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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
⁶ alternate between externally- and internally-oriented modes of sensory analysis. During
⁷ external mode, perception aligns more closely with the external sensory information, whereas
⁸ internal mode is characterized by enhanced biases toward perceptual history. Computational
⁹ modeling indicated that dynamic changes in mode are enabled by two interlinked factors:
¹⁰ (i), the integration of subsequent inputs over time and, (ii), slow anti-phase oscillations in
¹¹ the perceptual impact of external sensory information versus internal predictions that are
¹² provided by perceptual history. **We propose that between-mode fluctuations generate**
¹³ **unambiguous error signals that enable optimal inference in volatile environments.**

¹⁴ 3 One sentence summary

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

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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}.
²⁰ Intriguingly, 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 to
²⁴ seconds and even minutes⁴. Yet breaking from external information is risky, as swift responses
²⁵ to the environment are often crucial to survival.

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

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

⁴⁴ perceptual choices^{22–33}. These serial dependencies may be understood as driven by internal
⁴⁵ predictions that reflect the autocorrelation of natural environments³⁴ and bias perception
⁴⁶ toward preceding experiences^{30,31,35}. Computational modeling indicated that ongoing changes
⁴⁷ in perceptual performance may be driven by systematic fluctuations between externally- and
⁴⁸ internally-oriented *modes* of sensory analysis. **We suggest that such *bimodal inference***
⁴⁹ **may help to build stable internal representations of the sensory environment**
⁵⁰ **despite an ongoing stream of sensory information.**

⁵¹ 5 Results

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

⁵⁴ We began by selecting 66 studies from the Confidence Database²⁰ that investigated how
⁵⁵ human participants ($N = 4317$) perform binary perceptual decisions (Figure 1A; see Methods
⁵⁶ for details on inclusion criteria). As a metric for perceptual performance (i.e., the sensitivity
⁵⁷ to external sensory information), we asked whether the participant’s response and the
⁵⁸ presented stimulus matched (*stimulus-congruent* choices) or differed from each other (*stimulus-*
⁵⁹ *incongruent* choices; Figure 1B and C) in a total of 21.05 million trials.

⁶⁰ In a first step, we asked whether the ability to accurately perceive sensory stimuli is constant
⁶¹ over time or, alternatively, fluctuates in periods of enhanced and reduced sensitivity to
⁶² external information. We found perception to be stimulus-congruent in $73.46\% \pm 0.15\%$
⁶³ of trials (mean \pm standard error of the mean; Figure 2A), which was highly consistent
⁶⁴ across the selected studies (Supplemental Figure S1A). **In line with previous work⁸, we**
⁶⁵ **found that the probability of stimulus-congruence was not independent across**
⁶⁶ **successive trials: At the group level, stimulus-congruent perceptual choices were**
⁶⁷ **significantly autocorrelated for up to 15 trials (Figure 2B), controlling for task**

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

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

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

80 As a consequence of this autocorrelation, the dynamic probability of stimulus-congruent
81 perception (i.e., computed in sliding windows of ± 5 trials; Figure 1C) fluctuated considerably
82 within participants (average minimum: $35.46\% \pm 0.22\%$, maximum: $98.27\% \pm 0.07\%$). In
83 line with previous findings⁹, such fluctuations in the sensitivity to external information had a
84 power density that was inversely proportional to the frequency in the slow spectrum¹¹ (power
85 $\sim 1/f^\beta$, $\beta = -1.32 \pm 3.14 \times 10^{-3}$, $T(1.84 \times 10^5) = -419.48$, $p < 2.2 \times 10^{-308}$; Figure 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**
90 **sensory processing**

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

93 rely more strongly on internal information, i.e., on predictions about the environment that
94 are constructed from previous 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 preceding
105 experiences ($\beta = 16.18 \pm 1.07$, $T(1.09 \times 10^3) = 15.07$, $p = 10^{-46}$; Figure 2A) that was largely
106 consistent across studies (Supplemental Figure 1B) and more pronounced in participants who
107 were less sensitive to external sensory information (Supplemental Figure 1C). Importantly,
108 history-congruence was not a corollary of the sequence of presented stimuli: History-congruent
109 perceptual choices were more frequent at trials when perception was stimulus-incongruent
110 ($56.03\% \pm 0.2\%$) as opposed to stimulus-congruent ($51.77\% \pm 0.11\%$, $\beta = -4.26 \pm 0.21$,
111 $T(8.57 \times 10^3) = -20.36$, $p = 5.28 \times 10^{-90}$; Figure 2A, lower panel). Despite being adaptive
112 in autocorrelated real-world environments^{19,34,35,42}, perceptual history thus represented a
113 **source of bias** in the randomized experimental designs studied here^{24,28,30,31,43}. **These**
114 **serial biases were effects of choice history, i.e., driven by the experiences reported**
115 **at the preceding trial, and could not be attributed to stimulus history, i.e., to**
116 **effects of the stimuli presented at the preceding trial (Supplemental Section 9.1)**.

117 Second, we asked whether perception cycles through multi-trial epochs during which perception
118 is characterized by stronger or weaker biases toward preceding experiences. **In close**

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

¹²⁸ Third, we asked whether the impact of internal information fluctuates as **a scale-invariant**
¹²⁹ **process with a 1/f power law** (i.e., the feature typically associated with fluctuations
¹³⁰ in the sensitivity to external information^{9,10,13,39,40}). The dynamic probability of history-
¹³¹ congruent perception (i.e., computed in sliding windows of ± 5 trials; Figure 1C) varied
¹³² considerably over time, ranging between a minimum of $12.77\% \pm 0.14\%$ and a maximum
¹³³ $92.23\% \pm 0.14\%$. In analogy to stimulus-congruence, we found that history-congruence
¹³⁴ fluctuated as at power densities that were inversely proportional to the frequency in the
¹³⁵ slow spectrum¹¹ (power $\sim 1/f^\beta$, $\beta = -1.34 \pm 3.16 \times 10^{-3}$, $T(1.84 \times 10^5) = -423.91$, $p <$
¹³⁶ 2.2×10^{-308} ; Figure 2D).

¹³⁷ Finally, we ensured that fluctuations in stimulus- and history-congruence are linked to each
¹³⁸ other. When perceptual choices were less biased toward external information, participants
¹³⁹ relied more strongly on internal information acquired from perceptual history (and vice
¹⁴⁰ versa, $\beta = -0.05 \pm 5.63 \times 10^{-4}$, $T(2.1 \times 10^6) = -84.21$, $p < 2.2 \times 10^{-308}$, **controlling for**
¹⁴¹ **fluctuations in general response biases**; Supplemental Section 9.2). Thus, while sharing
¹⁴² the **1/f power law** characteristic, fluctuations in stimulus- and history-congruence were
¹⁴³ shifted against each other by approximately half a cycle and showed a squared coherence
¹⁴⁴ of $6.49 \pm 2.07 \times 10^{-3}\%$ (Figure 2E and F; we report the average phase and coherence for

¹⁴⁵ frequencies below $0.1 \text{ } 1/N_{trials}$; see Methods for details).

¹⁴⁶ In sum, our analyses indicate that perceptual decisions may result from a competition between
¹⁴⁷ external sensory signals with internal predictions provided by perceptual history. We show
¹⁴⁸ that the impact of these external and internal sources of information is not stable over time,
¹⁴⁹ but fluctuates systematically, emitting overlapping autocorrelation curves and antiphase $1/f$
¹⁵⁰ profiles.

¹⁵¹ These links between stimulus- and history-congruence suggest that the fluctuations in the
¹⁵² impact of external and internal information may be generated by a unifying mechanism that
¹⁵³ causes perception to alternate between two opposing *modes*¹⁸ (Figure 1D): During *external*
¹⁵⁴ *mode*, perception is more strongly driven by the available external stimulus information.
¹⁵⁵ Conversely, during *internal mode*, participants rely more heavily on internal predictions
¹⁵⁶ that are implicitly provided by preceding perceptual experiences. The fluctuations in the
¹⁵⁷ degree of bias toward external versus internal information created by such *bimodal inference*
¹⁵⁸ may thus provide a novel explanation for ongoing fluctuations in the sensitivity to external
¹⁵⁹ information^{4,5,18}.

¹⁶⁰ 5.3 Internal and external modes of processing facilitate response ¹⁶¹ behavior and enhance confidence in human perceptual decision- ¹⁶² making

¹⁶³ The above results point to systematic fluctuations in the *decision variable*⁴⁴
¹⁶⁴ that determines perceptual choices, causing enhanced sensitivity to external
¹⁶⁵ stimulus information during external mode and increased biases toward preceding
¹⁶⁶ choices during internal mode. As such, fluctuations in mode should influence
¹⁶⁷ downstream aspects of behavior and cognition that operate on the perceptual
¹⁶⁸ decision variable⁴⁴. To test this hypothesis with respect to motor behavior and
¹⁶⁹ metacognition, we asked how bimodal inference relates to response times (RTs)

¹⁷⁰ and confidence reports.

¹⁷¹ With respect to RTs, we observed faster responses for stimulus-congruent as opposed to
¹⁷² stimulus-incongruent choices ($\beta = -0.14 \pm 1.6 \times 10^{-3}$, $T(1.99 \times 10^6) = -85.84$, $p < 2.2 \times 10^{-308}$;
¹⁷³ Figure 2G). Intriguingly, whilst controlling for the effect of stimulus-congruence, we found
¹⁷⁴ that history-congruent (as opposed to history-incongruent) choices were also characterized by
¹⁷⁵ faster responses ($\beta = -9.56 \times 10^{-3} \pm 1.37 \times 10^{-3}$, $T(1.98 \times 10^6) = -6.97$, $p = 3.15 \times 10^{-12}$;
¹⁷⁶ Figure 2G).

¹⁷⁷ When analyzing the speed of response against the mode of sensory processing (Figure 2H),
¹⁷⁸ we found that RTs were shorter during externally-oriented perception ($\beta_1 = -11.07 \pm 0.55$,
¹⁷⁹ $T(1.98 \times 10^6) = -20.14$, $p = 3.17 \times 10^{-90}$). Crucially, as indicated by a quadratic relationship
¹⁸⁰ between the mode of sensory processing and RTs ($\beta_2 = -19.86 \pm 0.52$, $T(1.98 \times 10^6) =$
¹⁸¹ -38.43 , $p = 5 \times 10^{-323}$), participants became faster at indicating their perceptual decision
¹⁸² when biases toward both internal and external mode grew stronger.

¹⁸³ In analogy to the speed of response, confidence was higher for stimulus-congruent as opposed
¹⁸⁴ to stimulus-incongruent choices ($\beta = 0.04 \pm 1.18 \times 10^{-3}$, $T(2.06 \times 10^6) = 36.85$, $p =$
¹⁸⁵ 3.25×10^{-297} ; Figure 2I). Yet whilst controlling for the effect of stimulus-congruence, we found
¹⁸⁶ that history-congruence also increased confidence ($\beta = 0.48 \pm 1.38 \times 10^{-3}$, $T(2.06 \times 10^6) =$
¹⁸⁷ 351.54 , $p < 2.2 \times 10^{-308}$; Figure 2I).

¹⁸⁸ When depicted against the mode of sensory processing (Figure 2J), subjective confidence was
¹⁸⁹ indeed enhanced when perception was more externally-oriented ($\beta_1 = 92.63 \pm 1$, $T(2.06 \times 10^6)$
¹⁹⁰ $= 92.89$, $p < 2.2 \times 10^{-308}$). Importantly, however, participants were more confident in their
¹⁹¹ perceptual decision for stronger biases toward both internal and external mode ($\beta_2 = 39.3 \pm$
¹⁹² 0.94 , $T(2.06 \times 10^6) = 41.95$, $p < 2.2 \times 10^{-308}$). In analogy to RTs, subjective confidence thus
¹⁹³ showed a quadratic relationship to the mode of sensory processing (Figure 2J).

¹⁹⁴ Consequently, our findings predict that human participants lack full metacognitive insight
¹⁹⁵ into how strongly external signals and internal predictions contribute to perceptual decision-

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

²⁰⁷ In sum, the above results indicate that reporting behavior and metacognition do not map
²⁰⁸ linearly onto the mode of sensory processing. Rather, they suggest that slow fluctuations in the
²⁰⁹ respective impact of external and internal information are most likely to affect perception at
²¹⁰ an early level of sensory analysis^{46,47}. Such low-level processing may thus integrate perceptual
²¹¹ history with external inputs into a decision variable⁴⁴ that influences not only perceptual
²¹² choices, but also the speed and confidence at which they are made.

²¹³ **In what follows, we probe alternative explanations for between-mode fluctuations,**
²¹⁴ **test for the existence of modes in mice, and propose a predictive processing model**
²¹⁵ **that explains fluctuations in mode ongoing shifts in the precision afforded to**
²¹⁶ **external sensory information relative to internal predictions driven by perceptual**
²¹⁷ **history.**

218 5.4 Fluctuations between internal and external mode cannot be
219 reduced to general response biases or random choices

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

226 Logistic regression confirmed that perceptual history made a significant contrib-
227 ution to perception ($\beta = 0.11 \pm 5.79 \times 10^{-3}$, $z = 18.53$, $p = 1.1 \times 10^{-76}$) over and
228 above the ongoing stream of external sensory information ($\beta = 2.2 \pm 5.87 \times 10^{-3}$,
229 $z = 375.11$, $p < 2.2 \times 10^{-308}$) and general response biases toward ($\beta = 15.19 \pm 0.08$,
230 $z = 184.98$, $p < 2.2 \times 10^{-308}$).

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

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

²⁴⁴ internal mode processing reflects an enhanced impact of perceptual history,
²⁴⁵ one would expect a history-dependent increase in biases and lapses as well as a
²⁴⁶ history-independent increase in threshold. Conversely, if internal mode processing
²⁴⁷ were driven by random choices, one would expect a history-independent increase
²⁴⁸ in biases and threshold, and no change in bias. In line with our prediction, we
²⁴⁹ found that internal mode processing was associated with a history-dependent
²⁵⁰ increase in bias and lapse as well as a history-independent increase in threshold
²⁵¹ (Supplemental Section 9.3.1 and Supplemental Figure S6). This confirmed that
²⁵² internal mode processing is indeed driven by an enhanced impact of perceptual
²⁵³ history.

²⁵⁴ In line with this, the quadratic relationship between mode and confidence (Figure
²⁵⁵ 2J) suggested that biases toward internal information do not reflect a post-
²⁵⁶ perceptual strategy of repeating preceding choices when the subjective confidence
²⁵⁷ in the perceptual decision is low. Moreover, while responses became faster with
²⁵⁸ increased exposure to the experiments of the Confidence database, the frequency
²⁵⁹ of history-congruent choices increased over time, speaking against the proposition
²⁶⁰ that participants stereotypically repeat preceding choices when not yet familiar
²⁶¹ with the experimental task (Supplemental Section 9.4.1).

²⁶² Taken together, our results thus argue against recurring intervals of low task
²⁶³ engagement, which may be signaled by stereotypical or random responses, as an
²⁶⁴ alternative explanation for the phenomenon that we identify as bimodal inference.

²⁶⁵ 5.5 Mice fluctuate between external and internal modes of sensory ²⁶⁶ processing

²⁶⁷ In a prominent functional explanation for serial dependencies^{22–28,32,33,46}, perceptual history
²⁶⁸ is cast as an internal prediction that leverages the temporal autocorrelation of natural

²⁶⁹ environments for efficient decision-making^{30,31,34,35,41}. Since this autocorrelation is one of
²⁷⁰ the most basic features of our sensory world, fluctuating biases toward preceding perceptual
²⁷¹ choices should not be a uniquely human phenomenon.

²⁷² To test whether externally- and internally-oriented modes of processing exist beyond the
²⁷³ human mind, we analyzed data on perceptual decision-making in mice that were extracted
²⁷⁴ from the International Brain Laboratory (IBL) dataset²¹. We restricted our analyses to the
²⁷⁵ *basic* task²¹, in which mice responded to gratings of varying contrast that appeared either
²⁷⁶ in the left or right hemifield with equal probability. We excluded sessions in which mice
²⁷⁷ did not respond correctly to stimuli presented at a contrast above 50% in more than 80% of
²⁷⁸ trials (see Methods for details), which yielded a final sample of $N = 165$ adequately trained
²⁷⁹ mice that went through 1.46 million trials.

²⁸⁰ We found perception to be stimulus-congruent in $81.37\% \pm 0.3\%$ of trials (Figure 3A, upper
²⁸¹ panel). In line with humans, mice were biased toward perceptual history in $54.03\% \pm 0.17\%$
²⁸² of trials ($T(164) = 23.65$, $p = 9.98 \times 10^{-55}$; Figure 3A and Supplemental Figure S1D). Since
²⁸³ the *basic* task of the IBL dataset presented stimuli at random in either the left or right
²⁸⁴ hemifield²¹, we expected stronger biases toward perceptual history to decrease perceptual
²⁸⁵ performance. Indeed, history-congruent choices were more frequent when perception was
²⁸⁶ stimulus-incongruent ($61.59\% \pm 0.07\%$) as opposed to stimulus-congruent ($51.81\% \pm 0.02\%$,
²⁸⁷ $T(164) = 31.37$, $p = 3.36 \times 10^{-71}$; $T(164) = 31.37$, $p = 3.36 \times 10^{-71}$; Figure 3A, lower panel),
²⁸⁸ confirming that perceptual history was a **source of bias**^{24,28,30,31,43} as opposed to a feature
²⁸⁹ of the experimental paradigm.

²⁹⁰ **At the group level, we found significant autocorrelations in both stimulus-**
²⁹¹ **congruence (42 consecutive trials) and history-congruence (8 consecutive trials;**
²⁹² **Figure 3B), while controlling for the respective autocorrelation of task difficulty**
²⁹³ **and external stimulation (Supplemental Figure 2C-D).** In contrast to humans, mice
²⁹⁴ showed a negative autocorrelation coefficient of stimulus-congruence at trial 2, which was

²⁹⁵ due to a feature of the experimental design: Errors at a contrast above 50% were followed by
²⁹⁶ a high-contrast stimulus at the same location. Thus, stimulus-incongruent choices on easy
²⁹⁷ trials were more likely to be followed by stimulus-congruent perceptual choices that were
²⁹⁸ facilitated by high-contrast visual stimuli²¹.

²⁹⁹ At the level of individual mice, autocorrelation coefficients were elevated above randomly
³⁰⁰ permuted data within a lag of 4.59 ± 0.06 trials for stimulus-congruence and 2.58 ± 0.01 trials
³⁰¹ for history-congruence (Figure 3C). **We corroborated these autocorrelations in logistic**
³⁰² **regression models that successfully predicted the stimulus-/history-congruence**
³⁰³ **of perception at the index trial $t = 0$ from the stimulus-/history-congruence**
³⁰⁴ **at the 33 preceding trials for stimulus-congruence and 8 preceding trials for**
³⁰⁵ **history-congruence (Supplemental Figure S3)**. In analogy to humans, mice showed
³⁰⁶ anti-phase 1/f fluctuations in the sensitivity to internal and external information (Figure
³⁰⁷ 3D-F).

³⁰⁸ **The above results confirm that fluctuations between internally- and externally-**
³⁰⁹ **biased modes generalize to perceptual decision-making in mice. Following our**
³¹⁰ **hypothesis that bimodal inference operates at the level of perception, we predicted**
³¹¹ **that between-mode fluctuations modulate a decision variable⁴⁴ that determines**
³¹² **not only perceptual choices, but also downstream aspects of mouse behavior⁴⁴.**

³¹³ We therefore asked how external and internal modes relate to the trial duration (TD, a
³¹⁴ coarse measure of RT in mice that spans the interval from stimulus onset to feedback²¹).
³¹⁵ Stimulus-congruent (as opposed to stimulus-incongruent) choices were associated with shorter
³¹⁶ TDs ($\delta = -262.48 \pm 17.1$, $T(164) = -15.35$, $p = 1.55 \times 10^{-33}$), while history-congruent choices
³¹⁷ were characterized by longer TDs ($\delta = 30.47 \pm 5.57$, $T(164) = 5.47$, $p = 1.66 \times 10^{-7}$; Figure
³¹⁸ 3G).

³¹⁹ Across the full spectrum of the available data, TDs showed a linear relationship with the
³²⁰ mode of sensory processing, with shorter TDs during external mode ($\beta_1 = -4.16 \times 10^4 \pm$

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

³²⁶ As in humans, it is important to ensure that ongoing changes in the sensitivity to external
³²⁷ information are indeed driven by perceptual history and cannot be reduced to general choice
³²⁸ biases or random behavior. Logistic regression confirmed a significant effect perceptual
³²⁹ history on perceptual choices ($\beta = 0.51 \pm 4.49 \times 10^{-3}$, $z = 112.84$, $p < 2.2 \times 10^{-308}$),
³³⁰ while controlling for external sensory information ($\beta = 2.96 \pm 4.58 \times 10^{-3}$, $z = 646.1$, $p <$
³³¹ 2.2×10^{-308}) and general response biases toward one of the two outcomes ($\beta = -1.78 \pm 0.02$,
³³² $z = -80.64$, $p < 2.2 \times 10^{-308}$). **When eliminating perceptual history as a predictor of**
³³³ **individual choices, AIC increased by $\delta_{AIC} = 1.48 \times 10^4$, arguing against the notion**
³³⁴ **that choice randomness and general response bias are the only determinants of**
³³⁵ **perceptual performance in mice (see Supplemental Figure S4C-D for parameter-**
³³⁶ **and model-level inference in individual subjects).**

³³⁷ **In mice, fluctuations in the strength of history-congruent biases had a significant**
³³⁸ **effect on stimulus-congruence ($\beta_1 = -0.12 \pm 7.17 \times 10^{-4}$, $T(1.34 \times 10^6) = -168.39$, p**
³³⁹ **$< 2.2 \times 10^{-308}$) beyond the effect of ongoing changes in general response biases**
³⁴⁰ **($\beta_2 = -0.03 \pm 6.94 \times 10^{-4}$, $T(1.34 \times 10^6) = -48.14$, $p < 2.2 \times 10^{-308}$). Eliminating**
³⁴¹ **the dynamic fluctuations in history-congruence as a predictor of fluctuations**
³⁴² **in stimulus-congruence resulted in an increase in AIC by $\delta_{AIC} = 2.8 \times 10^4$ (see**
³⁴³ **Supplemental Section 9.2 and Supplemental Figure S5 for an in-depth assessment**
³⁴⁴ **of general response bias).**

³⁴⁵ **When fitting full and history-conditioned psychometric curves to the IBL data²¹,**
³⁴⁶ **we observed that internal mode processing was associated with a history-**

347 dependent increase in bias and lapse as well as a history-independent increase
348 in threshold (Supplemental Section 9.3.2 and Supplemental Figure S7). Over
349 time, the frequency of history-congruent choices increased alongside stimulus-
350 congruence and speed of response as mice were exposed to the experiment,
351 arguing against the proposition that biases toward perceptual history reflected
352 an unspecific response strategy in mice who were not sufficiently trained on the
353 IBL task (Supplemental Section 9.4.2 and Supplemental Figure S8).

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

358 5.6 Fluctuations in mode result from coordinated changes in the 359 impact of external and internal information on perception

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

368 Previous work has shown that such internal predictions can be built by dynamically updating
369 the estimated probability of being in a particular perceptual state from the sequence of
370 preceding experiences^{35,46,51}. The integration of sequential inputs may lead to accumulating
371 effects of perceptual history that progressively override incoming sensory information, enabling

³⁷² internal mode processing¹⁹. However, since such a process would lead to internal biases that
³⁷³ may eventually become impossible to overcome⁵², **changes in mode may require** ongoing
³⁷⁴ wave-like fluctuations^{9,13} in the perceptual impact of external and internal information that
³⁷⁵ occur *irrespective* of the sequence of previous experiences and temporarily de-couple the
³⁷⁶ decision variable from implicit internal representations of the environment¹⁹.

³⁷⁷ Following Bayes' theorem, binary perceptual decisions depend on the log posterior ratio L of
³⁷⁸ the two alternative states of the environment that participants learn about via noisy sensory
³⁷⁹ information⁵¹. We computed the posterior by combining the sensory evidence available at
³⁸⁰ time-point t (i.e., the log likelihood ratio LLR) with the prior probability ψ , **weighted by**
³⁸¹ **the respective precision terms** ω_{LLR} **and** ω_ψ :

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

³⁸² We derived the prior probability ψ at timepoint t from the posterior probability of perceptual
³⁸³ outcomes at timepoint L_{t-1} . Since a switch between the two states can occur at any time,
³⁸⁴ the effect of perceptual history varies according to both the sequence of preceding experiences
³⁸⁵ and the estimated stability of the external environment (i.e., the *hazard rate* H^{51}):

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

³⁸⁶ The LLR was computed from inputs s_t by applying a sigmoid function defined by parameter
³⁸⁷ α that controls the sensitivity of perception to the available sensory information (see Methods
³⁸⁸ for details on s_t in humans and mice):

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

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

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

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

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

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

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

402 We used a maximum likelihood procedure to fit the bimodal inference model
 403 (M1, Figure 1F) to the behavioral data from the Confidence database²⁰ and the
 404 IBL database²¹, optimizing the parameters α , H , amp_{LLR} , amp_ψ , f and p (see

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

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

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

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

426 As a second validation of the bimodal inference model, we tested whether the
427 posterior model predicted within-training and out-of-training variables. The
428 bimodal inference model characterizes each subject by a sensitivity parameter
429 α (humans: $\alpha = 0.5 \pm 1.12 \times 10^{-4}$; mice: $\alpha = 1.06 \pm 2.88 \times 10^{-3}$) that captures
430 how strongly perception is driven by the available sensory information, and a

431 hazard rate parameter H (humans: $H = 0.45 \pm 4.8 \times 10^{-5}$; mice: $H = 0.46 \pm$
432 2.97×10^{-4}) that controls how heavily perception is biased by perceptual history.
433 The parameter f captures the dominant time scale at which likelihood (amplitude
434 humans: $a_{LLR} = 0.5 \pm 2.02 \times 10^{-4}$; mice: $a_{LLR} = 0.39 \pm 1.08 \times 10^{-3}$) and prior
435 precision (amplitude humans: $a_\psi = 1.44 \pm 5.27 \times 10^{-4}$; mice: $a_\psi = 1.71 \pm 7.15 \times 10^{-3}$)
436 fluctuated and was estimated at $0.11 \pm 1.68 \times 10^{-5}$ $1/N_{trials}$ and $0.11 \pm 1.63 \times 10^{-4}$
437 $1/N_{trials}$ in mice.

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

447 Our behavioral analyses reveal that humans and mice show significant effects of perceptual
448 history that impaired performance in randomized psychophysical experiments^{24,28,30,31,43}
449 (Figure 2A and 3A). We therefore expected that humans and mice underestimated the true
450 hazard rate \hat{H} of the experimental environments (Confidence database²⁰: $\hat{H}_{Humans} = 0.5$
451 $\pm 1.58 \times 10^{-5}$); IBL database²¹: $\hat{H}_{Mice} = 0.49 \pm 6.47 \times 10^{-5}$). Indeed, when fitting the
452 bimodal inference model to the trial-wise perceptual choices, we found that the estimated (i.e.,
453 subjective) hazard rate H was lower than \hat{H} for both humans ($\beta = -6.87 \pm 0.94$, $T(61.87) =$
454 -7.33 , $p = 5.76 \times 10^{-10}$) and mice ($\beta = -2.91 \pm 0.34$, $T(112.57) = -8.51$, $p = 8.65 \times 10^{-14}$).

455 To further probe the validity of the bimodal inference model, we asked whether posterior
456 model quantities could explain aspects of the behavioral data that the model was not fitted

457 to. We predicted that the posterior decision variable L_t not only encodes perceptual choices
458 (i.e., the variable used for model estimation), but also predicts the speed of response and
459 subjective confidence^{30,44}. Indeed, the estimated trial-wise posterior decision certainty $|L_t|$
460 correlated negatively with RTs in humans ($\beta = -4.36 \times 10^{-3} \pm 4.64 \times 10^{-4}$, $T(1.98 \times 10^6)$
461 $= -9.41$, $p = 5.19 \times 10^{-21}$) and TDs mice ($\beta = -35.45 \pm 0.86$, $T(1.28 \times 10^6) = -41.13$, p
462 $< 2.2 \times 10^{-308}$). Likewise, subjective confidence reports were positively correlated with the
463 estimated posterior decision certainty in humans ($\beta = 7.63 \times 10^{-3} \pm 8.32 \times 10^{-4}$, $T(2.06 \times 10^6)$
464 $= 9.18$, $p = 4.48 \times 10^{-20}$).

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

475 **As a third validation of the bimodal inference model, we used the posterior**
476 **model parameters to simulate synthetic perceptual choices and repeated the**
477 **behavioral analyses conducted for the empirical data.** Simulations from the bimodal
478 inference model closely replicated our empirical results: Simulated perceptual decisions
479 resulted from a competition of perceptual history with incoming sensory signals (Figure 4A).
480 Stimulus- and history-congruence were significantly autocorrelated (Figure 4B-C), fluctuating
481 in anti-phase as a scale-invariant process with a 1/f power law (Figure 4D-F). Simulated
482 posterior certainty^{28,30,44} (i.e., the absolute of the log posterior ratio $|L_t|$) showed a quadratic

483 relationship to the mode of sensory processing (Figure 4H), mirroring the relation of RTs
484 and confidence reports to external and internal biases in perception (Figure 2G-H and Figure
485 3G-H). Crucially, the overlap between empirical and simulated data broke down when we
486 removed the anti-phase oscillations or the accumulation of evidence over time from the
487 bimodal inference model (Supplemental Figures S10-13).

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

493 6 Discussion

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

506 **6.1 Bimodal inference represents a pervasive aspect of perceptual**
507 **decision-making in humans and mice**

508 A growing body of literature has highlighted that perception is modulated by preceding
509 choices^{22–28,30,32,33}. Our work provides converging cross-species evidence supporting the
510 notion that such serial dependencies are a pervasive and general phenomenon of perceptual
511 decision-making (Figures 2 and 3). While introducing errors in randomized psychophysical
512 designs^{24,28,30,31,43} (Figures 2A and 3A), we found that perceptual history facilitates post-
513 perceptual processes such as speed of response⁴² (Figure 2G and 3G) and subjective confidence
514 in humans (Figure 2I).

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

522 In computational terms, serial dependencies may leverage the temporal autocorrelation of
523 natural environments^{31,46} to increase the efficiency of decision-making^{35,43}. Such temporal
524 smoothing⁴⁶ of sensory inputs may be achieved by updating dynamic predictions about the
525 world based on the sequence of noisy perceptual experiences^{22,31}, **using algorithms based**
526 **on sequential Bayes^{25,42,51} such as Kalman³⁵ or Hierarchical Gaussian filtering⁵⁴.**
527 At the level of neural mechanisms, the integration of internal with external information may
528 be realized by combining feedback from higher levels in the cortical hierarchy with incoming
529 sensory signals that are fed forward from lower levels⁵⁶.

530 Yet relying too strongly on serial dependencies may come at a cost: When accumulating over
531 time, internal predictions may eventually override external information, leading to circular

532 and false inferences about the state of the environment⁵⁷. Akin to the wake-sleep-algorithm
533 in machine learning⁵⁸, bimodal inference may help to determine whether errors result from
534 external input or from internally-stored predictions: During internal mode, sensory processing
535 is more strongly constrained by predictive processes that auto-encode the agent’s environment.
536 Conversely, during external mode, the network is driven predominantly by sensory inputs¹⁸.
537 Between-mode fluctuations may thus generate an unambiguous error signal that aligns internal
538 predictions with the current state of the environment in iterative test-update-cycles⁵⁸. On a
539 broader scale, between-mode fluctuations may thus regulate the balance between feedforward
540 versus feedback contributions to perception and thereby play a adaptive role in metacognition
541 and reality monitoring⁵⁹.

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

551 The empirical evidence above suggests that the timescale of this periodic schedul-
552 ing of evidence accumulation may be scale-invariant. This means that there
553 may exist a timescale of periodic fluctuations in precision over every window
554 or length of perceptual decision-making. Bimodal inference predicts perceptual
555 decisions under a generative model (based upon a hazard function to model
556 serial dependencies between subsequent trials) with periodic fluctuations in the
557 precision of sensory evidence relative to prior beliefs at a particular timescale.

558 Remarkably, a systematic model comparison based on AIC indicated that a
559 model with fluctuating precisions has much greater evidence, relative to a model
560 in the absence of fluctuating precisions. This ad-hoc addition of oscillations to a
561 normative Bayesian model of evidence accumulation⁵¹ allowed us to quantify the
562 dominant timescale of periodic fluctuations mode at approximately $0.11 \text{ } 1/N_{trials}$
563 in humans and mice that is appropriate for these kinds of paradigms.

564 **6.2 Bimodal inference versus normative Bayesian evidence accu-**
565 **mulation**

566 Could bimodal inference emerge spontaneously in normative models of perceptual
567 decision-making? In predictive processing, the relative precision of prior and
568 likelihood determines their integration into the posterior that determines the
569 content of perception. At the level of individual trials, the perceptual impact
570 of internal predictions generated from perceptual history (prior precision) and
571 external sensory information (likelihood precision) are thus necessarily anti-
572 correlated. The same holds for mechanistic models of drift diffusion, which
573 understand choice history biases as driven by changes in the starting point⁵¹
574 or the drift rate of evidence accumulation³². Under the former formulation,
575 perceptual history is bound to have a stronger influence on perception when less
576 weight is given to incoming sensory evidence, assuming that the last choice is
577 represented as a starting point bias. The effects of choice history in normative
578 Bayesian and mechanistic drift diffusion models can be mapped onto one another
579 via the Bayesian formulation of drift diffusion⁶⁰, where the inverse of likelihood
580 precision determines the amount of noise in the accumulation of new evidence,
581 and prior precision determines the absolute shift in its starting point⁶⁰.

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

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

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

606 **6.3 Task engagement and residual motor activation as alternative
607 explanations for bimodal inference**

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

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

628 **Outside of the predictive processing field, attention is often understood in the**
629 **context of task engagement**⁶³, which varies according to the availability of cognitive
630 resources that are modulated by factors such as tonic arousal, familiarity with
631 the task, or fatigue⁶³. Our results suggest that internal mode processing cannot

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

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

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

656 Residual activation of the motor system may provide another contribution to
657 serial biases in perceptual choices⁷². Such motor-driven priming may lead to

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

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

674 6.4 Limitations and open questions

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

678 First, this work sought to understand whether fluctuations between internal and
679 external mode, which we initially observed in an experiment on bistable perception
680 in humans¹⁹, are general phenomenon that occurs across a diverse set of perceptual
681 decision-making tasks. Our analysis of the Confidence database²⁰ therefore
682 collapsed across all available experiments on binary perceptual decision-making.

683 Individual experiments differed with respect to the stimuli, the manipulation
684 of difficulty, the timing of trials, and the way responses were collected, but
685 were highly comparable with respect to the central variables of stimulus- and
686 history-congruence (Supplemental Figure S1A-B).

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

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

709 not tied exclusively to repeating biases, but accommodates alternating biases
710 as well, such that both may lead to internally-biased processing and reduced
711 sensitivity to external sensory information. Future work could apply our approach
712 to paradigms that boost alternating as opposed to repeating biases, as this would
713 help to better understand how repetition and alternation are linked in terms of
714 their computational function and neural implementation²⁷.

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

731 A final important avenue for further research on bimodal inference is identify-
732 ing the neurobiological underpinnings of bimodal inference. Since between-mode
733 fluctuations were found in humans and mice, future studies can apply non-invasive and
734 invasive neuro-imaging and electrophysiology to better understand the neural mechanisms

⁷³⁵ that generate ongoing changes in mode in terms of their neuro-anatomy, -chemistry and
⁷³⁶ -circuitry.

⁷³⁷ Establishing the neural correlates of externally- an internally-biased modes will enable exiting
⁷³⁸ opportunities to investigate their role for adaptive perception and decision-making: Causal
⁷³⁹ interventions via pharmacological challenges, optogenetic manipulations or (non-)invasive
⁷⁴⁰ brain stimulation will help to understand whether between-mode fluctuations are implicated
⁷⁴¹ in resolving credit-assignment problems^{18,77} or in calibrating metacognition and reality
⁷⁴² monitoring⁵⁹. Answers to these questions may provide new insights into the pathophysiology
⁷⁴³ of hallucinations and delusions, which have been characterized by an imbalance in the impact
⁷⁴⁴ of external versus internal information^{56,78,79} and are typically associated with metacognitive
⁷⁴⁵ failures and a departure from consensual reality⁷⁹.

⁷⁴⁶ **7 Methods**

⁷⁴⁷ **7.1 Resource availability**

⁷⁴⁸ **7.1.1 Lead contact**

⁷⁴⁹ Further information and requests for resources should be directed to and will be fulfilled by
⁷⁵⁰ the lead contact, Veith Weilnhammer (veith.weilnhammer@gmail.com).

⁷⁵¹ **7.1.2 Materials availability**

⁷⁵² This study did not generate new unique reagents.

⁷⁵³ **7.1.3 Data and code availability**

⁷⁵⁴ All custom code and behavioral data are available on <https://github.com/veithweilnhammer/>
⁷⁵⁵ Modes. This manuscript was created using the *R Markdown* framework, which integrates all
⁷⁵⁶ data-related computations and the formatted text within one document. With this, we wish
⁷⁵⁷ to make our approach fully transparent and reproducible for reviewers and future readers.

⁷⁵⁸ **7.2 Experimental model and subject details**

⁷⁵⁹ **7.2.1 Confidence database**

⁷⁶⁰ We downloaded the human data from the Confidence database²⁰ on 10/21/2020,
⁷⁶¹ limiting our analyses to the category *perception*. Within this category, we
⁷⁶² selected studies in which participants made binary perceptual decisions between
⁷⁶³ two alternatives. We excluded two experiments in which the average perceptual
⁷⁶⁴ accuracy fell below 50%. After excluding these experiments, our sample consisted
⁷⁶⁵ of 21.05 million trials obtained from 4317 human participants and 66 individual
⁷⁶⁶ experiments (Supplemental Table 1). Out of the 66 included experiments, 62
⁷⁶⁷ investigated visual, 1 auditory, 2 proprioceptive, and 1 multimodal perception.

768 **59 experiments were based on discrimination and 6 on detection, with one**
769 **investigating both.**

770 **7.2.2 IBL database**

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

776 **7.3 Method details**

777 **7.3.1 Variables of interest**

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

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

790 **Secondary variables of interest:** From the Confidence Database²⁰, we furthermore
791 extracted trial-wise confidence reports and RTs. **Out of the 58 experiments that provide**

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

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

807 7.3.2 Control variables

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

818 **this precluded the computation of autocorrelation curves.** In analogy to RTs and
819 confidence, difficulty levels were normalized within individual studies. For the IBL Database²¹,
820 task difficulty was defined by the contrast of the presented grating.

821 **7.3.3 Autocorrelations**

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

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

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

844 the respective autocorrelation coefficients for the randomly permuted data; at the 6th trial
845 following the index trial, however, *less than 50%* of the autocorrelation coefficients exceeded
846 the respective permuted autocorrelation coefficients.

847 **7.3.4 Spectral analysis**

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

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

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

865 **7.4 Quantification and statistical procedures**

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

868 **7.4.1 Mixed effects modeling**

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

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

886 **7.4.2 Psychometric function**

887 We obtained psychometric curves by fitting the following error function to the behavioral
888 data:

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

889 We used the Broyden–Fletcher–Goldfarb–Shanno algorithm in maximum likelihood
890 estimation⁸⁰ to predict individual choices y (outcome A: $y = 0$; outcome B: $y = 1$) from the

891 choice probability y_p . In humans, we computed s_w by multiplying the inputs s (stimulus A:
 892 0; outcome B: 1) with the task difficulty D_b (binarized across 7 levels):

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

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

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

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

900 7.4.3 Computational modeling

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

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

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

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

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

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

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

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

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

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

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

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

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

926 To allow for long-range autocorrelation in stimulus- and history-congruence (Figure 2B and
 927 3B), our modeling approach differed from Glaze et al.⁵¹ in that it allowed for systematic
 928 fluctuation in the impact of sensory information (i.e., LLR) and the prior probability
 929 of choices ψ on the posterior probability L . This was achieved by multiplying the log
 930 likelihood ratio and the log prior ratio with coherent anti-phase fluctuations according to
 931 $\omega_{LLR} = a_{LLR} * \sin(f * t + phase) + 1$ and $\omega_\psi = a_\psi * \sin(f * t + phase + \pi) + 1$.

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

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

936 This allowed us to infer the free parameters H (lower bound = 0, upper bound = 1; human
 937 posterior = $0.45 \pm 4.8 \times 10^{-5}$; mouse posterior = $0.46 \pm 2.97 \times 10^{-4}$), α (lower bound
 938 = 0, upper bound = 5; human posterior = $0.5 \pm 1.12 \times 10^{-4}$; mouse posterior = $1.06 \pm$
 939 2.88×10^{-3}), a_ψ (lower bound = 0, upper bound = 10; human posterior = $1.44 \pm 5.27 \times 10^{-4}$;
 940 mouse posterior = $1.71 \pm 7.15 \times 10^{-3}$), amp_{LLR} (lower bound = 0, upper bound = 10;
 941 human posterior = $0.5 \pm 2.02 \times 10^{-4}$; mouse posterior = $0.39 \pm 1.08 \times 10^{-3}$), frequency f
 942 (lower bound = 1/40, upper bound = 1/5; human posterior = $0.11 \pm 1.68 \times 10^{-5}$; mouse
 943 posterior = $0.11 \pm 1.63 \times 10^{-4}$), p (lower bound = 0, upper bound = $2 * \pi$; human posterior
 944 = $2.72 \pm 4.41 \times 10^{-4}$; mouse posterior = $2.83 \pm 3.95 \times 10^{-3}$) and inverse decision temperature ζ

945 (lower bound = 1, upper bound = 10; human posterior = $4.63 \pm 1.95 \times 10^{-4}$; mouse posterior
946 = $4.82 \pm 3.03 \times 10^{-3}$) using maximum likelihood estimation with the Broyden–Fletcher–
947 Goldfarb–Shanno algorithm as implemented in the R-function *optimx*⁸⁰ (see Supplemental
948 **Table T2** for a description of our model parameters).

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

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

- 956 • The full *bimodal inference model* (M1; Figure 1F) incorporates the influ-
957 ence of sensory information according to the parameter α (likelihood); the
958 integration of evidence across trials according to the parameter H (prior);
959 anti-phase oscillations in between likelihood and prior precision according
960 to ω_{LLR} and ω_ψ with parameters a_{LLR} (amplitude likelihood fluctuation), a_ψ
961 (amplitude prior fluctuation), f (frequency) and p (phase).
- 962 • The *likelihood-oscillation-only model* (M2; Figure 1G) incorporates the
963 influence of sensory information according to parameter α (likelihood); the
964 integration of evidence across trials according to parameter H (prior); os-
965 cillations in likelihood precision according to ω_{LLR} with parameters a_{LLR}
966 (amplitude likelihood fluctuation), f (frequency) and p (phase).
- 967 • The *prior-oscillation-only model* (M3; Figure 1G) incorporates the influence
968 of sensory information according to parameter α (likelihood); the integration
969 of evidence across trials according to parameter H (prior); oscillations in

970 the prior precision according to ω_ψ with parameters a_ψ (amplitude prior
971 fluctuation), f (frequency) and p (phase). Please note that all models M1-3
972 lead to shifts in the relative precision of likelihood and prior.

- 973 • The *normative-evidence-accumulation* (M4; Figure 1G) incorporates the
974 influence of sensory information according to parameter α (likelihood); the
975 integration of evidence across trials according to parameter H (prior), There
976 are no additional oscillations. Model M4 thus corresponds to the model
977 proposed by Glaze et al. and captures normative evidence accumulation
978 in unpredictable environments using a Bayesian update scheme⁵¹. The
979 comparison against M4 tests the null hypothesis that fluctuations in mode
980 emerge from a normative Bayesian model without the ad-hoc addition of
981 oscillations as in models M1-3.
- 982 • The *no-evidence-accumulation* (M5; Figure 1G) incorporates the influence
983 of sensory information according to parameter α (likelihood). The model
984 lacks integration of evidence across trials (flat prior) and oscillations. The
985 comparison against M5 tests the null hypothesis that observers do not use
986 prior information derived from serial dependency in perception.

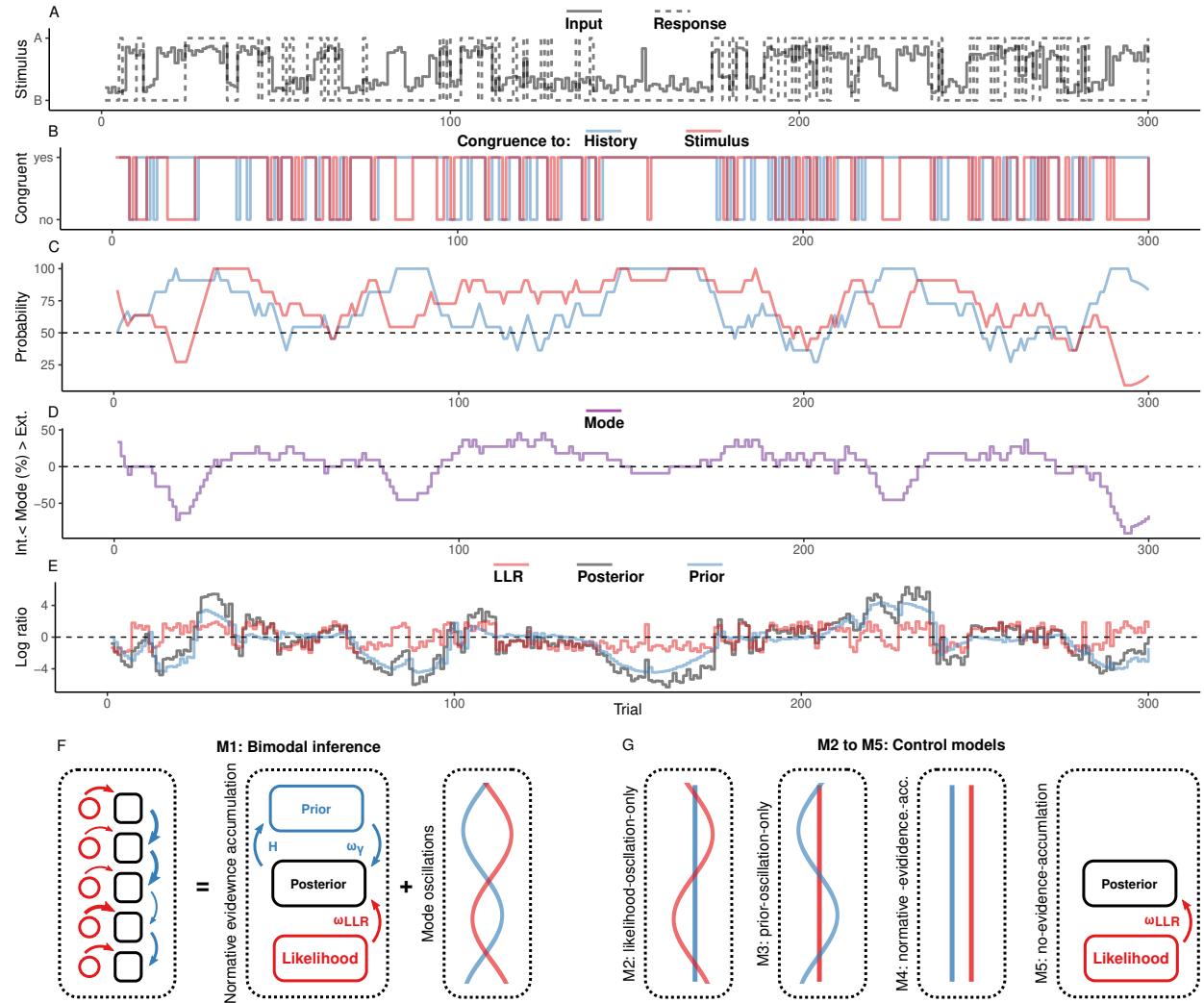
987 Prediction of within-training and out-of-training variables. To validate our model,
988 we correlated individual posterior parameter estimates with the respective con-
989 ventional variables. As a sanity check, we tested (i), whether the estimated hazard
990 rate H correlated negatively with the frequency of history-congruent choices
991 and, (ii), whether the estimated sensitivity to sensory information α correlated
992 positively with the frequency of stimulus-congruent choices. In addition, we
993 tested whether the posterior decision certainty (i.e.. the absolute of the log
994 posterior ratio) correlated negatively with RTs and positively with confidence.
995 This allowed us to assess whether our model could explain aspects of the data it

996 was not fitted to (i.e., RTs and confidence).

997 **Simulations.** Finally, we used simulations (Figure 4, Supplemental Figures S10-
998 13) to show that all model components, including the anti-phase oscillations
999 governed by a_ψ , a_{LLR} , f and p , were necessary for our model to reproduce the
1000 characteristics of the empirical data. This enabled us to assess over- or under-
1001 fitting in the bimodal inference model and all reduced models M2-M5. We used
1002 the posterior model parameters observed for humans (H , α , a_ψ , a_{LLR} , f and ζ)
1003 to define individual parameters for simulation in 4317 simulated participants
1004 (i.e., equivalent to the number of human participants). For each participant, the
1005 number of simulated trials was drawn at random between 300 to 700. Inputs s
1006 were drawn at random for each trial, such that the sequence of inputs to the
1007 simulation did not contain any systematic seriality. Noisy observations u were
1008 generated by applying the posterior parameter α to inputs s , thus generating
1009 stimulus-congruent choices in $71.36 \pm 2.6 \times 10^{-3}\%$ of trials. Choices were simulated
1010 based on the trial-wise choice probabilities y_p obtained from our model. Simulated
1011 data were analyzed in analogy to the human and mouse data. As a substitute of
1012 subjective confidence, we computed the absolute of the trial-wise log posterior
1013 ratio $|L|$ (i.e., the posterior decision certainty).

1014 **8 Figures**

1015 **8.1 Figure 1**

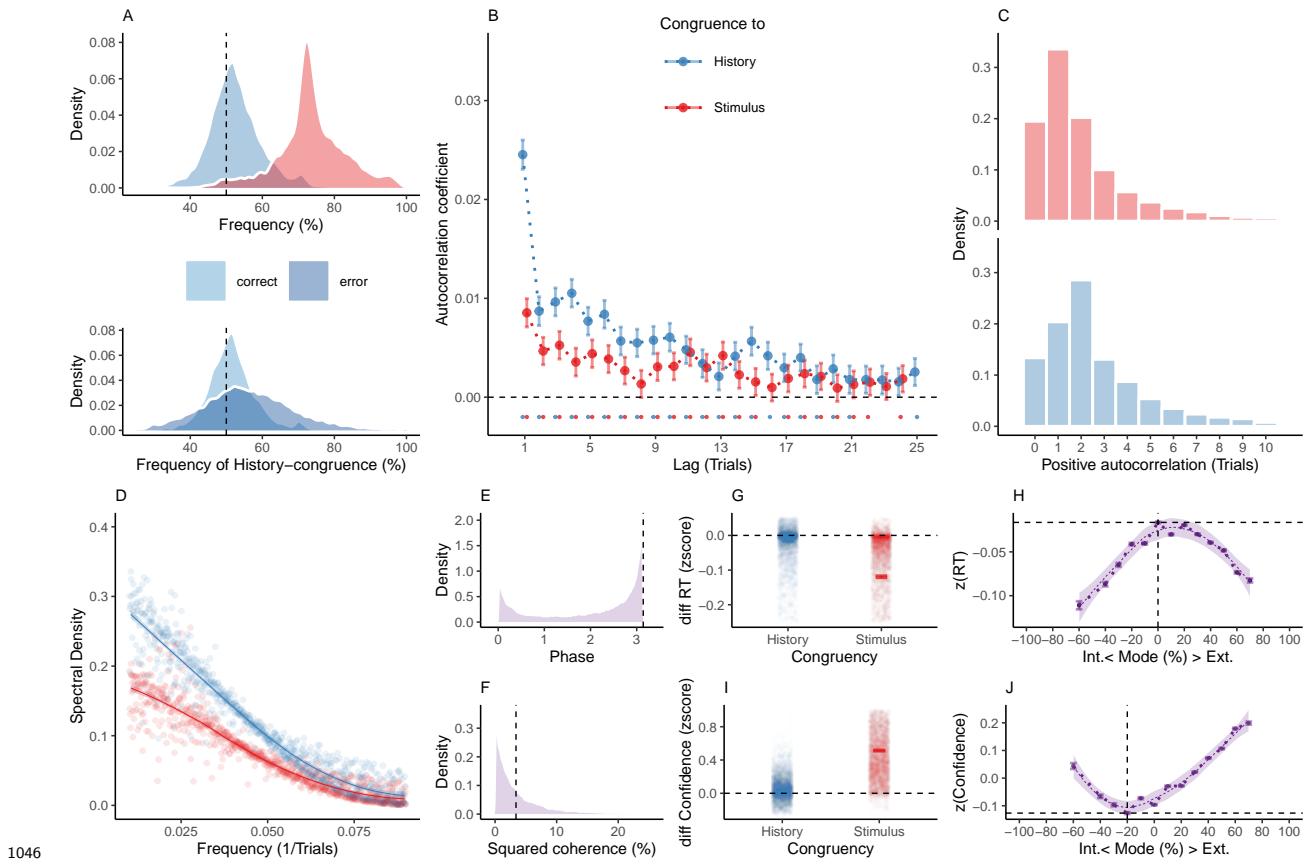


1016 **Figure 1. Concept.**

- 1017 A. In binary perceptual decision-making, a participant is presented with stimuli from two categories (A vs. B; dotted line) and reports consecutive perceptual choices via button presses (solid line). All panels below refer to these stimulated example data.
- 1018 B. When the response matches the external stimulus information (i.e., overlap between dotted
1019 and solid line in panel A), perceptual choices are *stimulus-congruent* (red line). When the
1020 response matches the response at the preceding trial, perceptual choices are *history-congruent*
- 1021 C. When the response does not match the external stimulus information (i.e., no overlap
1022 between dotted and solid line in panel A), perceptual choices are *stimulus-incongruent* (blue line).
- 1023 D. When the response does not match the response at the preceding trial, perceptual choices are *history-incongruent* (blue line).

- 1024 (blue line).
- 1025 C. The dynamic probabilities of stimulus- and history-congruence (i.e., computed in sliding
1026 windows of ± 5 trials) fluctuate over time.
- 1027 D. The *mode* of perceptual processing is derived by computing the difference between the
1028 dynamic probabilities of stimulus- and history-congruence. Values above 0% indicate a
1029 bias toward external information, whereas values below 0% indicate a bias toward internal
1030 information.
- 1031 E. In computational modeling, internal mode is caused by an enhanced impact of perceptual
1032 history. This causes the posterior (black line) to be close to the prior (blue line). Conversely,
1033 during external mode, the posterior is close to the sensory information (log likelihood ratio,
1034 red line).
- 1035 F. The bimodal inference model (M1) explains fluctuations between externally-
1036 and externally-biased modes (left panel) by two interacting factors: a normative
1037 accumulation of evidence according to parameters H (middle panel), and anti-
1038 phase oscillations in the precision terms ω_{LLR} and ω_ψ (right panel).
- 1039 G. The control models M2-M5 were constructed by successively removing the anti-
1040 phase oscillations and the integration of information from the bimodal inference
1041 model. Please note that the normative-evidence-accumulation-model (M4) corre-
1042 sponds to the model proposed by Glaze et al.⁵¹. In the no-evidence-accumulation
1043 model (M5), perceptual decisions depend only on likelihood information (flat
1044 priors).

1045 **8.2 Figure 2**



1046 **Figure 2. Internal and external modes in human perceptual decision-making.**

1047 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.

1048 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 $\gamma = -1.92 \times 10^{-3} \pm 4.5 \times 10^{-4}$ ($T(6.88 \times 10^4)$)

₁₀₅₉ $= -4.27$, $p = 1.98 \times 10^{-5}$) for stimulus-congruence and at a rate of $\gamma = -6.11 \times 10^{-3} \pm$
₁₀₆₀ 5.69×10^{-4} ($T(6.75 \times 10^4) = -10.74$, $p = 7.18 \times 10^{-27}$) for history-congruence.

₁₀₆₁ C. Here, we depict the number of consecutive trials at which autocorrelation coefficients
₁₀₆₂ exceeded the respective autocorrelation of randomly permuted data within individual partici-
₁₀₆₃ pants. For stimulus-congruence (upper panel), the lag of positive autocorrelation amounted
₁₀₆₄ to $3.24 \pm 2.39 \times 10^{-3}$ on average, showing a peak at trial $t+1$ after the index trial. For
₁₀₆₅ history-congruence (lower panel), the lag of positive autocorrelation amounted to $4.87 \pm$
₁₀₆₆ 3.36×10^{-3} on average, peaking at trial $t+2$ after the index trial.

₁₀₆₇ D. The smoothed probabilities of stimulus- and history-congruence (sliding windows of ± 5
₁₀₆₈ trials) fluctuated as a **scale-invariant process with a 1/f power law**, i.e., at power
₁₀₆₉ densities that were inversely proportional to the frequency.

₁₀₇₀ E. The distribution of phase shift between fluctuations in stimulus- and history-congruence
₁₀₇₁ peaked at half a cycle (π denoted by dotted line).

₁₀₇₂ F. The average squared coherence between fluctuations in stimulus- and history-congruence
₁₀₇₃ (black dotted line) amounted to $6.49 \pm 2.07 \times 10^{-3}\%$

₁₀₇₄ G. We observed faster RTs for both stimulus-congruence (as opposed to stimulus-incongruence,
₁₀₇₅ $\beta = -0.14 \pm 1.6 \times 10^{-3}$, $T(1.99 \times 10^6) = -85.84$, $p < 2.2 \times 10^{-308}$) and history-congruence
₁₀₇₆ ($\beta = -9.56 \times 10^{-3} \pm 1.37 \times 10^{-3}$, $T(1.98 \times 10^6) = -6.97$, $p = 3.15 \times 10^{-12}$).

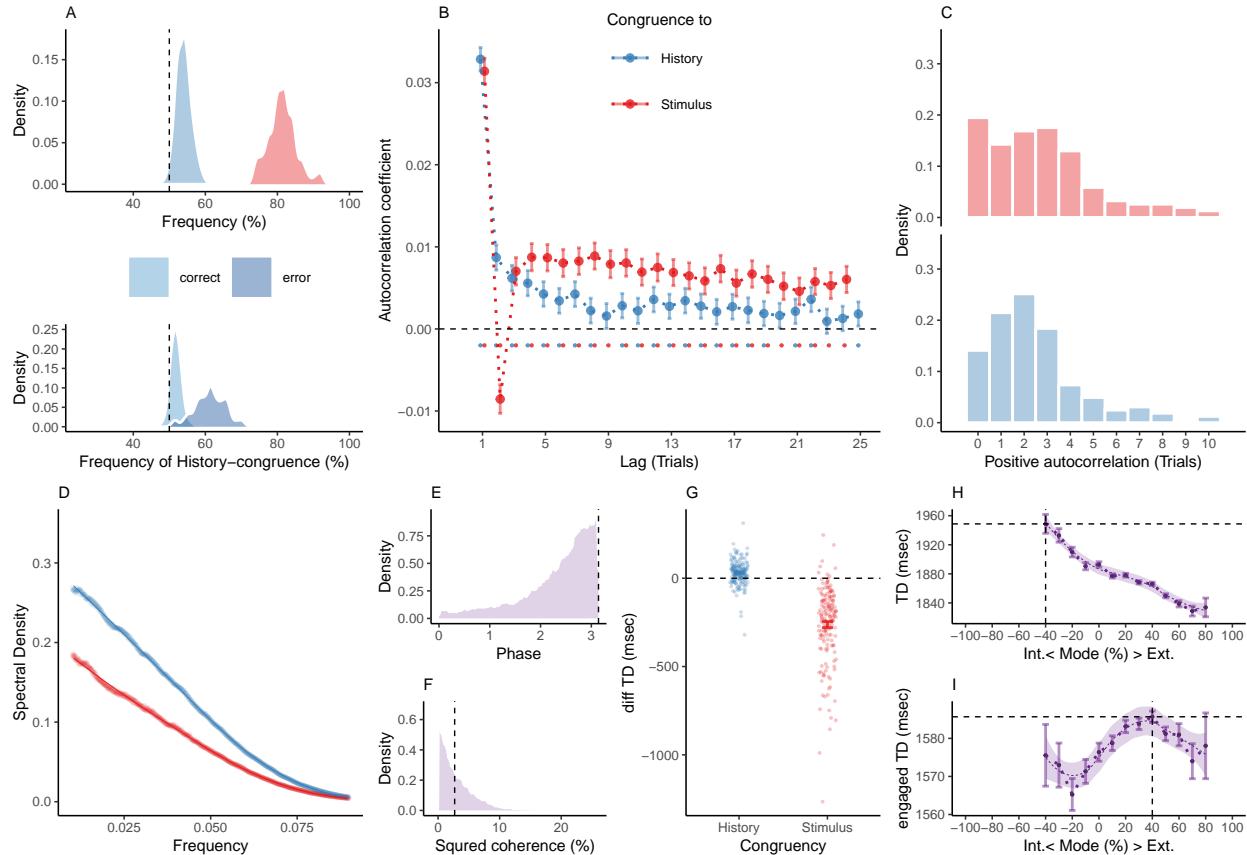
₁₀₇₇ H. The mode of perceptual processing (i.e., the difference between the smoothed probability
₁₀₇₈ of stimulus- vs. history-congruence) showed a quadratic relationship to RTs, with faster
₁₀₇₉ RTs for stronger biases toward both external sensory information and internal predictions
₁₀₈₀ provided by perceptual history ($\beta_2 = -19.86 \pm 0.52$, $T(1.98 \times 10^6) = -38.43$, $p = 5 \times 10^{-323}$).
₁₀₈₁ The horizontal and vertical dotted lines indicate maximum RT and the associated mode,
₁₀₈₂ respectively.

₁₀₈₃ I. Confidence was enhanced for both stimulus-congruence (as opposed to stimulus-

1084 incongruence, $\beta = 0.48 \pm 1.38 \times 10^{-3}$, $T(2.06 \times 10^6) = 351.54$, $p < 2.2 \times 10^{-308}$) and
 1085 history-congruence ($\beta = 0.04 \pm 1.18 \times 10^{-3}$, $T(2.06 \times 10^6) = 36.85$, $p = 3.25 \times 10^{-297}$).

1086 J. In analogy to RTs, we found a quadratic relationship between the mode of perceptual
 1087 processing and confidence, which increased when both externally- and internally-biased modes
 1088 grew stronger ($\beta_2 = 39.3 \pm 0.94$, $T(2.06 \times 10^6) = 41.95$, $p < 2.2 \times 10^{-308}$). The horizontal
 1089 and vertical dotted lines indicate minimum confidence and the associated mode, respectively.

1090 8.3 Figure 3



1091 1092 **Figure 3. Internal and external modes in mouse perceptual decision-making.**

1093 A. In mice, $81.37\% \pm 0.3\%$ of trials were stimulus-congruent (in red) and $54.03\% \pm 0.17\%$ of
 1094 trials were history-congruent (in blue; upper panel). History-congruent perceptual choices
 1095 were not a consequence of the experimental design, but a source of error, as they were more
 1096 frequent on stimulus-incongruent trials (lower panel).

- 1097 B. Relative to randomly permuted data, we found highly significant autocorrelations of
1098 stimulus-congruence and history-congruence (dots indicate intercepts $\neq 0$ in trial-wise linear
1099 mixed effects modeling at $p < 0.05$). Please note that the negative autocorrelation of
1100 stimulus-congruence at trial 2 was a consequence of the experimental design (Supplemental
1101 Figure 2D-F). As in humans, autocorrelation coefficients were best fit by an exponential
1102 function (adjusted R^2 for stimulus-congruence: 0.44; history-congruence: 0.52) as compared
1103 to a linear function (adjusted R^2 for stimulus-congruence: 3.16×10^{-3} ; history-congruence:
1104 0.26), decaying at a rate of $\gamma = -6.2 \times 10^{-4} \pm 5.93 \times 10^{-4}$ ($T(3.55 \times 10^4) = -1.05$, $p = 0.3$)
1105 for stimulus-congruence and at a rate of $\gamma = -6.7 \times 10^{-3} \pm 5.94 \times 10^{-4}$ ($T(3.69 \times 10^4) =$
1106 -11.27 , $p = 2.07 \times 10^{-29}$) for history-congruence.
- 1107 C. For stimulus-congruence (upper panel), the lag of positive autocorrelation was longer in
1108 comparison to humans (4.59 ± 0.06 on average). For history-congruence (lower panel), the
1109 lag of positive autocorrelation was slightly shorter relative to humans (2.58 ± 0.01 on average,
1110 peaking at trial $t+2$ after the index trial).
- 1111 D. In mice, the dynamic probabilities of stimulus- and history-congruence (sliding windows
1112 of ± 5 trials) fluctuated as **a scale-invariant process with a 1/f power law**.
- 1113 E. The distribution of phase shift between fluctuations in stimulus- and history-congruence
1114 peaked at half a cycle (π denoted by dotted line).
- 1115 F. The average squared coherence between fluctuations in stimulus- and history-congruence
1116 (black dotted line) amounted to $3.45 \pm 0.01\%$.
- 1117 G. We observed shorter trial durations (TDs) for stimulus-congruence (as opposed to stimulus-
1118 incongruence, $\beta = -1.12 \pm 8.53 \times 10^{-3}$, $T(1.34 \times 10^6) = -131.78$, $p < 2.2 \times 10^{-308}$), but
1119 longer TDs for history-congruence ($\beta = 0.06 \pm 6.76 \times 10^{-3}$, $T(1.34 \times 10^6) = 8.52$, $p =$
1120 1.58×10^{-17}).
- 1121 H. TDs decreased monotonically for stronger biases toward external mode ($\beta_1 = -4.16 \times 10^4$
1122 $\pm 1.29 \times 10^3$, $T(1.35 \times 10^6) = -32.31$, $p = 6.03 \times 10^{-229}$). The horizontal and vertical dotted

₁₁₂₃ lines indicate maximum TD and the associated mode, respectively.

₁₁₂₄ I. For TDs that differed from the median TD by no more than $1.5 \times \text{MAD}$ (median absolute

₁₁₂₅ distance⁴⁹), mice exhibited a quadratic component in the relationship between the mode of

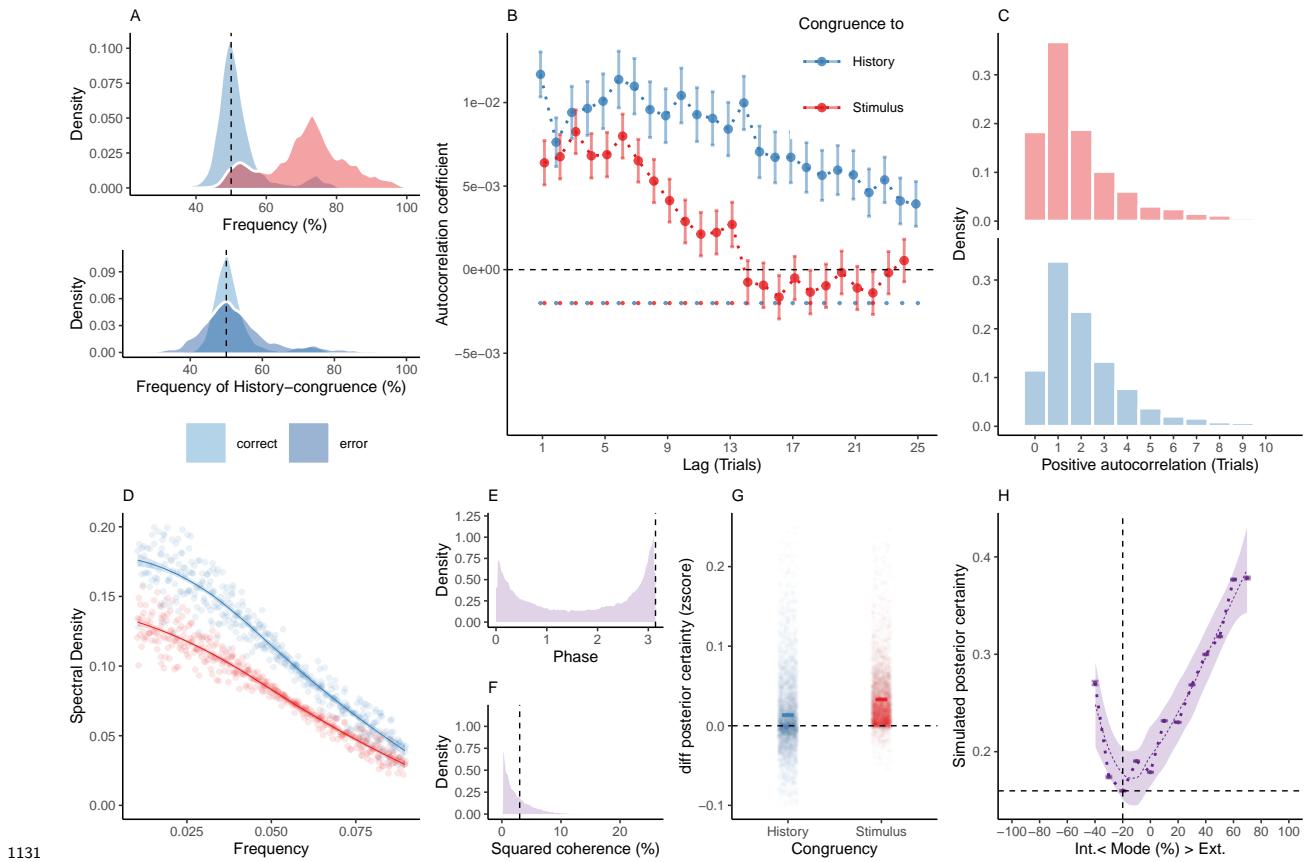
₁₁₂₆ sensory processing and TDs ($\beta_2 = -1.97 \times 10^3 \pm 843.74$, $T(1.19 \times 10^6) = -2.34$, $p = 0.02$).

₁₁₂₇ This explorative post-hoc analysis focuses on trials at which mice engage more swiftly with

₁₁₂₈ the experimental task. The horizontal and vertical dotted lines indicate maximum TD and

₁₁₂₉ the associated mode, respectively.

1130 **8.4 Figure 4**



1131 **Figure 4. Internal and external modes in simulated perceptual decision-making.**

1132 A. Simulated perceptual choices were stimulus-congruent in $71.36\% \pm 0.17\%$ (in red) and
 1133 history-congruent in $51.99\% \pm 0.11\%$ of trials (in blue; $T(4.32 \times 10^3) = 17.42$, $p = 9.89 \times 10^{-66}$;
 1134 upper panel). Due to the competition between stimulus- and history-congruence, history-
 1135 congruent perceptual choices were more frequent when perception was stimulus-incongruent
 1136 (i.e., on *error* trials; $T(4.32 \times 10^3) = 11.19$, $p = 1.17 \times 10^{-28}$; lower panel) and thus impaired
 1137 performance in the randomized psychophysical design simulated here.
 1138

1139 B. At the simulated group level, we found significant autocorrelations in both stimulus-
 1140 congruence (13 consecutive trials) and history-congruence (30 consecutive trials).

1141 C. On the level of individual simulated participants, autocorrelation coefficients exceeded the
 1142 autocorrelation coefficients of randomly permuted data within a lag of $2.46 \pm 1.17 \times 10^{-3}$

₁₁₄₃ trials for stimulus-congruence and $4.24 \pm 1.85 \times 10^{-3}$ trials for history-congruence.

₁₁₄₄ D. The smoothed probabilities of stimulus- and history-congruence (sliding windows of ± 5
₁₁₄₅ trials) fluctuated as a **scale-invariant process with a $1/f$ power law**, i.e., at power
₁₁₄₆ densities that were inversely proportional to the frequency (power $\sim 1/f^\beta$; stimulus-congruence:
₁₁₄₇ $\beta = -0.81 \pm 1.18 \times 10^{-3}$, $T(1.92 \times 10^5) = -687.58$, $p < 2.2 \times 10^{-308}$; history-congruence: β
₁₁₄₈ $= -0.83 \pm 1.27 \times 10^{-3}$, $T(1.92 \times 10^5) = -652.11$, $p < 2.2 \times 10^{-308}$).

₁₁₄₉ E. The distribution of phase shift between fluctuations in simulated stimulus- and history-
₁₁₅₀ congruence peaked at half a cycle (π denoted by dotted line). The dynamic probabilities of
₁₁₅₁ simulated stimulus- and history-congruence were therefore were strongly anti-correlated ($\beta =$
₁₁₅₂ $-0.03 \pm 8.22 \times 10^{-4}$, $T(2.12 \times 10^6) = -40.52$, $p < 2.2 \times 10^{-308}$).

₁₁₅₃ F. The average squared coherence between fluctuations in simulated stimulus- and history-
₁₁₅₄ congruence (black dotted line) amounted to $6.49 \pm 2.07 \times 10^{-3}\%$.

₁₁₅₅ G. Simulated confidence was enhanced for stimulus-congruence ($\beta = 0.03 \pm 1.71 \times 10^{-4}$,
₁₁₅₆ $T(2.03 \times 10^6) = 178.39$, $p < 2.2 \times 10^{-308}$) and history-congruence ($\beta = 0.01 \pm 1.5 \times 10^{-4}$,
₁₁₅₇ $T(2.03 \times 10^6) = 74.18$, $p < 2.2 \times 10^{-308}$).

₁₁₅₈ H. In analogy to humans, the simulated data showed a quadratic relationship between the
₁₁₅₉ mode of perceptual processing and posterior certainty, which increased for stronger external
₁₁₆₀ and internal biases ($\beta_2 = 31.03 \pm 0.15$, $T(2.04 \times 10^6) = 205.95$, $p < 2.2 \times 10^{-308}$). The
₁₁₆₁ horizontal and vertical dotted lines indicate minimum posterior certainty and the associated
₁₁₆₂ mode, respectively.

₁₁₆₃ **9 Supplemental Items**

₁₁₆₄ **9.1 Internal mode processing is driven by choice history as opposed
₁₁₆₅ to stimulus history**

₁₁₆₆ The main manuscript reports the effects of perceptual history, which we defined
₁₁₆₇ as the impact of the choice at the preceding trial on the choice at the current trial
₁₁₆₈ (henceforth *choice history*). *Stimulus history*, which is defined as the impact of
₁₁₆₉ the stimulus presented at the preceding trial on the choice at the present trial,
₁₁₇₀ represents an alternative approach to this. Here, we compare the effects of choice
₁₁₇₁ history to the effects of stimulus history.

₁₁₇₂ We observed a significant bias toward stimulus history (humans: $49.76\% \pm 0.1\%$
₁₁₇₃ of trials, $\beta = 1.26 \pm 0.94$, $T(373.62) = 1.34$, $p = 0.18$; mice: $51.11\% \pm 0.08\%$ of
₁₁₇₄ trials, $T(164) = 13.4$, $p = 3.86 \times 10^{-28}$). The bias toward stimulus history was
₁₁₇₅ smaller than the bias toward choice history (humans: $\beta = -3.53 \pm 0.5$, $T(66.53)$
₁₁₇₆ $= -7.01$, $p = 1.48 \times 10^{-9}$; mice: $T(164) = -17.21$, $p = 1.43 \times 10^{-38}$).

₁₁₇₇ The attraction of choices toward both preceding choices and stimuli is expected,
₁₁₇₈ as perception was *stimulus-congruent* on approximately 75% of trials, causing
₁₁₇₉ choices and stimuli to be highly correlated. We therefore compared the effects
₁₁₈₀ of choice history and stimulus history after *stimulus-incongruent* (i.e., *error*)
₁₁₈₁ trials, since those trials lead to opposite predictions regarding the perceptual
₁₁₈₂ choice at the subsequent trial.

₁₁₈₃ As expected from the findings presented in the main manuscript, perceptual
₁₁₈₄ choices were attracted toward perceptual choices when the inducing trial was
₁₁₈₅ stimulus-incongruent (i.e., a positive effect of choice history; humans: $\beta = 0.19 \pm$
₁₁₈₆ 1.4×10^{-4} , $z = 1.36 \times 10^3$, $p < 2.2 \times 10^{-308}$; mice: $\beta = 0.92 \pm 0.01$, $z = 88.82$, $p <$
₁₁₈₇ 2.2×10^{-308}). By contrast, perceptual choices tended to be repelled away from

1188 the stimulus presented at preceding stimulus-incongruent trial (i.e., a negative
1189 effect of stimulus history; humans: $\beta = -0.19 \pm 0.01$, $z = -16.47$, $p = 5.99 \times 10^{-61}$:
1190 mice: $\beta = -0.92 \pm 0.01$, $z = -88.76$, $p < 2.2 \times 10^{-308}$). This repulsion of choices
1191 away from stimuli presented at stimulus-incongruent trials confirmed that choices
1192 (which are anti-correlated to stimuli at stimulus-incongruent trials) were the
1193 primary driver of attracting serial effects in perception.

1194 In sum, the above results suggest that, in both humans and mice, serial depen-
1195 dencies were better explained by the effects of choice history as opposed to the
1196 effects of stimulus history. This aligns with a result recently published for the
1197 IBL database, where mice were shown to follow an *action-kernel* as opposed to a
1198 *stimulus-kernel* model when integrating information across trials⁸¹.

1199 9.2 Fluctuations between internal and external mode modulate 1200 perceptual performance beyond the effect of general response 1201 biases

1202 The hypothesis that perception cycles through opposing internally- and externally-biased
1203 modes is motivated by the assumption that recurring intervals of stronger perceptual history
1204 temporally reduce the participants' sensitivity to external information. Importantly, the
1205 history-dependent biases that characterize internal mode processing must be differentiated
1206 from general response biases. In binary perceptual decision-making, general response biases
1207 are defined by a propensity to choose one of the two outcomes more often than the alternative.
1208 Indeed, human participants selected the more frequent of the two possible outcomes in 58.71%
1209 $\pm 0.22\%$ of trials, and mice selected the more frequent of the two possible outcomes in 54.6%
1210 $\pm 0.3\%$ of trials.

1211 Two caveats have to be considered to make sure that the effect of history-congruence is
1212 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: $\beta = 0.24 \pm 6.93 \times 10^{-4}$, $T(2.09 \times 10^6) = 342.43$, $p < 2.2 \times 10^{-308}$; mice: $\beta = 0.15 \pm 8.25 \times 10^{-4}$, $T(1.32 \times 10^6) = 181.93$, $p < 2.2 \times 10^{-308}$). One may thus ask whether the autocorrelation of history-congruence could be entirely driven by general response biases.

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

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

Crucially, ongoing fluctuations in history-congruence had a significant negative effect on stimulus-congruence (humans: $\beta_1 = -0.05 \pm 5.63 \times 10^{-4}$, $T(2.1 \times 10^6) = -84.21$, $p < 2.2 \times 10^{-308}$; mice: $\beta_1 = -0.12 \pm 7.17 \times 10^{-4}$, $T(1.34 \times 10^6) = -168.39$, $p < 2.2 \times 10^{-308}$) beyond the effect of ongoing changes in general response biases (humans: $\beta_2 = -0.06 \pm 5.82 \times 10^{-4}$, $T(2.1 \times 10^6) = -103.51$, $p < 2.2 \times 10^{-308}$; mice: $\beta_2 = -0.03 \pm 6.94 \times 10^{-4}$, $T(1.34 \times 10^6) = -48.14$, $p < 2.2 \times 10^{-308}$). In sum, the above control analyses confirmed

1239 that, in both humans and mice, the observed influence of preceding choices on perceptual
1240 decision-making cannot be reduced to general response biases.

1241 **9.3 Internal mode is characterized by lower thresholds as well as**
1242 **by history-dependent changes in biases and lapses**

1243 Random or stereotypical responses may provide an alternative explanation for the reduced
1244 sensitivity to external sensory information that we attribute to internal mode processing. To
1245 test this hypothesis, we asked whether history-independent changes in biases and lapses may
1246 provide an alternative explanation of the reduced sensitivity during internal mode.

1247 To this end, we estimated full and history-conditioned psychometric curves to investigate how
1248 internal and external mode relate to biases (i.e., the horizontal position of the psychometric
1249 curve), lapses (i.e., the asymptotes of the psychometric curve) and thresholds (i.e., 1/sensitivity,
1250 estimated from the slope of the psychometric curve). We used a maximum likelihood procedure
1251 to predict trial-wise choices y ($y = 0$ and $y = 1$ for outcomes A and B respectively) from
1252 the choice probabilities y_p . y_p was computed from the difficulty-weighted inputs s_w via a
1253 parametric error function defined by the parameters γ (lower lapse), δ (upper lapse), μ (bias)
1254 and t (threshold; see Methods for details):

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

1255 Under our main hypothesis that periodic reductions in sensitivity to external information
1256 are driven by increases in the impact of perceptual history, one would expect (i) a history-
1257 dependent increase in biases and lapses (effects of perceptual history), and (ii), a history-
1258 independent increase in threshold (reduced sensitivity to external information). Conversely,
1259 if what we identified as internal mode processing was in fact driven by random choices, one
1260 would expect (i), a history-independent increase in lapse (choice randomness), (ii), no change

1261 in bias (no effect of perceptual history), and (iii), reduced thresholds (reduced sensitivity to
1262 external information).

1263 **9.3.1 Humans**

1264 Across all data provided by the Confidence database²⁰ (i.e., irrespective of the preceding
1265 perceptual choice y_{t-1}), biases μ were distributed around zero (-0.05 ± 0.03 ; $\beta_0 = 7.37 \times 10^{-3}$
1266 ± 0.09 , $T(36.8) = 0.08$, $p = 0.94$; Supplemental Figure 6A-B, upper panel). When conditioned
1267 on perceptual history, biases μ varied according to the preceding perceptual choice, with
1268 negative biases for $y_{t-1} = 0$ (-0.22 ± 0.04 ; $\beta_0 = 0.56 \pm 0.12$, $T(43.39) = 4.6$, $p = 3.64 \times 10^{-5}$;
1269 Supplemental Figure 6A-B, upper panel) and positive biases for $y_{t-1} = 1$ (0.29 ± 0.03 ; β_0
1270 $= 0.56 \pm 0.12$, $T(43.39) = 4.6$, $p = 3.64 \times 10^{-5}$; Supplemental Figure 6A-B, lower panel).
1271 Absolute biases $|\mu|$ were larger in internal mode (1.84 ± 0.03) as compared to external
1272 mode (0.86 ± 0.02 ; $\beta_0 = -0.62 \pm 0.07$, $T(45.62) = -8.38$, $p = 8.59 \times 10^{-11}$; controlling for
1273 differences in lapses and thresholds).

1274 Lower and upper lapses amounted to $\gamma = 0.13 \pm 2.83 \times 10^{-3}$ and $\delta = 0.1 \pm 2.45 \times 10^{-3}$
1275 (Supplemental Figure 6A, C and D). Lapses were larger in internal mode ($\gamma = 0.17 \pm$
1276 3.52×10^{-3} , $\delta = 0.14 \pm 3.18 \times 10^{-3}$) as compared to external mode ($\gamma = 0.1 \pm 2.2 \times 10^{-3}$, $\delta =$
1277 $0.08 \pm 2 \times 10^{-3}$; $\beta_0 = -0.05 \pm 5.73 \times 10^{-3}$, $T(47.03) = -9.11$, $p = 5.94 \times 10^{-12}$; controlling
1278 for differences in biases and thresholds).

1279 Conditioning on the previous perceptual choice revealed that the between-mode difference in
1280 lapse was not general, but depended on perceptual history: For $y_{t-1} = 0$, only higher lapses δ
1281 differed between internal and external mode ($\beta_0 = -0.1 \pm 9.58 \times 10^{-3}$, $T(36.87) = -10.16$, p
1282 $= 3.06 \times 10^{-12}$), whereas lower lapses γ did not ($\beta_0 = 0.01 \pm 7.77 \times 10^{-3}$, $T(33.1) = 1.61$, p
1283 $= 0.12$). Vice versa, for $y_{t-1} = 1$, lower lapses γ differed between internal and external mode
1284 ($\beta_0 = -0.11 \pm 0.01$, $T(40.11) = -9.59$, $p = 6.14 \times 10^{-12}$), whereas higher lapses δ did not
1285 ($\beta_0 = 0.01 \pm 7.74 \times 10^{-3}$, $T(33.66) = 1.58$, $p = 0.12$).

1286 Thresholds t were estimated at 3 ± 0.06 (Supplemental Figure 6A and E). Thresholds t were
1287 larger in internal mode (3.66 ± 0.09) as compared to external mode (2.02 ± 0.03 ; $\beta_0 = -1.77$
1288 ± 0.25 , $T(50.45) = -7.14$, $p = 3.48 \times 10^{-9}$; controlling for differences in biases and lapses).
1289 In contrast to the bias μ and the lapse rates γ and δ , thresholds t were not modulated by
1290 perceptual history ($\beta_0 = 0.04 \pm 0.06$, $T(2.97 \times 10^3) = 0.73$, $p = 0.47$).

1291 **9.3.2 Mice**

1292 When estimated based on the full dataset provided in the IBL database²¹ (i.e., irrespective
1293 of the preceding perceptual choice y_{t-1}), biases μ were distributed around zero (3.87×10^{-3}
1294 $\pm 9.81 \times 10^{-3}$; $T(164) = 0.39$, $p = 0.69$; Supplemental Figure 7A-B, upper panel). When
1295 conditioned on the preceding perceptual choice, biases were negative for $y_{t-1} = 0$ (-0.02
1296 $\pm 8.7 \times 10^{-3}$; $T(164) = -1.99$, $p = 0.05$; Supplemental Figure 7A-B, middle panel) and
1297 positive for $y_{t-1} = 1$ ($0.02 \pm 9.63 \times 10^{-3}$; $T(164) = 1.91$, $p = 0.06$; Supplemental Figure
1298 7A-B, lower panel). As in humans, mice showed larger biases during internal mode (0.14
1299 $\pm 7.96 \times 10^{-3}$) as compared to external mode ($0.07 \pm 8.7 \times 10^{-3}$; $\beta_0 = -0.18 \pm 0.03$, $T =$
1300 -6.38 , $p = 1.77 \times 10^{-9}$; controlling for differences in lapses and thresholds).

1301 Lower and upper lapses amounted to $\gamma = 0.1 \pm 4.35 \times 10^{-3}$ and $\delta = 0.11 \pm 4.65 \times 10^{-3}$
1302 (Supplemental Figure 7A, C and D). Lapse rates were higher in internal mode ($\gamma = 0.15 \pm$
1303 5.14×10^{-3} , $\delta = 0.16 \pm 5.79 \times 10^{-3}$) as compared to external mode ($\gamma = 0.06 \pm 3.11 \times 10^{-3}$,
1304 $\delta = 0.07 \pm 3.34 \times 10^{-3}$; $\beta_0 = -0.11 \pm 4.39 \times 10^{-3}$, $T = -24.8$, $p = 4.91 \times 10^{-57}$; controlling
1305 for differences in biases and thresholds).

1306 For $y_{t-1} = 0$, the difference between internal and external mode was more pronounced for
1307 higher lapses δ ($T(164) = 21.44$, $p = 1.93 \times 10^{-49}$). Conversely, for $y_{t-1} = 1$, the difference
1308 between internal and external mode was more pronounced for lower lapses γ ($T(164) =$
1309 -18.24 , $p = 2.68 \times 10^{-41}$). In contrast to the human data, higher lapses δ and lower lapses
1310 γ were significantly elevated during internal mode irrespective of the preceding perceptual
1311 choice (higher lapses δ for $y_{t-1} = 1$: $T(164) = -2.65$, $p = 8.91 \times 10^{-3}$; higher lapses δ for

₁₃₁₂ $y_{t-1} = 0$: $T(164) = -28.29$, $p = 5.62 \times 10^{-65}$; lower lapses γ for $y_{t-1} = 1$: $T(164) = -32.44$, p
₁₃₁₃ $= 2.92 \times 10^{-73}$; lower lapses γ for $y_{t-1} = 0$: $T(164) = -2.5$, $p = 0.01$.

₁₃₁₄ In mice, thresholds t amounted to $0.15 \pm 6.52 \times 10^{-3}$ (Supplemental Figure 7A and E) and
₁₃₁₅ were higher in internal mode (0.27 ± 0.01) as compared to external mode ($0.09 \pm 4.44 \times 10^{-3}$;
₁₃₁₆ $\beta_0 = -0.28 \pm 0.04$, $T = -7.26$, $p = 1.53 \times 10^{-11}$; controlling for differences in biases and
₁₃₁₇ lapses). Thresholds t were not modulated by perceptual history ($T(164) = 0.94$, $p = 0.35$).

₁₃₁₈ In sum, the above analyses showed that, in both humans and mice, internal and external
₁₃₁₉ mode differ with respect to biases, lapses and thresholds. Internally-biased processing was
₁₃₂₀ characterized by higher thresholds, indicating a reduced sensitivity to sensory information,
₁₃₂₁ as well as by larger biases and lapses. Importantly, between-mode differences in biases and
₁₃₂₂ lapses strongly depended on perceptual history. This confirmed that internal mode processing
₁₃₂₃ cannot be explained solely on the ground of a general (i.e., history-independent) increase in
₁₃₂₄ lapses or bias indicative of random or stereotypical responses.

₁₃₂₅ **9.4 Internal mode processing can not be reduced to insufficient 1326 task familiarity**

₁₃₂₇ It may be assumed that participants tend to repeat preceding choices when they are not yet
₁₃₂₈ familiar with the experimental task, leading to history-congruent choices that are caused by
₁₃₂₉ insufficient training. To assess this alternative explanation, we contrasted the correlates of
₁₃₃₀ bimodal inference with training effects in humans and mice.

₁₃₃₁ **9.4.1 Humans**

₁₃₃₂ In the Confidence database²⁰, training effects were visible from RTs that were shortened by
₁₃₃₃ 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
₁₃₃₄ $< 2.2 \times 10^{-308}$). Intriguingly, however, history-congruent choices became more frequent with
₁₃₃₅ increased exposure to the task ($\beta = 3.6 \times 10^{-5} \pm 2.54 \times 10^{-6}$, $z = 14.19$, $p = 10^{-45}$), speaking

₁₃₃₆ against the proposition that insufficient training induces seriality in response behavior.

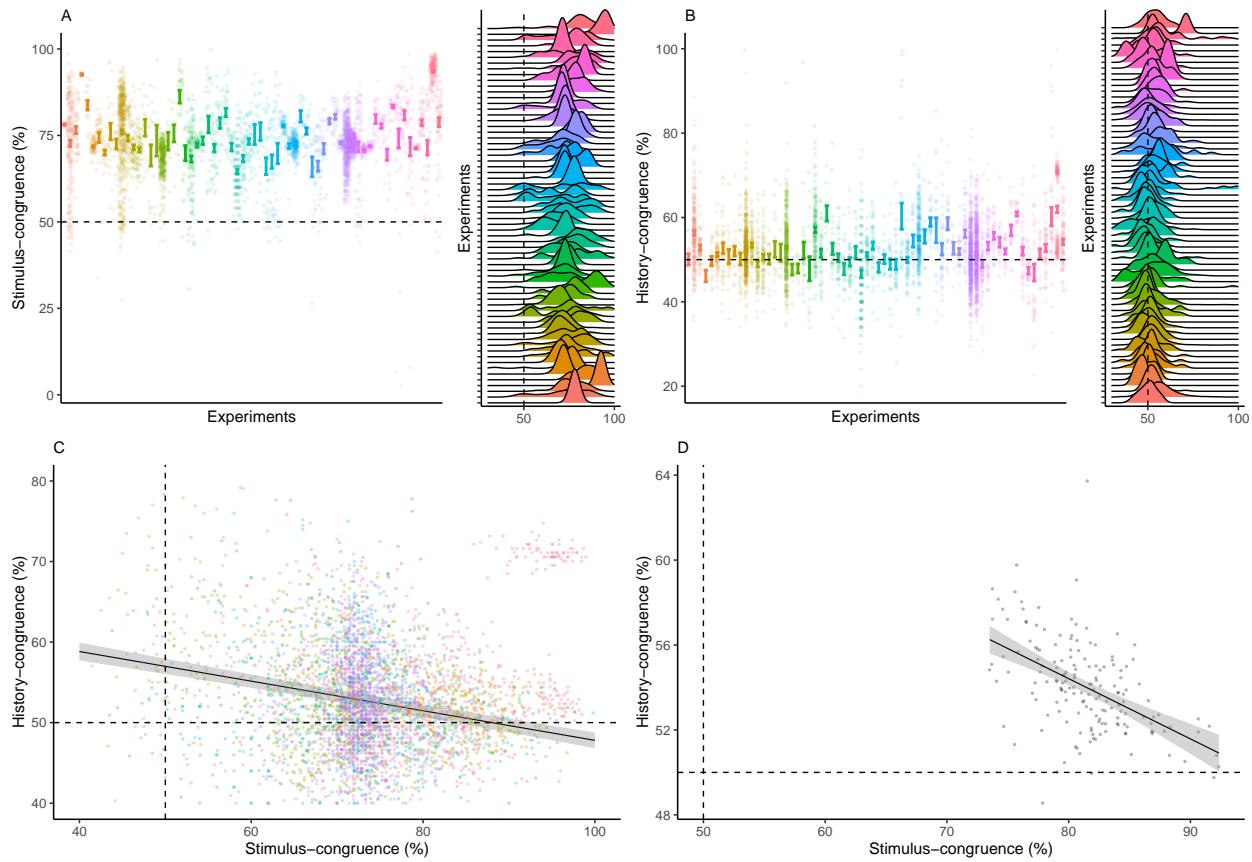
₁₃₃₇ **9.4.2 Mice**

₁₃₃₈ As in humans, it is an important caveat to consider whether the observed serial dependencies
₁₃₃₉ in mice reflect a phenomenon of perceptual inference, or, alternatively, an unspecific strategy
₁₃₄₀ that occurs at the level of reporting behavior. We reasoned that, if mice indeed tended to
₁₃₄₁ repeat previous choices as a general response pattern, history effects should decrease during
₁₃₄₂ training of the perceptual task. We therefore analyzed how stimulus- and history-congruent
₁₃₄₃ perceptual choices evolved across sessions in mice that, by the end of training, achieved
₁₃₄₄ proficiency (i.e., stimulus-congruence $\geq 80\%$) in the *basic* task of the IBL dataset²¹.

₁₃₄₅ Across sessions, we found that stimulus-congruent perceptual choices became more frequent
₁₃₄₆ ($\beta = 0.34 \pm 7.13 \times 10^{-3}$, $T(8.51 \times 10^3) = 47.66$, $p < 2.2 \times 10^{-308}$) and TDs were progressively
₁₃₄₇ shortened ($\beta = -22.14 \pm 17.06$, $T(1.14 \times 10^3) = -1.3$, $p < 2.2 \times 10^{-308}$). Crucially, the
₁₃₄₈ frequency of history-congruent perceptual choices also increased during training ($\beta = 0.13 \pm$
₁₃₄₉ 4.67×10^{-3} , $T(8.4 \times 10^3) = 27.04$, $p = 1.96 \times 10^{-154}$; Supplemental Figure S8).

₁₃₅₀ Within individual session, longer task exposure was associated with an increase in history-
₁₃₅₁ 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
₁₃₅₂ $= -0.1 \pm 3.96 \times 10^{-3}$, $T(1.34 \times 10^6) = -24.99$, $p = 9.45 \times 10^{-138}$). In sum, these findings
₁₃₅₃ strongly argue against the proposition that mice show biases toward perceptual history due
₁₃₅₄ to an unspecific response strategy.

1355 **9.5 Supplemental Figure S1**



1356 **1357 Supplemental Figure S1. Stimulus- and history-congruence.**

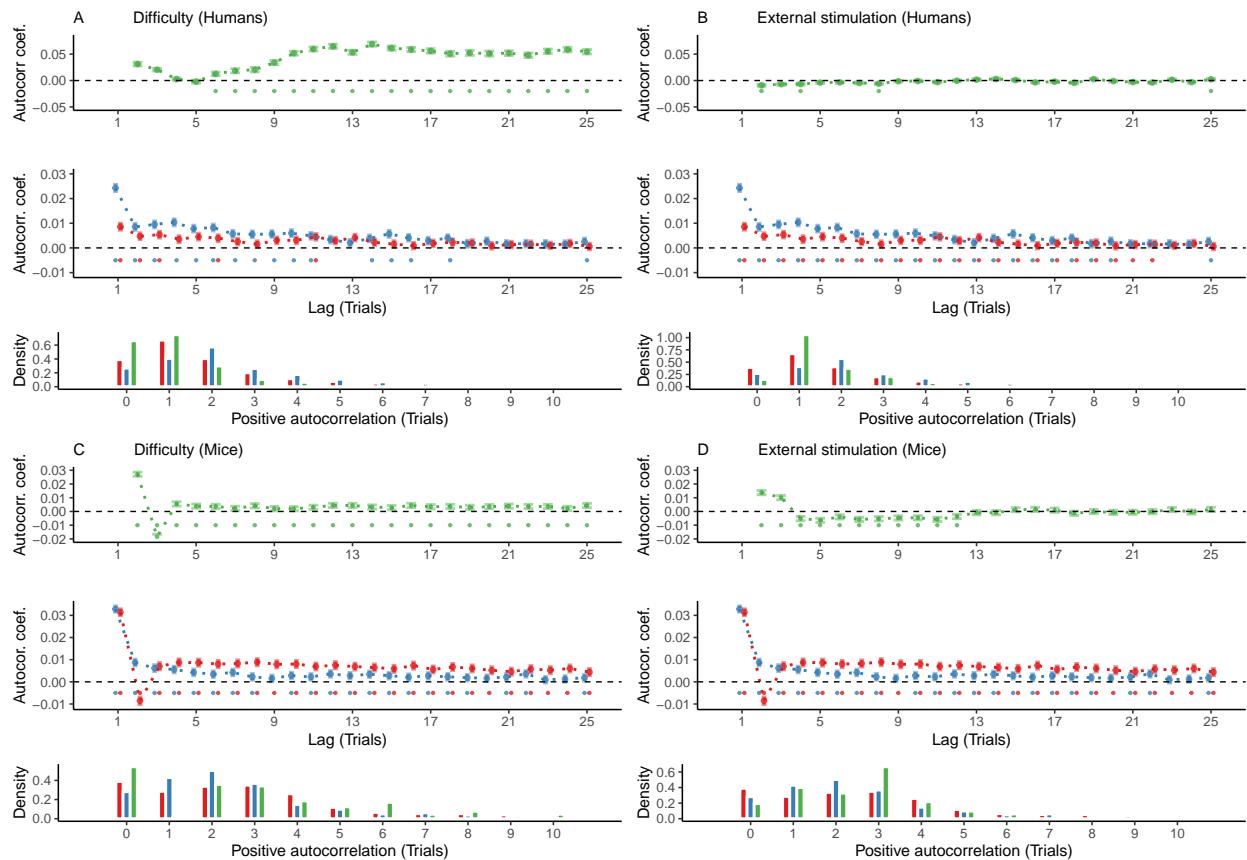
1358 A. Stimulus-congruent choices in humans amounted to $73.46\% \pm 0.15\%$ of trials and were
1359 highly consistent across the experiments selected from the Confidence Database.

1360 B. History-congruent choices in humans amounted to $52.7\% \pm 0.12\%$ of trials. In analogy
1361 to stimulus-congruence, the prevalence of history-congruence was highly consistent across
1362 the experiments selected from the Confidence Database. 48.48% of experiments showed
1363 significant ($p < 0.05$) biases toward preceding choices, whereas 2 of the 66 of the included
1364 experiments showed significant repelling biases.

1365 C. In humans, we found an enhanced impact of perceptual history in participants who were
1366 less sensitive to external sensory information ($T(4.3 \times 10^3) = -14.27$, $p = 3.78 \times 10^{-45}$),
1367 suggesting that perception results from the competition of external with internal information.

₁₃₆₈ D. In analogy to humans, mice that were less sensitive to external sensory information
₁₃₆₉ showed stronger biases toward perceptual history ($T(163) = -7.52$, $p = 3.44 \times 10^{-12}$, Pearson
₁₃₇₀ correlation).

1371 **9.6 Supplemental Figure S2**



1372

1373 **Supplemental Figure S2. Controlling for task difficulty and external stimulation.**

1374 In this study, we found highly significant autocorrelations of stimulus- and history-congruence
 1375 in humans as well as in mice, while controlling for task difficulty and the sequence of external
 1376 stimulation. **Here, we confirm that the autocorrelations of stimulus- and history-**
 1377 **congruence were not a trivial consequence of the experimental design or the**
 1378 **addition of task difficulty and external stimulation as control variables in the**
 1379 **computation of group-level autocorrelations.**

1380 A. In humans, task difficulty (in green) showed a significant autocorrelation starting at the
 1381 5th trial (upper panel, dots at the bottom indicate intercepts $\neq 0$ in trial-wise linear mixed
 1382 effects modeling at $p < 0.05$). When controlling for task difficulty only, linear mixed effects
 1383 modeling indicated a significant autocorrelation of stimulus-congruence (in red) for the first 3
 1384 consecutive trials (middle panel). 20% of trials within the displayed time window remained

1385 significantly autocorrelated. The autocorrelation of history-congruence (in blue) remained
1386 significant for the first 11 consecutive trials (64% significantly autocorrelated trials within
1387 the displayed time window). At the level of individual participants, the autocorrelation of
1388 task difficulty exceeded the respective autocorrelation of randomly permuted within a lag of
1389 $21.66 \pm 8.37 \times 10^{-3}$ trials (lower panel).

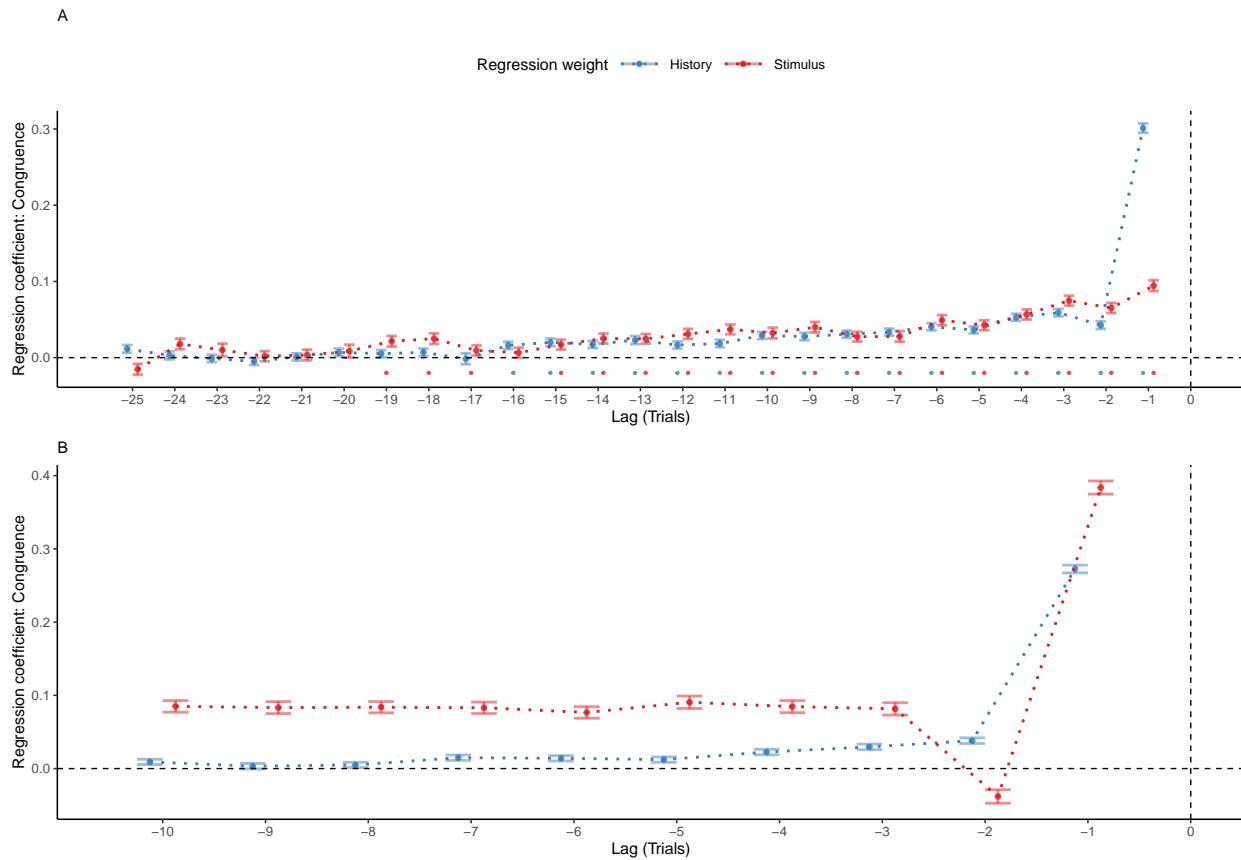
1390 B. In humans, the sequence of external stimulation (i.e., which of the two binary outcomes
1391 was supported by the presented stimuli; depicted in green) was negatively autocorrelated
1392 for 1 trial. When controlling for the autocorrelation of external stimulation only, stimulus-
1393 congruence remained significantly autocorrelated for 22 consecutive trials (88% of trials
1394 within the displayed time window; lower panel) and history-congruence remained significantly
1395 autocorrelated for 20 consecutive trials (84% of trials within the displayed time window). At
1396 the level of individual participants, the autocorrelation of external stimulation exceeded the
1397 respective autocorrelation of randomly permuted within a lag of $2.94 \pm 4.4 \times 10^{-3}$ consecutive
1398 trials (lower panel).

1399 C. In mice, task difficulty showed a significant autocorrelated for the first 25 consecutive trials
1400 (upper panel). When controlling only for task difficulty only, linear mixed effects modeling
1401 indicated a significant autocorrelation of stimulus-congruence for the first 36 consecutive trials
1402 (middle panel). In total, 100% of trials within the displayed time window remained significantly
1403 autocorrelated. The autocorrelation of history-congruence remained significant for the first
1404 8 consecutive trials, with 84% significantly autocorrelated trials within the displayed time
1405 window. At the level of individual mice, autocorrelation coefficients for difficulty were elevated
1406 above randomly permuted data within a lag of 15.13 ± 0.19 consecutive trials (lower panel).

1407 D. In mice, the sequence of external stimulation (i.e., which of the two binary outcomes was
1408 supported by the presented stimuli) was negatively autocorrelated for 11 consecutive trials
1409 (upper panel). When controlling only for the autocorrelation of external stimulation, stimulus-
1410 congruence remained significantly autocorrelated for 86 consecutive trials (100% of trials

¹⁴¹¹ within the displayed time window; middle) and history-congruence remained significantly
¹⁴¹² autocorrelated for 8 consecutive trials (84% of trials within the displayed time window). At
¹⁴¹³ the level of individual mice, autocorrelation coefficients for external stimulation were elevated
¹⁴¹⁴ above randomly permuted data within a lag of $2.53 \pm 9.8 \times 10^{-3}$ consecutive trials (lower
¹⁴¹⁵ panel).

1416 **9.7 Supplemental Figure S3**



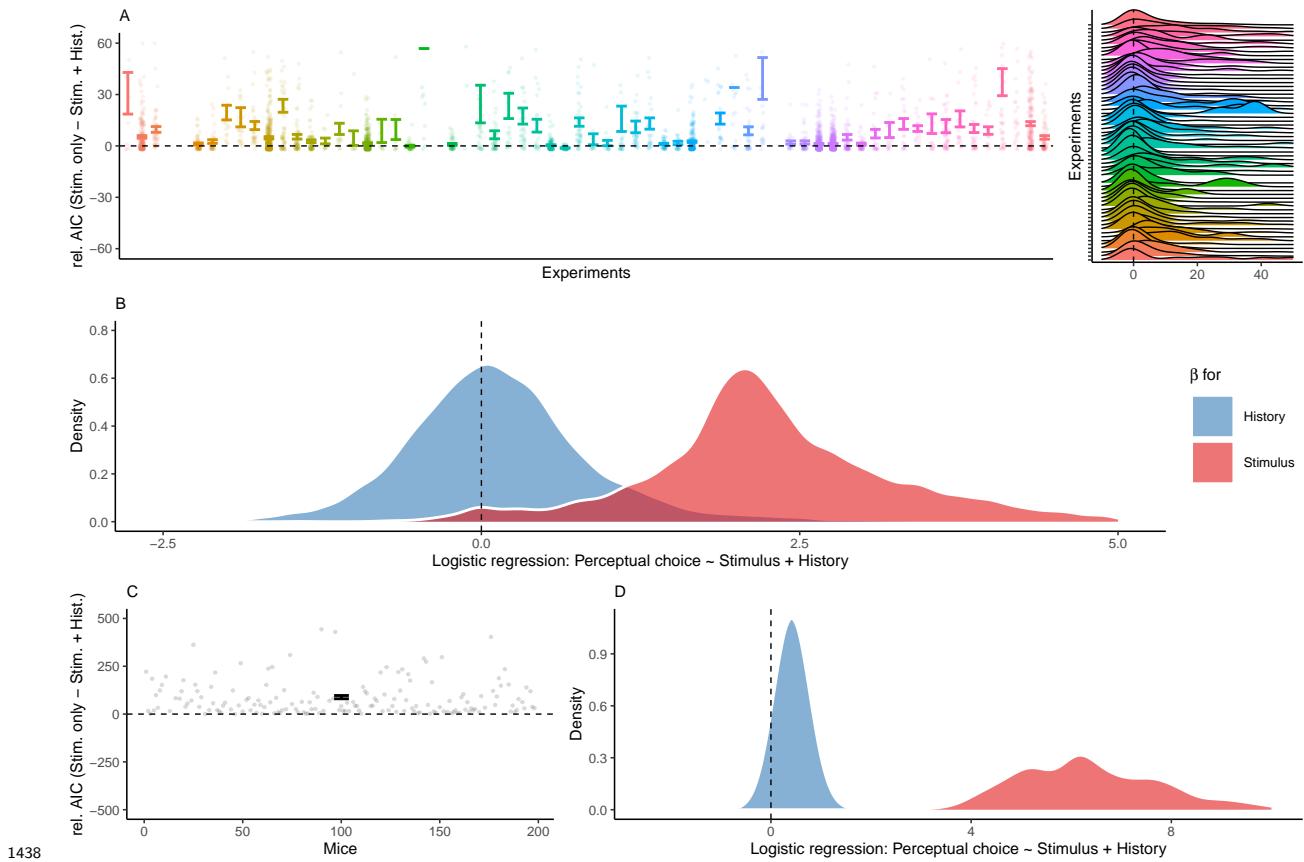
1418 **Supplemental Figure S3. Reproducing group-level autocorrelations using logistic
1419 regression.**

1420 A. As an alternative to group-level autocorrelation coefficients, we used trial-wise logistic
1421 regression to quantify serial dependencies in stimulus- and history-congruence. This analysis
1422 predicted stimulus- and history-congruence at the index trial (trial $t = 0$, vertical line) based
1423 on stimulus- and history-congruence at the 100 preceding trials. Mirroring the shape of the
1424 group-level autocorrelations, trial-wise regression coefficients (depicted as mean \pm SEM, dots
1425 mark trials with regression weights significantly greater than zero at $p < 0.05$) increased
1426 toward the index trial $t = 0$ for the human data.

1427 B. Following our results in human data, regression coefficients that predicted history-
1428 congruence at the index trial (trial $t = 0$, vertical line) increased exponentially for trials
1429 closer to the index trial in mice. In contrast to history-congruence, stimulus-congruence

¹⁴³⁰ showed a negative regression weight (or autocorrelation coefficient; Figure 3B) at trial -2.
¹⁴³¹ This was due to the experimental design (see also the autocorrelations of difficulty and
¹⁴³² external stimulation in Supplemental Figure S2C and D): When mice made errors at easy
¹⁴³³ trials (contrast $\geq 50\%$), the upcoming stimulus was shown at the same spatial location and at
¹⁴³⁴ high contrast. This increased the probability of stimulus-congruent perceptual choices after
¹⁴³⁵ stimulus-incongruent perceptual choices at easy trials, thereby creating a negative regression
¹⁴³⁶ weight (or autocorrelation coefficient) of stimulus-congruence at trial -2.

1437 **9.8 Supplemental Figure S4**



1438

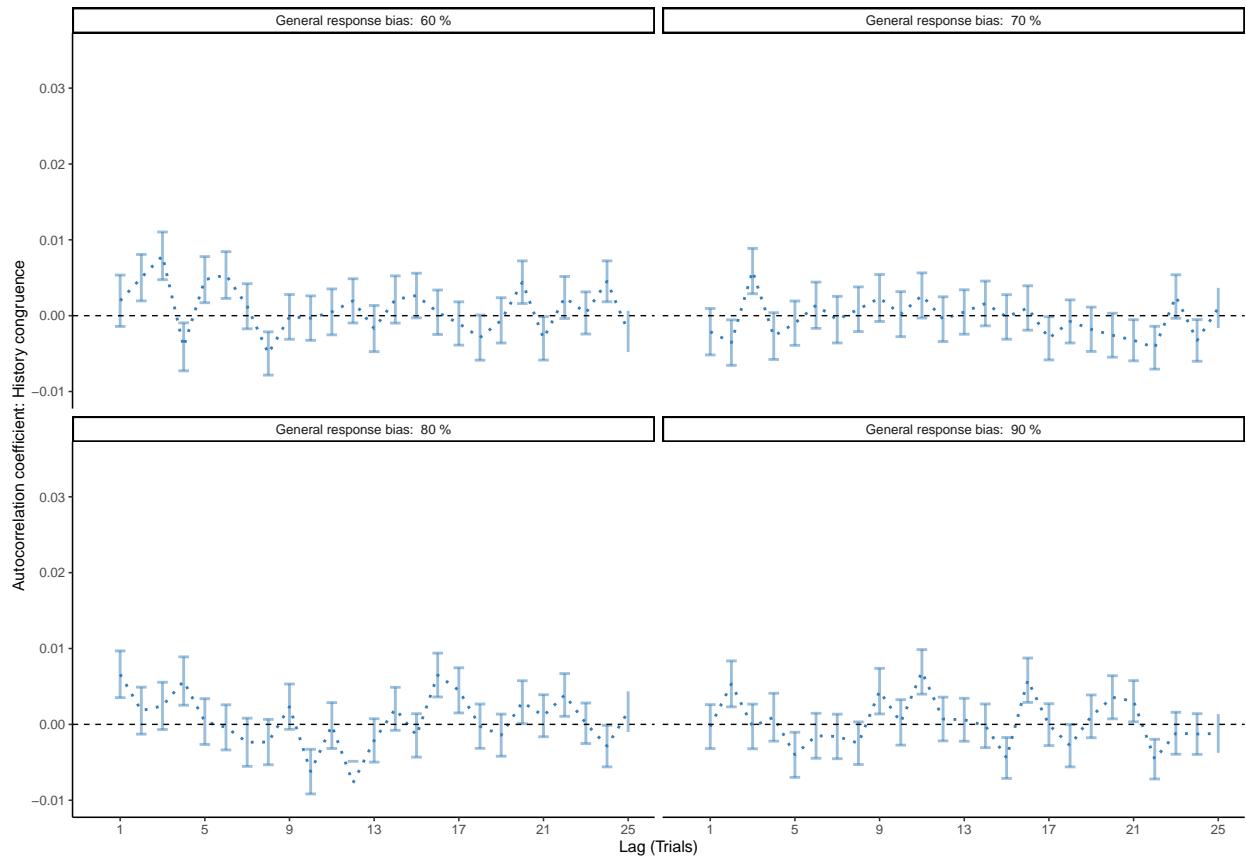
1439 **Supplemental Figure S4. History-congruence in logistic regression.**

1440 A. To ensure that perceptual history played a significant role in perception despite the ongoing
 1441 stream of external information, we tested whether human perceptual decision-making was
 1442 better explained by the combination of external and internal information or, alternatively,
 1443 by external information alone. To this end, we compared AIC between logistic regression
 1444 models that predicted trial-wise perceptual responses either by both current external sensory
 1445 information and the preceding percept, or by external sensory information alone (values above
 1446 zero indicate a superiority of the full model). With high consistency across the experiments
 1447 selected from the Confidence Database, this model-comparison confirmed that perceptual
 1448 history contributed significantly to perception (difference in AIC = 8.07 ± 0.53 , $T(57.22) =$
 1449 4.1 , $p = 1.31 \times 10^{-4}$).

1450 B. Participant-wise regression coefficients amount to 0.18 ± 0.02 for the effect of perceptual

- ₁₄₅₁ history and 2.51 ± 0.03 for external sensory stimulation.
- ₁₄₅₂ C. In mice, an AIC-based model comparison indicated that perception was better explained
₁₄₅₃ by logistic regression models that predicted trial-wise perceptual responses based on both
₁₄₅₄ current external sensory information and the preceding percept (difference in AIC = $88.62 \pm$
₁₄₅₅ 8.57 , $T(164) = -10.34$, $p = 1.29 \times 10^{-19}$).
- ₁₄₅₆ D. In mice, individual regression coefficients amounted to 0.42 ± 0.02 for the effect of
₁₄₅₇ perceptual history and 6.91 ± 0.21 for external sensory stimulation.

1458 **9.9 Supplemental Figure S5**



1459

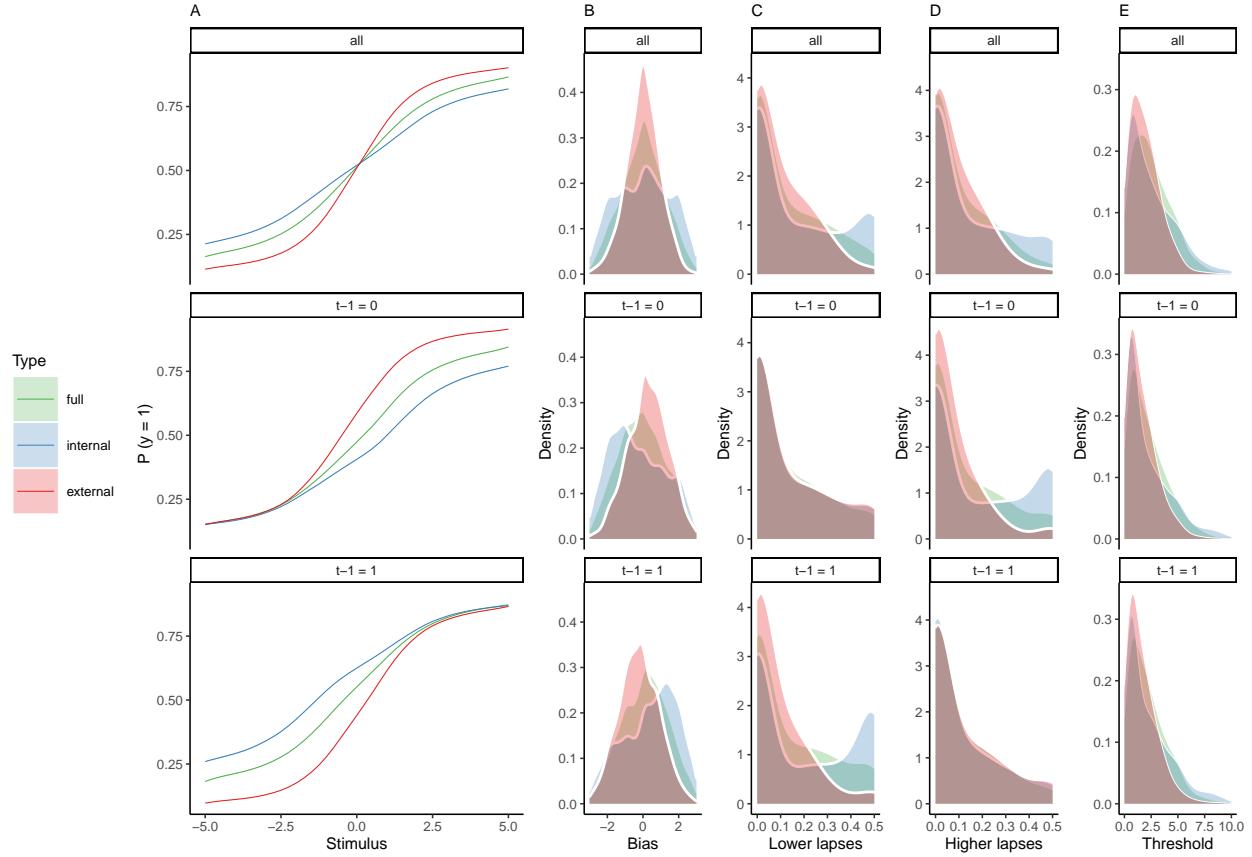
1460 **Supplemental Figure S5. Correcting for general response biases.**

1461 Here, we ask whether the autocorrelation of history-congruence (as shown in Figure 2-3C)
1462 may be driven by general response biases (i.e., a general propensity to choose one of the two
1463 possible outcomes more frequently than the alternative). To this end, we generated sequences
1464 of 100 perceptual choices with general response biases ranging from 60 to 90% for 1000
1465 simulated participants each. We then computed the autocorrelation of history-congruence
1466 for these simulated data. Crucially, we used the correction procedure that is applied to the
1467 autocorrelation curves shown in this manuscript: All reported autocorrelation coefficients are
1468 computed relative to the average autocorrelation coefficients obtained for 100 iterations of
1469 randomly permuted trial sequences. The above simulation show that this correction procedure
1470 removes any potential contribution of general response biases to the autocorrelation of history-
1471 congruence. This indicates that the autocorrelation of history-congruence (as shown in Figure

₁₄₇₂ 2-3C) is not driven by general response biases that were present in the empirical data at a

₁₄₇₃ level of $58.71\% \pm 0.22\%$ in humans and $54.6\% \pm 0.3\%$ in mice.

1474 **9.10 Supplemental Figure S6**



1475

1476 **Supplemental Figure S6. Full and history-conditioned psychometric functions**
 1477 **across modes in humans.**

1478 A. Here, we show average psychometric functions for the full dataset (upper panel) and
 1479 conditioned on perceptual history ($y_{t-1} = 1$ and $y_{t-1} = 0$; middle and lower panel) across
 1480 modes (green line) and for internal mode (blue line) and external mode (red line) separately.

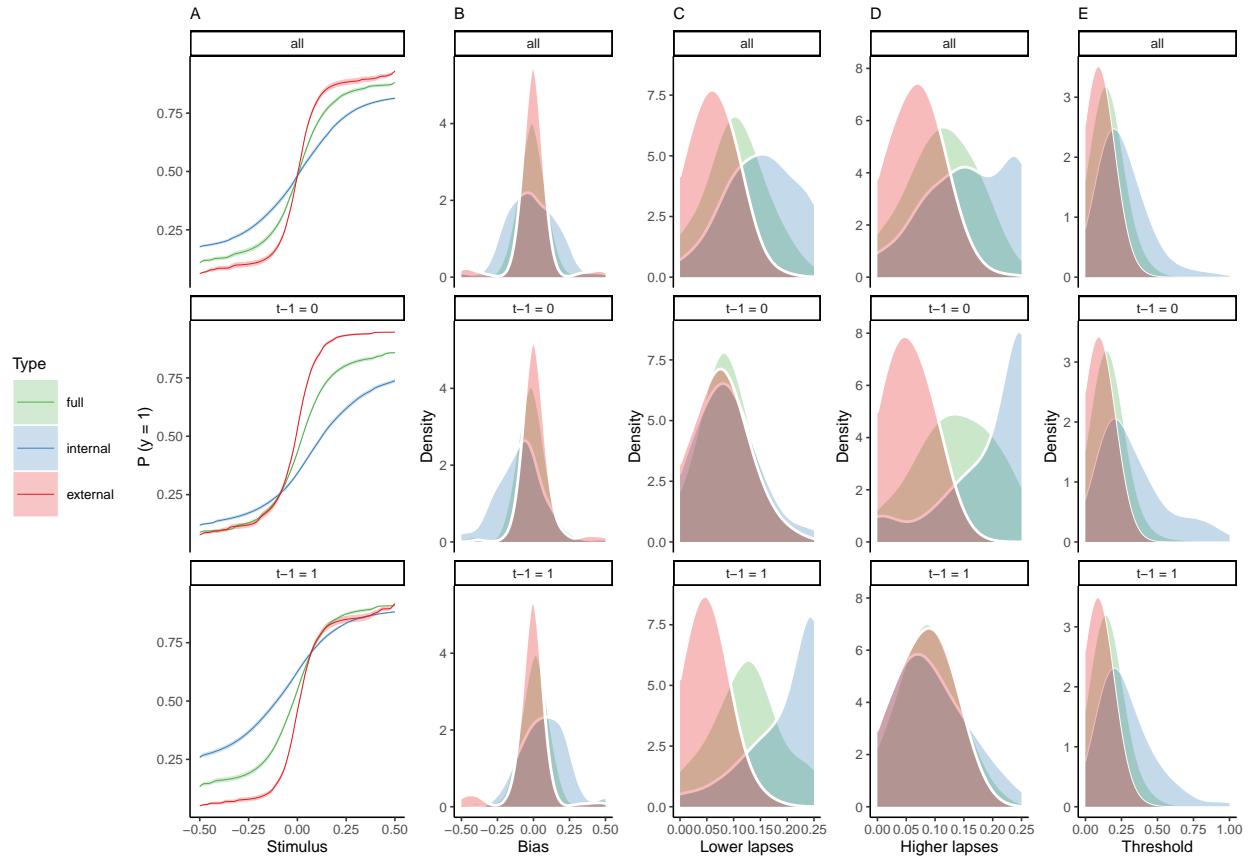
1481 B. Across the full dataset, biases μ were distributed around zero ($\beta_0 = 7.37 \times 10^{-3} \pm 0.09$,
 1482 $T(36.8) = 0.08$, $p = 0.94$; upper panel), with larger absolute biases $|\mu|$ for internal as compared
 1483 to external mode ($\beta_0 = -0.62 \pm 0.07$, $T(45.62) = -8.38$, $p = 8.59 \times 10^{-11}$; controlling for
 1484 differences in lapses and thresholds). When conditioned on perceptual history, we observed
 1485 negative biases for $y_{t-1} = 0$ ($\beta_0 = 0.56 \pm 0.12$, $T(43.39) = 4.6$, $p = 3.64 \times 10^{-5}$; middle
 1486 panel) and positive biases for $y_{t-1} = 1$ ($\beta_0 = 0.56 \pm 0.12$, $T(43.39) = 4.6$, $p = 3.64 \times 10^{-5}$;
 1487 lower panel).

₁₄₈₈ C. Lapse rates were higher in internal mode as compared to external mode ($\beta_0 = -0.05 \pm$
₁₄₈₉ 5.73×10^{-3} , $T(47.03) = -9.11$, $p = 5.94 \times 10^{-12}$; controlling for differences in biases and
₁₄₉₀ thresholds; see upper panel and subplot D). Importantly, the between-mode difference in
₁₄₉₁ lapses depended on perceptual history: We found no significant difference in lower lapses
₁₄₉₂ 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
₁₄₉₃ significant difference for $y_{t-1} = 1$ ($\beta_0 = -0.11 \pm 0.01$, $T(40.11) = -9.59$, $p = 6.14 \times 10^{-12}$;
₁₄₉₄ lower panel).

₁₄₉₅ D. Conversely, higher lapses δ were significantly increased for $y_{t-1} = 0$ ($\beta_0 = -0.1 \pm$
₁₄₉₆ 9.58×10^{-3} , $T(36.87) = -10.16$, $p = 3.06 \times 10^{-12}$; middle panel), but not for $y_{t-1} = 1$ ($\beta_0 =$
₁₄₉₇ $0.01 \pm 7.74 \times 10^{-3}$, $T(33.66) = 1.58$, $p = 0.12$; lower panel).

₁₄₉₈ E. The thresholds t were larger in internal as compared to external mode ($\beta_0 = -1.77 \pm 0.25$,
₁₄₉₉ $T(50.45) = -7.14$, $p = 3.48 \times 10^{-9}$; controlling for differences in biases and lapses) and were
₁₅₀₀ not modulated by perceptual history ($\beta_0 = 0.04 \pm 0.06$, $T(2.97 \times 10^3) = 0.73$, $p = 0.47$).

1501 **9.11 Supplemental Figure S7**



1502 **1503 Supplemental Figure S7. Full and history-conditioned psychometric functions**

1504 **across modes in mice.**

1505 A. Here, we show average psychometric functions for the full IBL dataset (upper panel) and
 1506 conditioned on perceptual history ($y_{t-1} = 1$ and $y_{t-1} = 0$; middle and lower panel) across
 1507 modes (green line) and for internal mode (blue line) and external mode (red line) separately.

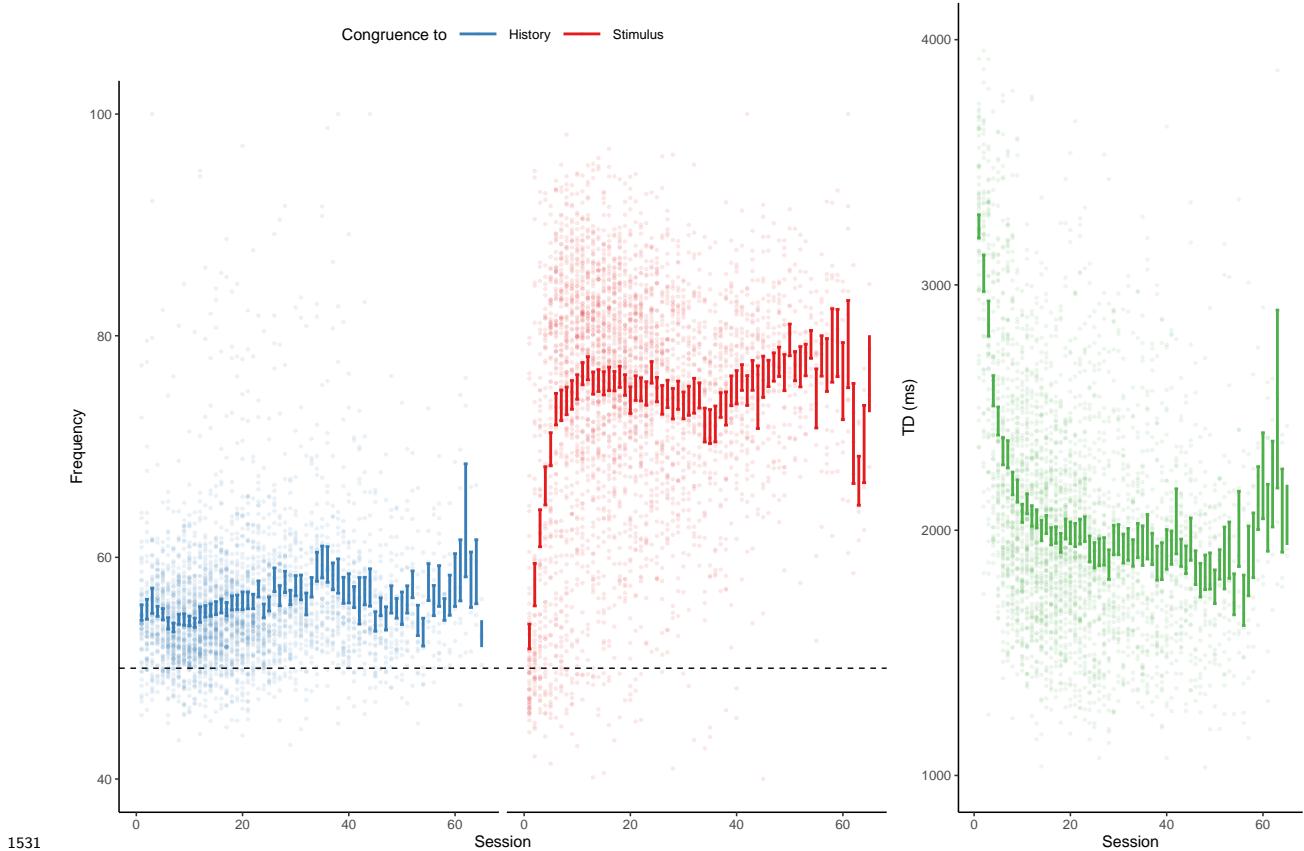
1508 B. Across the full dataset, biases μ were distributed around zero ($T(164) = 0.39$, $p = 0.69$;
 1509 upper panel), with larger absolute biases $|\mu|$ for internal as compared to external mode ($\beta_0 =$
 1510 -0.18 ± 0.03 , $T = -6.38$, $p = 1.77 \times 10^{-9}$; controlling for differences in lapses and thresholds).
 1511 When conditioned on perceptual history, we observed negative biases for $y_{t-1} = 0$ ($T(164)$
 1512 $= -1.99$, $p = 0.05$; middle panel) and positive biases for $y_{t-1} = 1$ ($T(164) = 1.91$, $p = 0.06$;
 1513 lower panel).

₁₅₁₄ C. Lapse rates were higher in internal as compared to external mode ($\beta_0 = -0.11 \pm 4.39 \times 10^{-3}$,
₁₅₁₅ $T = -24.8$, $p = 4.91 \times 10^{-57}$; controlling for differences in biases and thresholds; upper
₁₅₁₆ panel, see subplot D). For $y_{t-1} = 1$, the difference between internal and external mode was
₁₅₁₇ more pronounced for lower lapses γ ($T(164) = -18.24$, $p = 2.68 \times 10^{-41}$) as compared to
₁₅₁₈ higher lapses δ (see subplot D). In mice, lower lapses γ were significantly elevated during
₁₅₁₉ internal mode irrespective of the preceding perceptual choice (middle panel: lower lapses γ
₁₅₂₀ for $y_{t-1} = 0$; $T(164) = -2.5$, $p = 0.01$, lower panel: lower lapses γ for $y_{t-1} = 1$; $T(164) =$
₁₅₂₁ -32.44 , $p = 2.92 \times 10^{-73}$).

₁₅₂₂ D. For $y_{t-1} = 0$, the difference between internal and external mode was more pronounced
₁₅₂₃ for higher lapses δ ($T(164) = 21.44$, $p = 1.93 \times 10^{-49}$, see subplot C). Higher lapses were
₁₅₂₄ significantly elevated during internal mode irrespective of the preceding perceptual choice
₁₅₂₅ (middle panel: higher lapses δ for $y_{t-1} = 0$; $T(164) = -28.29$, $p = 5.62 \times 10^{-65}$ lower panel:
₁₅₂₆ higher lapses δ for $y_{t-1} = 1$; $T(164) = -2.65$, $p = 8.91 \times 10^{-3}$;).

₁₅₂₇ E. Thresholds t were higher in internal as compared to external mode ($\beta_0 = -0.28 \pm 0.04$,
₁₅₂₈ $T = -7.26$, $p = 1.53 \times 10^{-11}$; controlling for differences in biases and lapses) and were not
₁₅₂₉ modulated by perceptual history ($T(164) = 0.94$, $p = 0.35$).

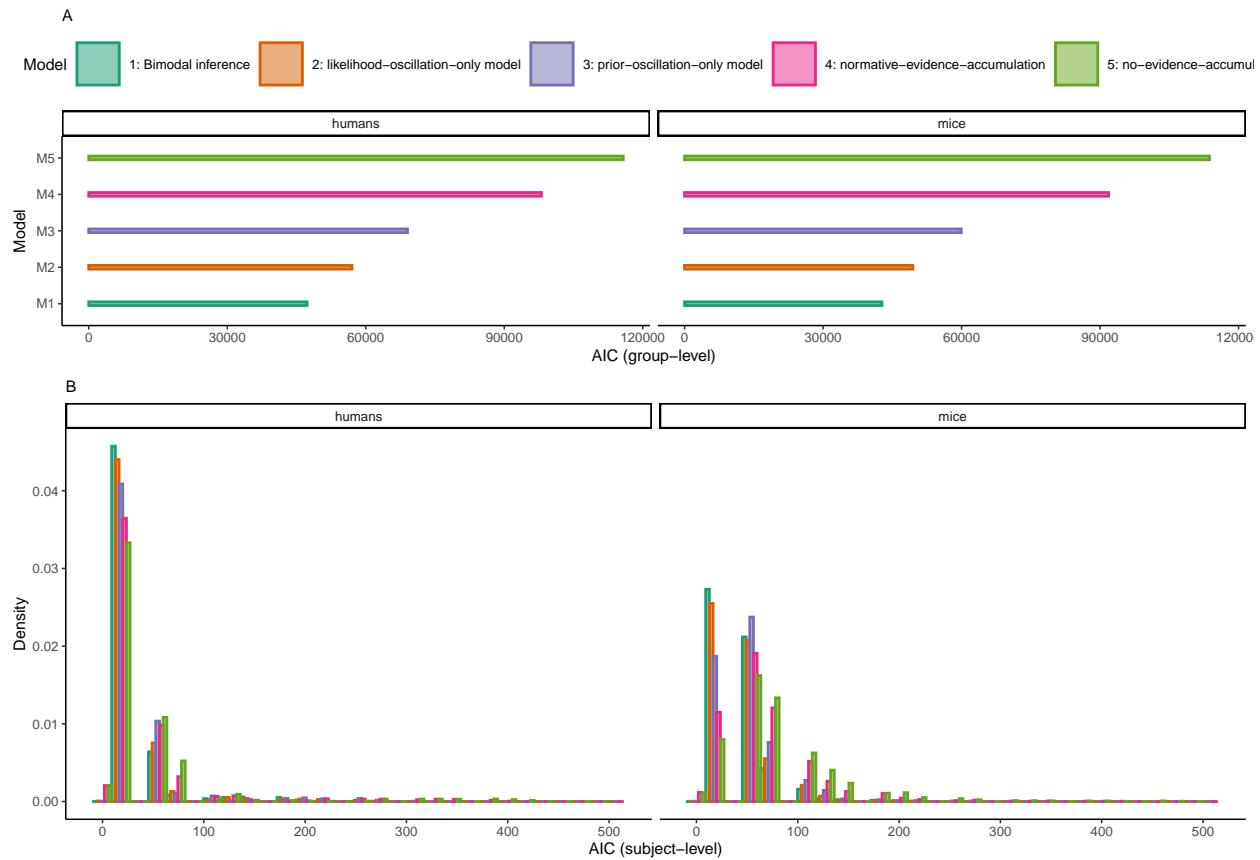
1530 **9.12 Supplemental Figure S8**



1531 **Supplemental Figure S8. History-/stimulus-congruence and TDs during training
of the basic task.**

1532 Here, we depict the progression of history- and stimulus-congruence (depicted in blue and
1533 red, respectively; left panel) as well as TDs (in green; right panel) across training sessions in
1534 mice that achieved proficiency (i.e., stimulus-congruence $\geq 80\%$) in the *basic* task of the IBL
1535 dataset. We found that both history-congruent perceptual choices ($\beta = 0.13 \pm 4.67 \times 10^{-3}$,
1536 $T(8.4 \times 10^3) = 27.04$, $p = 1.96 \times 10^{-154}$) and stimulus-congruent perceptual choices ($\beta =$
1537 $0.34 \pm 7.13 \times 10^{-3}$, $T(8.51 \times 10^3) = 47.66$, $p < 2.2 \times 10^{-308}$) became more frequent with
1538 training. As in humans, mice showed shorter TDs with increased exposure to the task ($\beta =$
1539 -22.14 ± 17.06 , $T(1.14 \times 10^3) = -1.3$, $p < 2.2 \times 10^{-308}$).

1542 **9.13 Supplemental Figure S9**



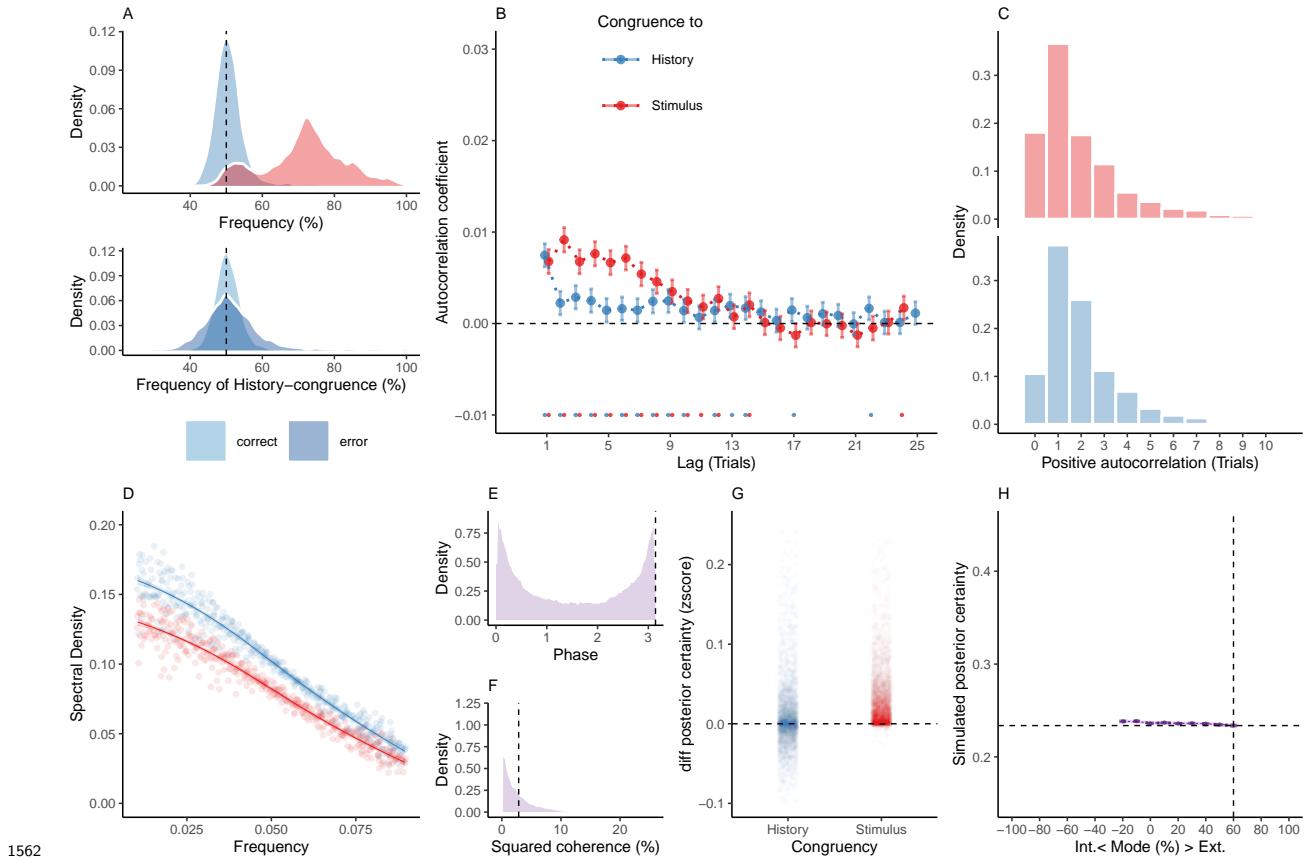
1543

1544 **Supplemental Figure S9. Comparison of the bimodal inference model against**
1545 **reduced control models.**

1546 **A. Group-level AIC.** The bimodal inference model (M1) achieved the lowest AIC
1547 across the full model space ($AIC_1 = 4.73 \times 10^4$ in humans and 4.28×10^4 in mice).
1548 Model M2 ($AIC_2 = 5.7 \times 10^4$ in humans and 4.94×10^4 in mice) and Model M3
1549 ($AIC_3 = 6.9 \times 10^4$ in humans and 5.99×10^4 in mice) incorporated only oscillations
1550 of either likelihood or prior precision. Model M4 ($AIC_4 = 9.8 \times 10^4$ in humans
1551 and 9.19×10^4 in mice) lacked any oscillations of likelihood and prior precision
1552 and corresponded to the normative model proposed by Glaze et al.⁵¹. In model
1553 M5 ($AIC_5 = 1.16 \times 10^5$ in humans and 1.14×10^5 in mice), we furthermore removed
1554 the integration of information across trials, such that perception depended only
1555 in incoming sensory information.

1556 **B. Subject-level AIC.** Here, we show the distribution of AIC values at the subject-
1557 level. AIC for the bimodal inference model tended to be smaller than AIC for
1558 the comparator models (statistical comparison to the second-best model M2 in
1559 humans: $\beta = -1.81 \pm 0.27$, $T(5.07 \times 10^3) = -6.82$, $p = 1.02 \times 10^{-11}$; mice: $T(1.5 \times 10^3)$
1560 = **-6.28**, $p = 4.38 \times 10^{-10}$).

1561 **9.14 Supplemental Figure S10**



1562 **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 .

1563 A. Similar to the full model M1 (Figure 1F and Figure 4), simulated perceptual choices
 1564 were stimulus-congruent in $71.97\% \pm 0.17\%$ of trials (in red). History-congruent amounted
 1565 to $50.76\% \pm 0.07\%$ of trials (in blue). As in the full model, the likelihood-oscillation-only
 1566 model showed a significant bias toward perceptual history $T(4.32 \times 10^3) = 10.29$, $p =$
 1567 1.54×10^{-24} ; upper panel). Similarly, history-congruent choices were more frequent at error
 1573 trials ($T(4.32 \times 10^3) = 9.71$, $p = 4.6 \times 10^{-22}$; lower panel).

1574 B. In the likelihood-oscillation-only model, we observed that the autocorrelation coefficients for

1575 history-congruence were reduced below the autocorrelation coefficients of stimulus-congruence.

1576 This is an approximately five-fold reduction relative to the empirical results observed in humans

1577 (Figure 2B), where the autocorrelation of history-congruence was above the autocorrelation of

1578 stimulus-congruence. Moreover, in the reduced model shown here, the number of consecutive

1579 trials that showed significant autocorrelation of history-congruence was reduced to 11.

1580 C. In the likelihood-oscillation-only model, the number of consecutive trials at which true

1581 autocorrelation coefficients exceeded the autocorrelation coefficients for randomly permuted

1582 data did not differ with respect to stimulus-congruence ($2.62 \pm 1.39 \times 10^{-3}$ trials; $T(4.32 \times 10^3)$

1583 = 1.85, $p = 0.06$), but decreased with respect to history-congruence ($2.4 \pm 8.45 \times 10^{-4}$ trials;

1584 $T(4.32 \times 10^3) = -15.26$, $p = 3.11 \times 10^{-51}$) relative to the full model.

1585 D. In the likelihood-oscillation-only model, the smoothed probabilities of stimulus- and

1586 history-congruence (sliding windows of ± 5 trials) fluctuated as **a scale-invariant process**

1587 **with a 1/f power law**, i.e., at power densities that were inversely proportional to the

1588 frequency (power $\sim 1/f^\beta$; stimulus-congruence: $\beta = -0.81 \pm 1.17 \times 10^{-3}$, $T(1.92 \times 10^5) =$

1589 -688.65 , $p < 2.2 \times 10^{-308}$; history-congruence: $\beta = -0.79 \pm 1.14 \times 10^{-3}$, $T(1.92 \times 10^5) =$

1590 -698.13 , $p < 2.2 \times 10^{-308}$).

1591 E. In the likelihood-oscillation-only model, the distribution of phase shift between fluctuations

1592 in simulated stimulus- and history-congruence peaked at half a cycle (π denoted by dotted

1593 line). In contrast to the full model, the dynamic probabilities of simulated stimulus- and

1594 history-congruence were positively correlated ($\beta = 2.7 \times 10^{-3} \pm 7.6 \times 10^{-4}$, $T(2.02 \times 10^6) =$

1595 3.55 , $p = 3.8 \times 10^{-4}$).

1596 F. In the likelihood-oscillation-only model, the average squared coherence between fluctuations

1597 in simulated stimulus- and history-congruence (black dotted line) was reduced in comparison

1598 to the full model ($T(3.51 \times 10^3) = -4.56$, $p = 5.27 \times 10^{-6}$) and amounted to $3.43 \pm 1.02 \times 10^{-3}\%$.

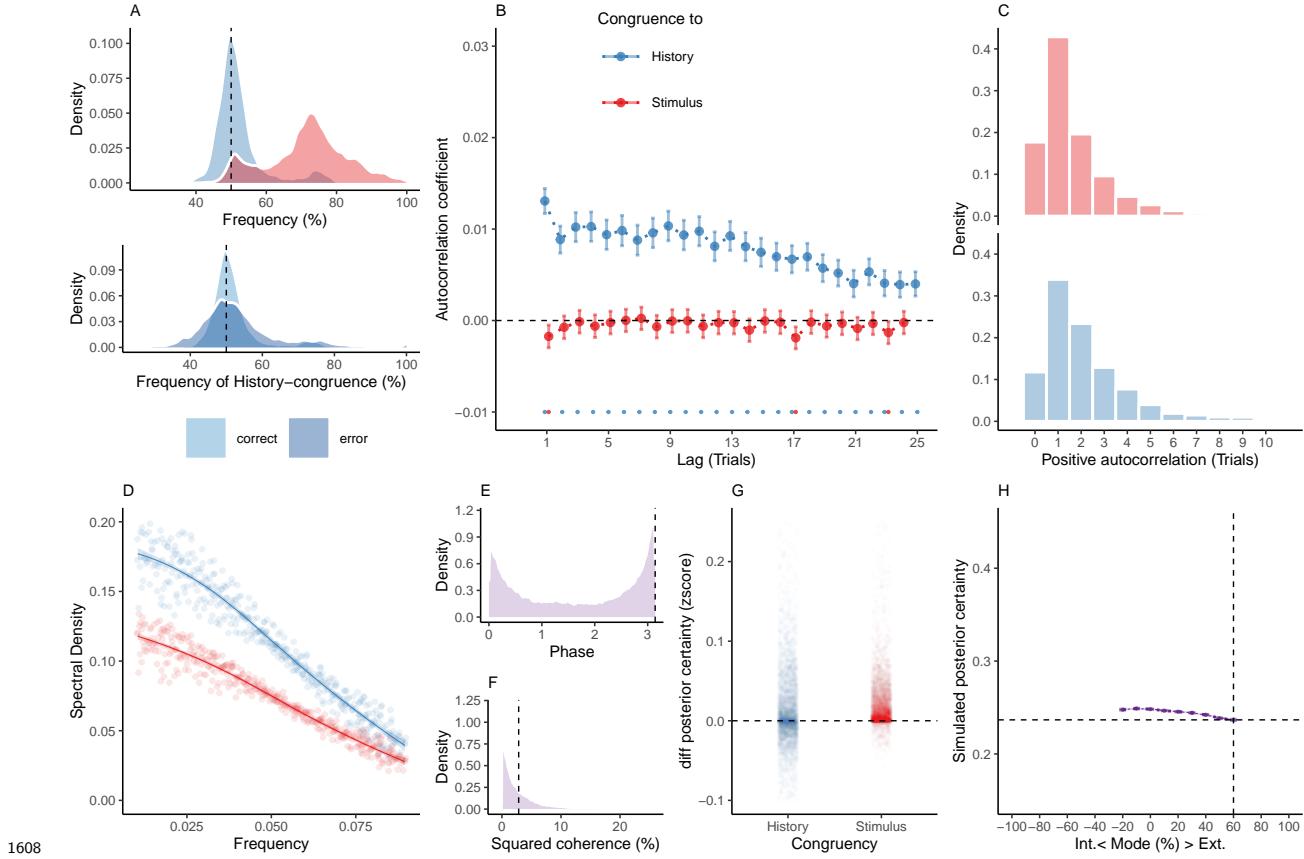
1599 G. Similar to the full bimodal inference model, confidence simulated from the likelihood-

1600 oscillation-only model was enhanced for stimulus-congruent choices ($\beta = 0.03 \pm 1.42 \times 10^{-4}$,

₁₆₀₁ $T(2.1 \times 10^6) = 191.78$, $p < 2.2 \times 10^{-308}$) and history-congruent choices ($\beta = 9.1 \times 10^{-3} \pm$
₁₆₀₂ 1.25×10^{-4} , $T(2.1 \times 10^6) = 72.51$, $p < 2.2 \times 10^{-308}$).

₁₆₀₃ H. In the likelihood-oscillation-only model, the positive quadratic relationship between the
₁₆₀₄ mode of perceptual processing and confidence was markedly reduced in comparison to the full
₁₆₀₅ 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
₁₆₀₆ dotted lines indicate minimum posterior certainty and the associated mode, respectively.

1607 **9.15 Supplemental Figure S11**



1608 **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 .

1614 A. Similar to the full model (Figure 1F and Figure 4), simulated perceptual choices were
 1615 stimulus-congruent in $71.97\% \pm 0.17\%$ of trials (in red). History-congruent amounted to
 1616 $52.1\% \pm 0.11\%$ of trials (in blue). As in the full model, the prior-oscillation-only showed a
 1617 significant bias toward perceptual history $T(4.32 \times 10^3) = 18.34$, $p = 1.98 \times 10^{-72}$; upper
 1618 panel). Similarly, history-congruent choices were more frequent at error trials ($T(4.31 \times 10^3)$
 1619 $= 12.35$, $p = 1.88 \times 10^{-34}$; lower panel).

1620 B. In the prior-oscillation-only model, we did not observe any significant positive autocor-

₁₆₂₁ relation of stimulus-congruence , whereas the autocorrelation of history-congruence was
₁₆₂₂ preserved.

₁₆₂₃ C. In the prior-oscillation-only model, the number of consecutive trials at which true au-
₁₆₂₄ tocorrelation coefficients exceeded the autocorrelation coefficients for randomly permuted
₁₆₂₅ data did was decreased with respect to stimulus-congruence relative to the full model ($1.8 \pm$
₁₆₂₆ 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
₁₆₂₇ model with respect to history-congruence ($4.25 \pm 1.84 \times 10^{-3}$ trials; $T(4.32 \times 10^3) = 0.07$, p
₁₆₂₈ = 0.95).

₁₆₂₉ D. In the prior-oscillation-only model, the smoothed probabilities of stimulus- and history-
₁₆₃₀ congruence (sliding windows of ± 5 trials) fluctuated as **a scale-invariant process with a**
₁₆₃₁ **1/f power law**, i.e., at power densities that were inversely proportional to the frequency
₁₆₃₂ (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
₁₆₃₃ $< 2.2 \times 10^{-308}$; history-congruence: $\beta = -0.83 \pm 1.27 \times 10^{-3}$, $T(1.92 \times 10^5) = -651.6$, $p <$
₁₆₃₄ 2.2×10^{-308}).

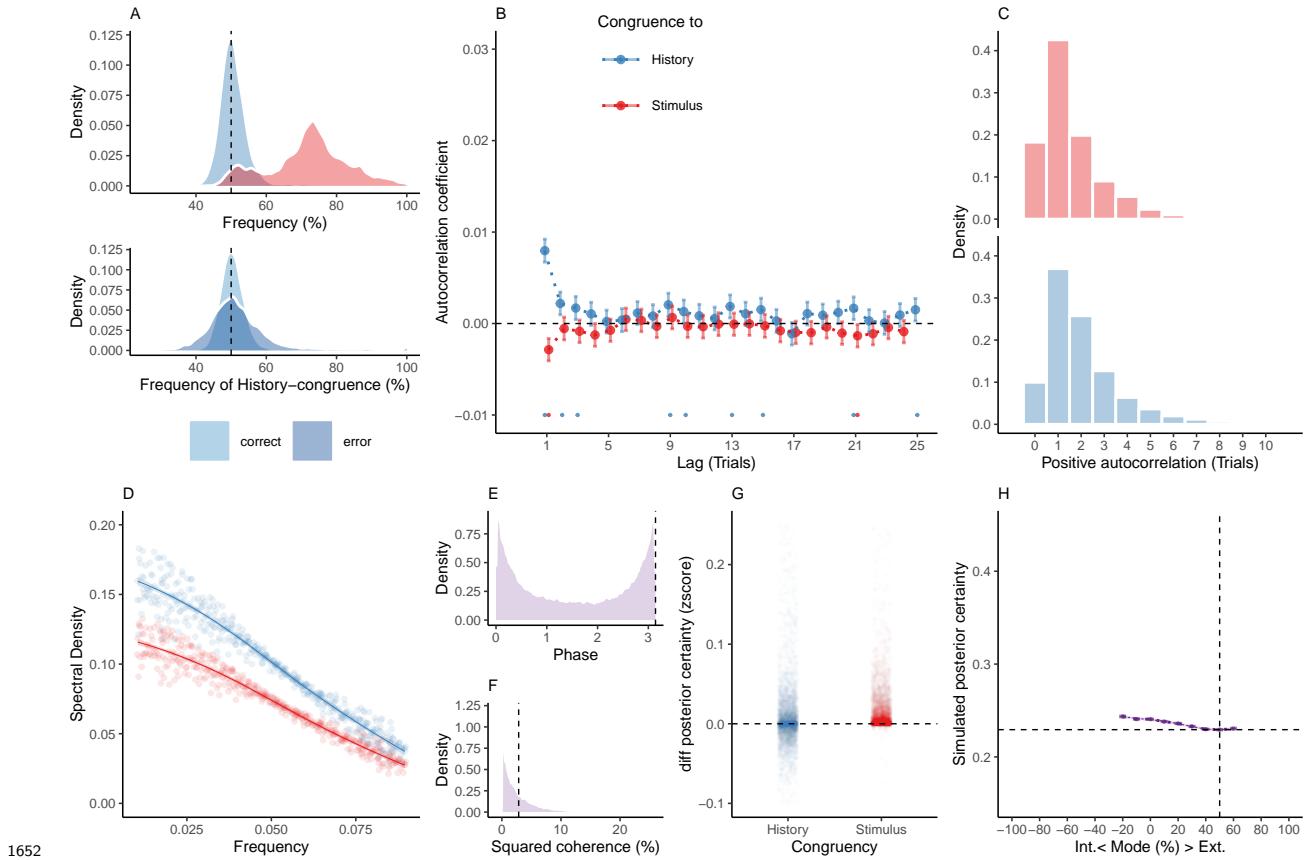
₁₆₃₅ E. In the prior-oscillation-only model, the distribution of phase shift between fluctuations
₁₆₃₆ in simulated stimulus- and history-congruence peaked at half a cycle (π denoted by dotted
₁₆₃₇ line). Similar to the full model, the dynamic probabilities of simulated stimulus- and history-
₁₆₃₈ congruence were anti-correlated ($\beta = -0.03 \pm 8.61 \times 10^{-4}$, $T(2.12 \times 10^6) = -34.03$, $p =$
₁₆₃₉ 8.17×10^{-254}).

₁₆₄₀ F. In the prior-oscillation-only model, the average squared coherence between fluctuations in
₁₆₄₁ simulated stimulus- and history-congruence (black dotted line) was reduced in comparison to
₁₆₄₂ the full model ($T(3.54 \times 10^3) = -3.22$, $p = 1.28 \times 10^{-3}$) and amounted to $3.52 \pm 1.04 \times 10^{-3}\%$.

₁₆₄₃ G. Similar to the full bimodal inference model, confidence simulated from the prior-oscillation-
₁₆₄₄ only model was enhanced for stimulus-congruent choices ($\beta = 0.02 \pm 1.44 \times 10^{-4}$, $T(2.03 \times 10^6)$
₁₆₄₅ = 128.53, $p < 2.2 \times 10^{-308}$) and history-congruent choices ($\beta = 0.01 \pm 1.26 \times 10^{-4}$, $T(2.03 \times 10^6)$
₁₆₄₆ = 88.24, $p < 2.2 \times 10^{-308}$).

₁₆₄₇ H. In contrast to the full bimodal inference model, the prior-oscillation-only model did
₁₆₄₈ not yield a positive quadratic relationship between the mode of perceptual processing and
₁₆₄₉ confidence ($\beta_2 = -0.17 \pm 0.1$, $T(2.04 \times 10^6) = -1.66$, $p = 0.1$). The horizontal and vertical
₁₆₅₀ dotted lines indicate minimum posterior certainty and the associated mode, respectively.

1651 **9.16 Supplemental Figure S12**



1652 **1653 Supplemental Figure S12. Reduced Control Model M4: Normative evidence**

1654 **accumulation.** When simulating data for the *normative-evidence-accumulation model*, we
 1655 removed the oscillation from the likelihood and prior terms by setting the amplitudes a_{LLR}
 1656 and a_ψ to zero. Simulated data thus depended only on the participant-wise estimates for
 1657 hazard rate H and inverse decision temperature ζ .

1658 A. Similar to the full model (Figure 1F and Figure 4), simulated perceptual choices were
 1659 stimulus-congruent in $71.97\% \pm 0.17\%$ of trials (in red). History-congruent amounted to
 1660 $50.73\% \pm 0.07\%$ of trials (in blue). As in the full model, the no-oscillation model showed
 1661 a significant bias toward perceptual history $T(4.32 \times 10^3) = 9.94$, $p = 4.88 \times 10^{-23}$; upper
 1662 panel). Similarly, history-congruent choices were more frequent at error trials ($T(4.31 \times 10^3)$
 1663 $= 10.59$, $p = 7.02 \times 10^{-26}$; lower panel).

1664 B. In the normative-evidence-accumulation model, we did not find significant autocor-

₁₆₆₅ relations for stimulus-congruence. Likewise, we did not observe any autocorrelation of
₁₆₆₆ history-congruence beyond the first three consecutive trials.

₁₆₆₇ C. In the normative-evidence-accumulation model, the number of consecutive trials at
₁₆₆₈ which true autocorrelation coefficients exceeded the autocorrelation coefficients for randomly
₁₆₆₉ permuted data decreased with respect to both stimulus-congruence ($1.8 \pm 1.59 \times 10^{-3}$ trials;
₁₆₇₀ $T(4.31 \times 10^3) = -5.21$, $p = 2 \times 10^{-7}$) and history-congruence ($2.18 \pm 5.48 \times 10^{-4}$ trials;
₁₆₇₁ $T(4.32 \times 10^3) = -17.1$, $p = 1.75 \times 10^{-63}$) relative to the full model.

₁₆₇₂ D. In the normative-evidence-accumulation model, the smoothed probabilities of stimulus- and
₁₆₇₃ history-congruence (sliding windows of ± 5 trials) fluctuated as **a scale-invariant process**
₁₆₇₄ **with a $1/f$ power law**, i.e., at power densities that were inversely proportional to the
₁₆₇₅ frequency (power $\sim 1/f^\beta$; stimulus-congruence: $\beta = -0.78 \pm 1.1 \times 10^{-3}$, $T(1.92 \times 10^5) =$
₁₆₇₆ -706.93 , $p < 2.2 \times 10^{-308}$; history-congruence: $\beta = -0.79 \pm 1.12 \times 10^{-3}$, $T(1.92 \times 10^5) =$
₁₆₇₇ -702.46 , $p < 2.2 \times 10^{-308}$).

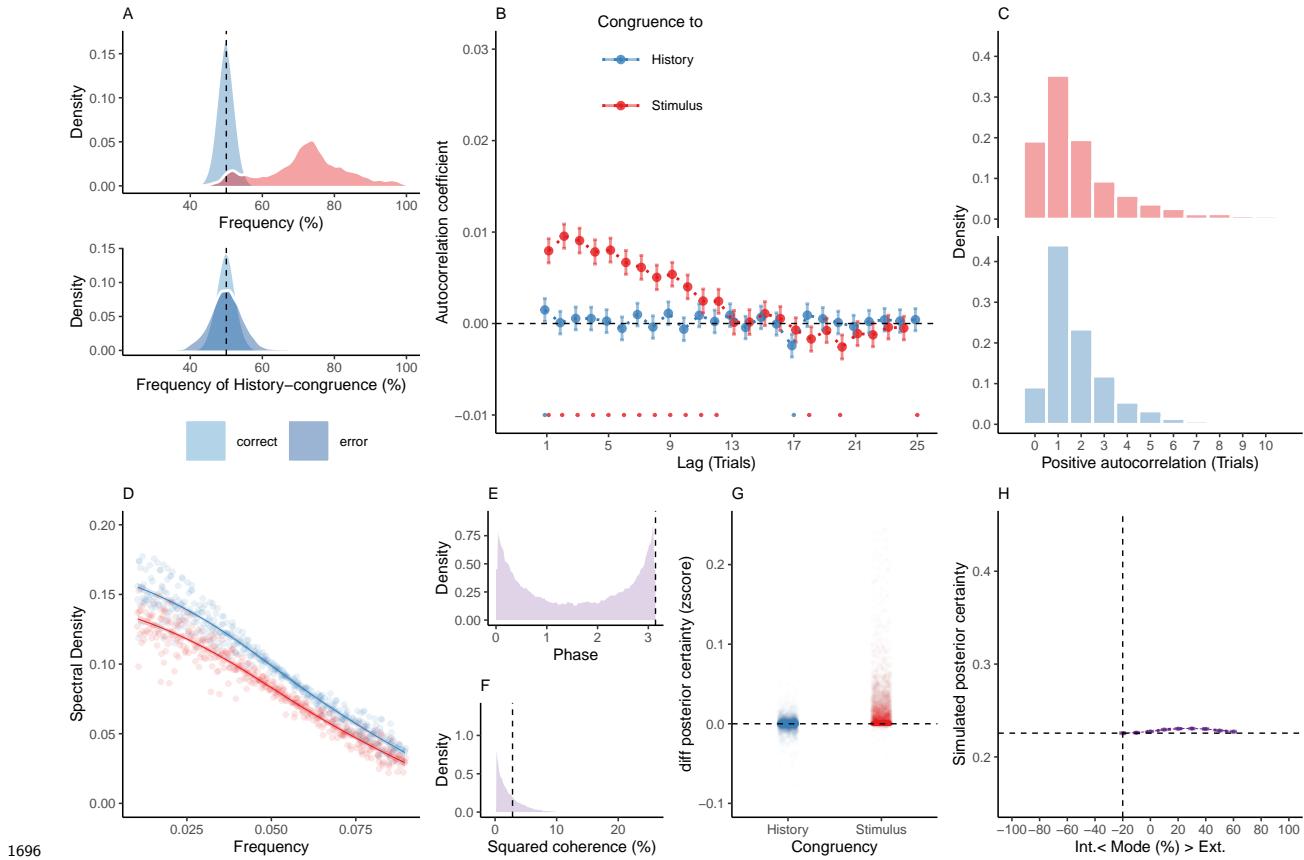
₁₆₇₈ E. In the normative-evidence-accumulation model, the distribution of phase shift between
₁₆₇₉ fluctuations in simulated stimulus- and history-congruence peaked at half a cycle (π denoted
₁₆₈₀ by dotted line). In contrast to the full model, the dynamic probabilities of simulated stimulus-
₁₆₈₁ and history-congruence were positively correlated ($\beta = 4.3 \times 10^{-3} \pm 7.97 \times 10^{-4}$, $T(1.98 \times 10^6)$
₁₆₈₂ $= 5.4$, $p = 6.59 \times 10^{-8}$).

₁₆₈₃ F. In the normative-evidence-accumulation model, the average squared coherence between
₁₆₈₄ fluctuations in simulated stimulus- and history-congruence (black dotted line) was reduced in
₁₆₈₅ comparison to the full model ($T(3.52 \times 10^3) = -6.27$, $p = 3.97 \times 10^{-10}$) and amounted to
₁₆₈₆ $3.26 \pm 8.88 \times 10^{-4}\%$.

₁₆₈₇ G. Similar to the full bimodal inference model, confidence simulated from the no-oscillation
₁₆₈₈ model was enhanced for stimulus-congruent choices ($\beta = 0.01 \pm 1.05 \times 10^{-4}$, $T(2.1 \times 10^6)$
₁₆₈₉ $= 139.17$, $p < 2.2 \times 10^{-308}$) and history-congruent choices ($\beta = 8.05 \times 10^{-3} \pm 9.2 \times 10^{-5}$,
₁₆₉₀ $T(2.1 \times 10^6) = 87.54$, $p < 2.2 \times 10^{-308}$).

₁₆₉₁ H. In the normative-evidence-accumulation model, the positive quadratic relationship between
₁₆₉₂ the mode of perceptual processing and confidence was markedly reduced in comparison to
₁₆₉₃ the full model ($\beta_2 = 0.14 \pm 0.07$, $T(2.1 \times 10^6) = 1.95$, $p = 0.05$). The horizontal and vertical
₁₆₉₄ dotted lines indicate minimum posterior certainty and the associated mode, respectively.

1695 **9.17 Supplemental Figure S13**



1696 **Supplemental Figure S13. Reduced Control Model M5: No accumulation of**
 1697 **information across trials.** When simulating data for the *no-evidence-accumulation model*,
 1698 we removed the accumulation of information across trials by setting the Hazard rate H to
 1699 0.5. Simulated data thus depended only on the participant-wise estimates for the amplitudes
 1700 $a_{LLR/\psi}$, frequency f , phase p and inverse decision temperature ζ .

1701 A. Similar to the full model (Figure 1F and Figure 4), simulated perceptual choices were
 1702 stimulus-congruent in $72.14\% \pm 0.17\%$ of trials (in red). History-congruent amounted to
 1703 $49.89\% \pm 0.03\%$ of trials (in blue). In contrast to the full model, the no-accumulation model
 1704 showed a significant bias against perceptual history $T(4.32 \times 10^3) = -3.28$, $p = 1.06 \times 10^{-3}$;
 1705 upper panel). In contrast to the full model, there was no difference in the frequency of
 1706 history-congruent choices between correct and error trials ($T(4.31 \times 10^3) = 0.76$, $p = 0.44$;
 1707 lower panel).

₁₇₀₉ B. In the no-evidence-accumulation model, we found no significant autocorrelation of history-
₁₇₁₀ congruence beyond the first trial, whereas the autocorrelation of stimulus-congruence was
₁₇₁₁ preserved.

₁₇₁₂ C. In the no-evidence-accumulation model, the number of consecutive trials at which true
₁₇₁₃ autocorrelation coefficients exceeded the autocorrelation coefficients for randomly permuted
₁₇₁₄ data increased with respect to stimulus-congruence ($2.83 \pm 1.49 \times 10^{-3}$ trials; $T(4.31 \times 10^3) =$
₁₇₁₅ 3.45 , $p = 5.73 \times 10^{-4}$) and decreased with respect to history-congruence ($1.85 \pm 3.49 \times 10^{-4}$
₁₇₁₆ trials; $T(4.32 \times 10^3) = -19.37$, $p = 3.49 \times 10^{-80}$) relative to the full model.

₁₇₁₇ D. In the no-evidence-accumulation model, the smoothed probabilities of stimulus- and
₁₇₁₈ history-congruence (sliding windows of ± 5 trials) fluctuated as **a scale-invariant process**
₁₇₁₉ **with a 1/f power law**, i.e., at power densities that were inversely proportional to the
₁₇₂₀ frequency (power $\sim 1/f^\beta$; stimulus-congruence: $\beta = -0.82 \pm 1.2 \times 10^{-3}$, $T(1.92 \times 10^5) =$
₁₇₂₁ -681.98 , $p < 2.2 \times 10^{-308}$; history-congruence: $\beta = -0.78 \pm 1.11 \times 10^{-3}$, $T(1.92 \times 10^5) =$
₁₇₂₂ -706.57 , $p < 2.2 \times 10^{-308}$).

₁₇₂₃ E. In the no-evidence-accumulation model, the distribution of phase shift between fluctuations
₁₇₂₄ in simulated stimulus- and history-congruence peaked at half a cycle (π denoted by dotted
₁₇₂₅ line). In contrast to the full model, the dynamic probabilities of simulated stimulus- and
₁₇₂₆ history-congruence were not significantly anti-correlated ($\beta = 6.39 \times 10^{-4} \pm 7.22 \times 10^{-4}$,
₁₇₂₇ $T(8.89 \times 10^5) = 0.89$, $p = 0.38$).

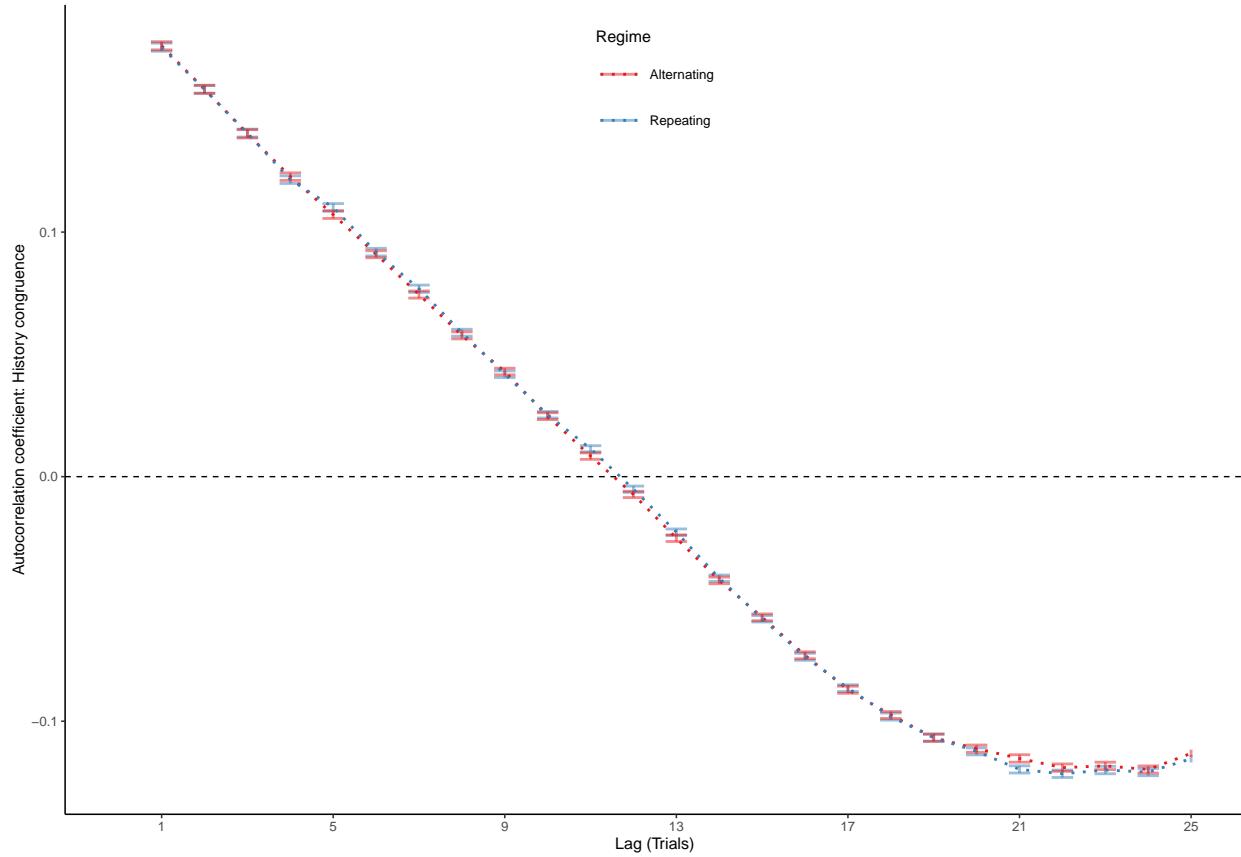
₁₇₂₈ F. In the no-evidence-accumulation model, the average squared coherence between fluctuations
₁₇₂₉ in simulated stimulus- and history-congruence (black dotted line) was reduced in comparison
₁₇₃₀ to the full model ($T(3.56 \times 10^3) = -9.96$, $p = 4.63 \times 10^{-23}$) and amounted to $2.8 \pm 7.29 \times 10^{-4}\%$.

₁₇₃₁ G. Similar to the full bimodal inference model, confidence simulated from the no-evidence-
₁₇₃₂ accumulation model was enhanced for stimulus-congruent choices ($\beta = 0.01 \pm 9.4 \times 10^{-5}$,
₁₇₃₃ $T(2.11 \times 10^6) = 158.1$, $p < 2.2 \times 10^{-308}$). In contrast to the full bimodal inference model,
₁₇₃₄ history-congruent choices were not characterized by enhanced confidence ($\beta = 8.78 \times 10^{-5} \pm$

₁₇₃₅ 8.21×10^{-5} , $T(2.11 \times 10^6) = 1.07$, $p = 0.29$).

₁₇₃₆ H. In the no-evidence-accumulation model, the positive quadratic relationship between the
₁₇₃₇ mode of perceptual processing and confidence was markedly reduced in comparison to the full
₁₇₃₈ 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
₁₇₃₉ dotted lines indicate minimum posterior certainty and the associated mode, respectively.

1740 **9.18 Supplemental Figure S14**



1741 **Supplemental Figure S14. Autocorrelation of history-congruence of alternating
1742 and repeating biases.** Here, we simulate the autocorrelation of history-congruence in 10^3
1743 synthetic participants. In the repeating regime (blue), history-congruence fluctuated between
1744 50% and 80% (blue) in interleaved blocks (10 blocks per condition with a random duration
1745 between 15 and 30 trials). In the alternation regime (red), history-congruence fluctuated
1746 between 50% and 20%. The resulting autocorrelation curves for history-congruence overlap,
1747 indicating that our analysis is able to accommodate both repeating and alternating biases.
1748

₁₇₄₉ **9.19 Supplemental Table T1**

₁₇₅₀ **9.20 Supplemental Table T2**

1751 10 Response to Reviewers

1752 10.1 Reviewer 1

1753 This was an interesting and thought-provoking submission. I note that it is
1754 a revision: I am therefore supposing that the authors have already responded
1755 to one round of reviewer comments and that you are potentially interested in
1756 publishing this work. In brief, I think there are many elements of this report that
1757 warrant publication; however, there are some parts that are less compelling and
1758 could be deferred to a subsequent paper. The paper is far too long and would
1759 benefit greatly from being streamlined. Furthermore, some of the modeling is
1760 overengineered and is difficult to follow. I have tried to suggest how the authors
1761 might improve the presentation of their work in my comments to authors.

1762 I enjoyed reading this long but thought-provoking report of fluctuations in the
1763 sensitivity to sensory evidence in perceptual decision-making tasks. There were
1764 some parts of this report that were compelling and interesting. Other parts were
1765 less convincing and difficult to understand. Overall, this paper is far too long. An
1766 analogy that might help here is that a dinner guest is very entertaining for the
1767 first hour or so - and then overstays their welcome; until you start wishing they
1768 would leave. Another analogy, which came to mind, was that the modeling—and
1769 its interpretation—was a bit autistic (i.e., lots of fascinating if questionable detail
1770 with a lack of central coherence).

1771 I think that both issues could be resolved by shortening the paper and removing
1772 (or, at least, greatly simplifying) the final simulation studies of metacognition. I
1773 try to unpack this suggestion in the following.

1774 We would like to thank Prof. Friston for the very insightful and helpful comments on our
1775 manuscript. We fully agree that our ideas about the computational function of between-mode

1776 fluctuations and the associated simulations may be presented in a more accessible form in a
1777 standalone paper. As we outlined in more detail below, we have streamlined our findings
1778 and rewrote the paper and reduced it's length by shortening the sections on computational
1779 modeling. We have also followed Prof. Friston's suggestion to interpret the effects of mode
1780 on RT and confidence in the context of predictive processing definitions of attention, namely
1781 the allocation of precision between prior and likelihood.

1782 **Major points:**

1783 **As I understand it, you have used publicly available data on perceptual decision-**
1784 **making to demonstrate slow fluctuations in the tendency to predicate perceptual**
1785 **decisions on the stimuli and on the history of recent decisions. You find scale-free**
1786 **fluctuations in this tendency — that are anti-correlated — and interpret this as**
1787 **fluctuations in the precision afforded sensory evidence, relative to prior beliefs.**
1788 **This interpretation is based upon a model of serial dependencies (parameterised**
1789 **with a hazard function).**

1790 **The stimulus and history (i.e., likelihood and prior) sensitivities are anti-correlated**
1791 **and both show scale free behavior. This is reproduced in men and mice. You**
1792 **then proceed to model this with periodic fluctuations in the precisions or weights**
1793 **applied to the likelihood and prior that are in anti-phase - and then estimate the**
1794 **parameters of the ensuing model. Finally, you then simulate the learning of the**
1795 **hazard parameter — and something called metacognition - to show that periodic**
1796 **fluctuations improve estimates of metacognition (based upon a Rescorla-Wagner**
1797 **model of learning). You motivate this by suggesting that the fluctuations in**
1798 **sensitivity are somehow necessary to elude circular inference and provide better**
1799 **estimates of precision.**

1800 **Note that I am reading the parameters omega_LL and omega_psi as the**
1801 **precision of the likelihood and prior, where the precision of the likelihood is**

1802 called sensory precision. This contrasts with your use of sensory precision, which
1803 seems to be attributed to a metacognitive construct M.

1804 As noted above, all of this is fascinating but there are too many moving parts
1805 that do not fit together comfortably. I will list a few examples:

1806 **10.1.1 Comment 1**

1807 If, empirically, the fluctuations in sensitivity are scale-free with a 1/f power law,
1808 why did you elect to model fluctuations in precision as a periodic function with
1809 one unique timescale (i.e., f).?

1810 The reason for choosing a unique timescale f was to enable our model to depict the dominant
1811 timescale at which prior and likelihood precision fluctuate in their impact on perceptual
1812 decision-making, giving rise to what constitutes between-mode fluctuations. We think that
1813 identifying this timescale is important for planning future experiments targeted at between-
1814 mode fluctuations and their manipulation by causal interventions (e.g., pharmacology or
1815 TMS). The posterior value for f lies at approximately $0.11 \text{ } 1/N_{trials}$ in both humans and
1816 mice. The value of f approximately matches the transition probabilities between *engaged* and
1817 *disengaged* states in work assessing fluctuations in perceptual decision-making using Hidden
1818 Markov models (stay probabilities ranged between 0.94 and 0.98, see Ashwood et al., Nature
1819 Neuroscience 2022). Simulating from our model (Figure 4) replicates the 1/f feature of the
1820 empirical data. Please note that the individual trial is the smallest unit of *measurement*
1821 for these fluctuations, such that our analysis is limited by definition to frequencies below 1
1822 ($1/N_{trials}$).

1823 We now provide a rationale for choosing one value for f - identifying the dominant timescale
1824 for fluctuations in mode - in the results section:

- 1825 • To allow for *bimodal inference*, i.e., alternating periods of internally- and externally-
1826 biased modes of perceptual processing that occur irrespective of the sequence of preceding

experiences, we assumed that likelihood and prior vary in their influence on the perceptual decision according to fluctuations governed by ω_{LLR} and ω_ψ . These anti-phase sine functions (defined by amplitudes $a_{LLR/\psi}$, frequency f and phase p) determine the precision afforded to the likelihood and prior⁵³. The implicit anti-phase fluctuations are mandated by Bayes-optimal formulations in which inference depends only on the relative values of prior and likelihood precision (i.e., the Kalman gain⁵⁴). As such, ω_{LLR} and ω_ψ implement a hyperprior⁵⁵ in which the likelihood and prior precisions are shifted against each other at a dominant timescale defined by f : (...)

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

10.1.2 Comment 2

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

In our model, the parameter α controls the encoding precision by governing the transformation from sensory stimuli to the log likelihood ratio (LLR) via the equations (13-16) (the LLR ends up closer to zero when α is low). Our simulations on the adaptive benefits of bimodal inference rest on the assumption that α may change unpredictably. The construct M is a belief about α that may be useful for, e.g., communicating the precision of sensory encoding to other cognitive domains or agents. To our mind, α is a feature of low-level

1852 sensory encoding that cannot be modulated by top-down beliefs such as M . This is why we
1853 did not include M in equation (2). Please note that we have removed this section following
1854 Comment 9 of Reviewer 1.

1855 **10.1.3 Comment 3**

1856 **Why do you assume that non-specific increases in attention and arousal will**
1857 **increase reaction times? If one has very precise prior beliefs (and is not attending**
1858 **to stimuli), would you not expect a decrease in reaction time?**

1859 Thanks a lot for pointing this out (see also the Comment below and Comment 6 by Reviewer
1860 3). Both high prior and high likelihood precision lead to higher absolute values of the log
1861 posterior ratio (reflecting certainty encoded by the decision variable), and thus faster RTs.
1862 This is reflected empirically by RTs in humans (Figure 2) and to a lesser degree in mice
1863 (Figure 3): RTs tended to be shorter for stronger biases toward both external and internal
1864 mode. Our model, which incorporates (i), the accumulation of information across trials, and
1865 (ii), fluctuations in the likelihood precision relative to the prior precision, recapitulates this
1866 feature of the data, which is lost or greatly attenuated when eliminating process (i) and/or
1867 (ii) (see model comparison and simulations below). Our data thus confirm the hypothesis
1868 that both high prior and likelihood precision lead to faster RTs.

1869 In the previous version of the manuscript, we had included the relation between mode and
1870 RTs and confidence primarily as a defensive analysis against the proposition that what we
1871 call between-mode fluctuations is not a perceptual phenomenon, but occurs downstream of
1872 perception. One may imagine that fluctuations in perceptual performance are not influenced
1873 by periods of relative increases in prior precision (which decrease performance in fully
1874 randomized designs), but by periods when participants do not attend to the task at all, i.e.,
1875 neither to sensory information nor to prior precision. We propose that the analyses of RTs
1876 and confidence can give some insight into whether such alternative mechanisms may be at
1877 play, as we would assume longer RTs and lower confidence if participants failed to attend to

₁₈₇₈ the task at all.

₁₈₇₉ That being said, we realize that, due to the potential non-linearity in their relation to arousal
₁₈₈₀ (see also Comment 6 by Reviewer 3), RTs and confidence cannot provide a definitive map
₁₈₈₁ of where fluctuations in mode are situated in relation to arousal. Such a delineation may
₁₈₈₂ potentially be provided by tracking of pupil size, response behavior or by neural data (e.g.,
₁₈₈₃ noise correlations of fluctuations in LFP). These data are not available for the studies in
₁₈₈₄ the Confidence Database, but were very recently published for the IBL database (after this
₁₈₈₅ manuscript was submitted). While we believe that this is beyond the scope of this manuscript,
₁₈₈₆ we will assess the relation of pupil diameter, motor behavior (turning of the response wheel)
₁₈₈₇ and LFPs to between-mode fluctuations in a future publication using the IBL dataset.

₁₈₈₈ In light of the considerations above and our response to Comment 6 by Reviewer 3, we now
₁₈₈₉ refer to attention in the predictive processing sense. We use the term “task engagement”
₁₈₉₀ instead of “on-task attention” to refer to situation in which participants may not attend to
₁₈₉₁ the task at all, e.g. due to low arousal or fatigue, and discuss these as alternative explanations
₁₈₉₂ for between-mode fluctuations. We have made three sets of changes to our manuscript:

₁₈₉₃ First, we present our results on the relation of mode to RT and Confidence in a more
₁₈₉₄ descriptive way, and do not use it as a strong defensive analysis against arousal:

- ₁₈₉₅ • The above results point to systematic fluctuations in the *decision variable*⁴⁴ that deter-
₁₈₉₆ mines perceptual choices, causing enhanced sensitivity to external stimulus information
₁₈₉₇ during external mode and increased biases toward preceding choices during internal
₁₈₉₈ mode. As such, fluctuations in mode should influence downstream aspects of behavior
₁₈₉₉ and cognition that operate on the perceptual decision variable⁴⁴. To test this hypothesis
₁₉₀₀ with respect to motor behavior and metacognition, we asked how bimodal inference
₁₉₀₁ relates to response times (RTs) and confidence reports. (...)
- ₁₉₀₂ • (...) In sum, the above results indicate that reporting behavior and metacognition do

1903 not map linearly onto the mode of sensory processing. Rather, they suggest that slow
1904 fluctuations in the respective impact of external and internal information are most likely
1905 to affect perception at an early level of sensory analysis^{46,47}. Such low-level processing
1906 may thus integrate perceptual history with external inputs into a decision variable⁴⁴
1907 that influences not only perceptual choices, but also the speed and confidence at which
1908 they are made.

- 1909 • In what follows, we probe alternative explanations for between-mode fluctuations, test
1910 for the existence of modes in mice, and propose a predictive processing model that
1911 explains fluctuations in mode ongoing shifts in the precision afforded to external sensory
1912 information relative to internal predictions driven by perceptual history.

1913 Second, we have re-written our discussion of the quadratic relationship of mode to RTs and
1914 Confidence, focusing on predictive coding models of attention: - As a functional explanation
1915 for bimodal inference, we propose that perception temporarily disengages from internal
1916 predictions to form stable inferences about the statistical properties of the sensory environment.
1917 Between-mode fluctuations may thus elude circular inferences that occur when both the
1918 causes and the encoding of sensory stimuli are volatile^{19,57}.** By the same token, we suggest
1919 that fluctuations in mode occur at the level of perceptual processing^{26,30,46,47}, and are not a
1920 passive phenomenon that is primarily driven by factors situated up- or downstream of sensory
1921 analysis.

- 1922 • How does attention relate to between-mode fluctuations? According to predictive
1923 processing, attention corresponds to the precision afforded to the probability distributions
1924 that underlie perceptual inference⁵³. From this perspective, fluctuations between external
1925 and internal mode can be understood as ongoing shifts in the attention afforded to either
1926 external sensory information (regulated via likelihood precision) or internal predictions
1927 (regulated via precision precision). When the precision of either likelihood or prior

1928 increases, posterior precision increases, which leads to faster RTs and higher confidence.
1929 Therefore, when defined from the perspective of predictive processing as the precision
1930 afforded to likelihood and prior⁵³, fluctuations in attention may provide a plausible
1931 explanation for the quadratic relationship of mode to RTs and confidence (Figure 2H
1932 and J; Figure 3I; Figure 3I).

1933 Third, we have added a more general discussion of our findings in the light of fluctuations in
1934 task engagement:

1935 • Outside of the predictive processing field, attention is often understood in the context of
1936 task engagement⁶³, which varies according to the availability of cognitive resources that
1937 are modulated by factors such as tonic arousal, familiarity with the task, or fatigue⁶³. Our
1938 results suggest that internal mode processing cannot be completely reduced to intervals
1939 of low task engagement: In addition to shorter RTs and elevated confidence, choices
1940 during internal mode were not random or globally biased, but driven by perceptual
1941 history (Supplemental Figures S6-7). Moreover, our computational model identified
1942 the dominant timescale of between-mode fluctuations at $0.11 \text{ } 1/N_{trials}$, which may be
1943 compatible with fluctuations in arousal⁶⁴, but is faster than to be expected for the
1944 development of task familiarity or fatigue.

1945 • However, in interpreting the impact of between-mode fluctuations on perceptual accuracy,
1946 speed of response and confidence, it is important to consider that global modulators
1947 such as tonic arousal are known to have non-linear effects on task performance⁶⁵: In
1948 perceptual tasks, performance seems so be highest during mid-level arousal, whereas low-
1949 and high-level arousal lead to reduced accuracy and slower responses⁶⁵. This contrasts
1950 with the effects of bimodal inference, where accuracy increases linearly as one moves
1951 from internal to external mode, and responses become faster at both ends of the mode
1952 spectrum.

- 1953 • Of note, high phasic arousal has been shown to suppress multi-domain biases in decision-
1954 making in humans and mice^{66–68}, including the biases toward perceptual history²⁸ that
1955 we implicate in internal mode processing. The increase in response speed and history
1956 congruence over time (Supplemental Section 9.4) may argue against insufficient training
1957 as an alternative explanation for internal mode processing, but may also taken as a
1958 sign of waning arousal. The multiple mechanistic mappings to RTs and confidence
1959 therefore warrant more direct measures of arousal (such as pupil size^{28,65,66,68–70}, motor
1960 behavior^{69,70}, or neural data⁷¹) to better delineate bimodal inference from fluctuations
1961 in global modulators of task performance.

1962 **10.1.4 Comment 4**

1963 **In the predictive processing literature, attention is thought to correspond to**
1964 **fluctuations in sensory and prior precision. Why did you then consider attention**
1965 **as some additional or unrelated confound?**

1966 This point is closely related to the comment above. We realize that, in the predictive coding
1967 field, attention is equated with the precision of probability distributions that contribute to the
1968 perceptual decision, such that an observer can attend strongly to sensory information (high
1969 likelihood precision) or to internal predictions derived from the sequence of preceding percepts
1970 (high prior precision). Therefore, when following the above predictive coding definition,
1971 fluctuations in attention can be equated with fluctuations in mode.

1972 However, we feel that outside of the predictive coding field, attention is not always conceived
1973 in that way, such that low attention is often considered as low engagement with the task,
1974 i.e., relating to low likelihood and low prior precision in the predictive coding sense. It is
1975 against these caveats that our control analysis (based on psychometric functions, training
1976 effects, RTs and confidence) defend our conclusions on bimodal inference.

1977 We now provide a more nuanced interpretation of our findings of RTs and confidence in

¹⁹⁷⁸ relation to attention, with a specific focus on predictive coding and precision. We hope that
¹⁹⁷⁹ our responses to the comment above resolves the points raised in this comment.

¹⁹⁸⁰ **10.1.5 Comment 5**

¹⁹⁸¹ **What licences the assumption that “agents depend upon internal confidence**
¹⁹⁸² **signals” in the absence of feedback?**

¹⁹⁸³ In the absence of feedback, observers can only rely on internal estimates of performance to
¹⁹⁸⁴ guide updates to their model of the reliability of their sensory apparatus (inferences about
¹⁹⁸⁵ M). Previous work (e.g. Guggenmos et al., Elife 2106, <https://doi.org/10.7554/eLife.13388>)
¹⁹⁸⁶ has shown that confidence signals can provide signals that drive perceptual learning in the
¹⁹⁸⁷ absence of feedback. This has motivated our model simulation on the adaptive benefits of
¹⁹⁸⁸ bimodal inference for metacognition, where the learning signal ϵ_M (i.e., the difference between
¹⁹⁸⁹ the choice and its probability) drives inferences about M . Please note that we have removed
¹⁹⁹⁰ this section following Comment 9 of Reviewer 1.

¹⁹⁹¹ **10.1.6 Comment 6**

¹⁹⁹² **And what licences the assumption that internal confidence feedback corresponds**
¹⁹⁹³ **to “the absolute of the posterior log ratio” (did you mean the log of the posterior**
¹⁹⁹⁴ **ratio)?**

¹⁹⁹⁵ We mean the absolute of the log of the posterior ratio. Following first order models (see
¹⁹⁹⁶ e.g., Fleming & Daw, Self-evaluation of decision-making: A general Bayesian framework for
¹⁹⁹⁷ metacognitive computation, Psychol. Rev. 2017, <https://doi.org/10.1037/rev0000045>), the
¹⁹⁹⁸ perceptual decision and the confidence report rely on the posterior. The distance of the log
¹⁹⁹⁹ of the posterior ratio L_t from zero becomes a measure of decision-certainty or confidence.

2000 **10.1.7 Comment 7**

2001 I got a bit lost here when you say that “the precision of sensory coding M a
2002 function of u_t . This is largely because I couldn’t find a definition of u_t .

2003 We apologize for this lack of clarity. In the model simulations on the adaptive benefits of
2004 bimodal inference, we generated stimuli s_t from a Bernoulli-distribution with $p = q = 0.5$.
2005 The value of u_t was then defined via equation (13), following our modeling of the human
2006 data. Please note that we have removed this section following Comment 9 of Reviewer 1.

2007 **10.1.8 Comment 8**

2008 What licences an application of Rescorla-Wagner to learning the parameters (as
2009 in Equation 11) and, learning sensory precision as described by M_T (Equation
2010 13). Are you moving from a Bayesian framework to a reinforcement learning
2011 framework?

2012 We would like to thank the reviewer for pointing out this inconsistency. We have chosen the
2013 Rescorla-Wagner learning rule for simplicity: In our model, the speed of learning about H
2014 and M varied according to the current mode of perceptual processing and a constant learning
2015 rate. Allowing the learning rate itself to vary as a function of preceding experiences would
2016 add an additional level of complexity that we sought to omit in this analysis. However, we
2017 fully agree that choosing a Bayesian framework (e.g., a three-level HGF) would indeed be
2018 more consistent. Please note that we have removed this section following Comment 9 of
2019 Reviewer 1.

2020 **10.1.9 Comment 9**

2021 I am sure you have answers to these questions - but with each new question
2022 the reader is left more and more skeptical that there is a coherent story behind
2023 your analyses. It would have been more convincing had you just committed to

2024 a Bayesian filter and made your points using one update scheme, under ideal
2025 Bayesian observer assumptions.

2026 Unlike your piecemeal scheme, things like the hierarchical Gaussian filter estimates
2027 the sensory and prior decisions explicitly and these estimates underwrite posterior
2028 inference. In your scheme, the sensory precision M appears to have no influence
2029 on perceptual inference (which is why, presumably you call it metacognition).
2030 The problem with this is that your motivation for systematic fluctuations in
2031 precision is weakened. This is because improved metacognition does not improve
2032 perception — it only improves the perception of perception.

2033 In light of the above, can I suggest that you remove Section 5.8 and use your
2034 model in the preceding section to endorse your hypothesis along the following
2035 lines:

2036 “In summary, we hypothesized that subjects have certain hyperpriors that are
2037 apt for accommodating fluctuations in the predictability of their environment;
2038 i.e., people believe that their world is inherently volatile. This means that to be
2039 Bayes optimal it is necessary to periodically re-evaluate posterior beliefs about
2040 model parameters. One way to do this is to periodically suspend the precision
2041 of prior beliefs and increase the precision afforded to sensory evidence that
2042 updates (Bayesian) beliefs about model parameters. The empirical evidence above
2043 suggests that the timescale of this periodic scheduling of evidence accumulation
2044 may be scale-invariant. This means that there may exist a timescale of periodic
2045 fluctuations in precision over every window or length of perceptual decision-
2046 making. In what follows, we model perceptual decisions under a generative model
2047 (based upon a hazard function to model historical or serial dependencies) with, a
2048 periodic fluctuation in the precision of sensory evidence relative to prior beliefs
2049 at a particular timescale. Remarkably—using Bayesian model comparison—we

2050 find that a model with fluctuating precisions has much greater evidence, relative
2051 to a model in the absence of fluctuating precisions. Furthermore, we were able
2052 to quantify the dominant timescale of periodic fluctuations; appropriate for these
2053 kinds of paradigm.”

2054 Note, again, I am reading your omega_LL_R and omega_psi as precisions and
2055 that the periodic modulation is the hyperprior that you are characterizing—and
2056 have discovered.

2057 We would like to thank Prof. Friston for these very helpful and precise suggestions. In brief,
2058 we now provide a quantitative assessment of model space based on AIC (i) and have followed
2059 the suggestion of omitting section 5.8 (ii).

2060 In addition to the qualitative assessment of our models in the initial version of our manuscript,
2061 we have conducted a formal model comparison (i). Following the model comparisons in
2062 other sections of the manuscript, we based the model comparison on AIC. We furthermore
2063 show that the winning *bimodal inference model* predicts out-of-training variables (RT and
2064 confidence) and use simulations from posterior model parameters to show that, in contrast to
2065 reduced models, the bimodal inference model neither over- nor underfits the empirical data.

2066 We have added a description of our model comparison to the Method section:

2067 • We validated the bimodal inference model in three steps: a formal model comparison to
2068 reduced models based on AIC (Figure 1F-G; Supplemental Figure S9), the prediction of
2069 within-training (stimulus- and history-congruence) as well as out-of-training variables
2070 (RT and confidence), and a qualitative reproduction of the empirical data from model
2071 simulations based on estimated parameters (Figure 4).

2072 • **Model comparison.** We assessed the following model space based on AIC:
2073 • The full *bimodal inference model* (M1; Figure 1F) incorporates the influence of sensory
2074 information according to the parameter α (likelihood); the integration of evidence across

2075 trials according to the parameter H (prior); anti-phase oscillations in between likelihood
2076 and prior precision according to ω_{LLR} and ω_ψ with parameters a_{LLR} (amplitude likelihood
2077 fluctuation), a_ψ (amplitude prior fluctuation), f (frequency) and p (phase).

2078 • The *likelihood-oscillation-only model* (M2; Figure 1G) incorporates the influence of sen-
2079 sory information according to parameter α (likelihood); the integration of evidence across
2080 trials according to parameter H (prior); oscillations in likelihood precision according
2081 to ω_{LLR} with parameters a_{LLR} (amplitude likelihood fluctuation), f (frequency) and p
2082 (phase).

2083 • The *prior-oscillation-only model* (M3; Figure 1G) incorporates the influence of sensory
2084 information according to parameter α (likelihood); the integration of evidence across
2085 trials according to parameter H (prior); oscillations in the prior precision according
2086 to ω_ψ with parameters a_ψ (amplitude prior fluctuation), f (frequency) and p (phase).

2087 Please note that all models M1-3 lead to shifts in the relative precision of likelihood and
2088 prior.

2089 • The *normative-evidence-accumulation* (M4; Figure 1G) incorporates the influence of
2090 sensory information according to parameter α (likelihood); the integration of evidence
2091 across trials according to parameter H (prior). There are no additional oscillations.

2092 Model M4 thus corresponds to the model proposed by Glaze et al. and captures normative
2093 evidence accumulation in unpredictable environments using a Bayesian update scheme⁵¹.
2094 The comparison against M4 tests the null hypothesis that fluctuations in mode emerge
2095 from a normative Bayesian model without the ad-hoc addition of oscillations as in models
2096 M1-3.

2097 • The *no-evidence-accumulation* (M5; Figure 1G) incorporates the influence of sensory
2098 information according to parameter α (likelihood). The model lacks integration of
2099 evidence across trials (flat prior) and oscillations. The comparison against M5 tests

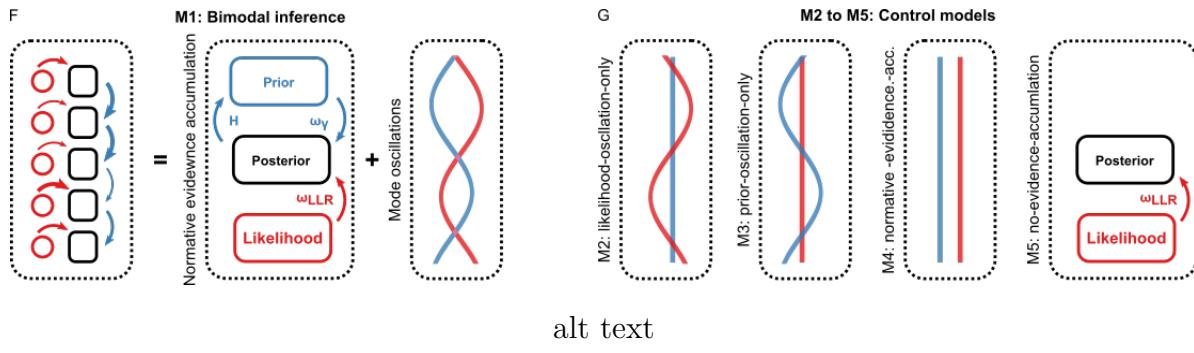
2100 the null hypothesis that observers do not use prior information derived from serial
2101 dependency in perception.

2102 • **Prediction of within-training and out-of-training variables.** To validate our
2103 model, we correlated individual posterior parameter estimates with the respective
2104 conventional variables. As a sanity check, we tested (i), whether the estimated hazard
2105 rate H correlated negatively with the frequency of history-congruent choices and, (ii),
2106 whether the estimated sensitivity to sensory information α correlated positively with the
2107 frequency of stimulus-congruent choices. In addition, we tested whether the posterior
2108 decision certainty (i.e.. the absolute of the log posterior ratio) correlated negatively with
2109 RTs and positively with confidence. This allowed us to assess whether our model could
2110 explain aspects of the data it was not fitted to (i.e., RTs and confidence).

2111 • **Simulations.** Finally, we used simulations (Figure 4, Supplemental Figures S10-13)
2112 to show that all model components, including the anti-phase oscillations governed by
2113 a_ψ , a_{LLR} , f and p , were necessary for our model to reproduce the characteristics of the
2114 empirical data. This enabled us to assess over- or under-fitting in the bimodal inference
2115 model and all reduced models M2-M5. We used the posterior model parameters observed
2116 for humans (H , α , a_ψ , a_{LLR} , f and ζ) to define individual parameters for simulation
2117 in 4317 simulated participants (i.e., equivalent to the number of human participants).
2118 For each participant, the number of simulated trials was drawn at random between
2119 300 to 700. Inputs s were drawn at random for each trial, such that the sequence of
2120 inputs to the simulation did not contain any systematic seriality. Noisy observations
2121 u were generated by applying the posterior parameter α to inputs s , thus generating
2122 stimulus-congruent choices in $71.36 \pm 2.6 \times 10^{-3}\%$ of trials. Choices were simulated
2123 based on the trial-wise choice probabilities y_p obtained from our model. Simulated data
2124 were analyzed in analogy to the human and mouse data. As a substitute of subjective
2125 confidence, we computed the absolute of the trial-wise log posterior ratio $|L|$ (i.e., the

2126 posterior decision certainty).

2127 We have also added a graphical depiction of the model space to Figure 1 (subpanels F and
2128 G):



2129 • F. The bimodal inference model (M1) explains fluctuations between externally- and
2130 externally-biased modes (left panel) by two interacting factors: a normative accumulation
2131 of evidence according to parameters H (middle panel), and anti-phase oscillations in the
2132 precision terms ω_{LLR} and ω_ψ (right panel).

2133 • G. The control models M2-M5 were constructed by successively removing the anti-phase
2134 oscillations and the integration of information from the bimodal inference model. Please
2135 note that the normative-evidence-accumulation-model (M4) corresponds to the model
2136 proposed by Glaze et al.⁵¹. In the no-evidence-accumulation model (M5), perceptual
2137 decisions depend only on likelihood information (flat priors).

2138 The formal model comparison yielded clear evidence for a superiority of the bimodal inference
2139 model, in particular over the normative Bayesian model of evidence accumulation. The model
2140 successfully predicted both within-training variables (as a sanity-check) and out-of-training
2141 variables. Simulations from posterior model parameters closely followed the empirical data
2142 (Figure 4), which was not the case for reduced models (Supplemental Figures S10-13). We
2143 summarize these findings in the Results section and have added a Supplemental Figure S9 to
2144 show the distribution of observer-level AIC at the session-level (see below):

2145 • We used a maximum likelihood procedure to fit the bimodal inference model (M1, Figure
2146 1F) to the behavioral data from the Confidence database²⁰ and the IBL database²¹,
2147 optimizing the parameters α , H , amp_{LLR} , amp_ψ , f and p (see Methods for details and
2148 Supplemental Table T2 for a summary of the parameters of the bimodal inference model).
2149 We validated our model in three steps: First, to show that bimodal inference does not
2150 emerge spontaneously in normative Bayesian models of evidence accumulation, but
2151 requires the ad-hoc addition of anti-phase oscillations in prior and likelihood precision,
2152 we compared the bimodal inference model to four control models (M2-5, Figure 1G).
2153 In these models, we successively removed the anti-phase oscillations (M2-M4) and the
2154 integration of information across trials (M5) from the bimodal inference model and
2155 performed a model comparison based on AIC.

- 2156 • Model M2 ($AIC_2 = 5.7 \times 10^4$ in humans and 4.94×10^4 in mice) and Model M3 (AIC_3
2157 $= 6.9 \times 10^4$ in humans and 5.99×10^4 in mice) incorporated only oscillations of either
2158 likelihood or prior precision. Model M4 ($AIC_4 = 9.8 \times 10^4$ in humans and 9.19×10^4 in
2159 mice) lacked any oscillations of likelihood and prior precision and corresponded to the
2160 normative model proposed by Glaze et al.⁵¹. In model M5 ($AIC_4 = 1.16 \times 10^5$ in humans
2161 and 1.14×10^5 in mice), we furthermore removed the integration of information across
2162 trials, such that perception depended only in incoming sensory information (Figure 1G).
- 2163 • The bimodal inference model achieved the lowest AIC across the full model space (AIC_1
2164 $= 4.73 \times 10^4$ in humans and 4.28×10^4 in mice) and was clearly superior to the normative
2165 Bayesian model of evidence accumulation ($\delta_{AIC} = -5.08 \times 10^4$ in humans and -4.91×10^4
2166 in mice; Supplemental Figure S9).
- 2167 • As a second validation of the bimodal inference model, we tested whether the posterior
2168 model predicted within-training and out-of-training variables. The bimodal inference
2169 model characterizes each subject by a sensitivity parameter α (humans: $\alpha = 0.5 \pm$
2170 1.12×10^{-4} ; mice: $\alpha = 1.06 \pm 2.88 \times 10^{-3}$) that captures how strongly perception is

2171 driven by the available sensory information, and a hazard rate parameter H (humans: H
2172 $= 0.45 \pm 4.8 \times 10^{-5}$; mice: $H = 0.46 \pm 2.97 \times 10^{-4}$) that controls how heavily perception
2173 is biased by perceptual history. The parameter f captures the dominant time scale at
2174 which likelihood (amplitude humans: $a_{LLR} = 0.5 \pm 2.02 \times 10^{-4}$; mice: $a_{LLR} = 0.39 \pm$
2175 1.08×10^{-3}) and prior precision (amplitude humans: $a_\psi = 1.44 \pm 5.27 \times 10^{-4}$; mice: a_ψ
2176 $= 1.71 \pm 7.15 \times 10^{-3}$) fluctuated and was estimated at $0.11 \pm 1.68 \times 10^{-5} 1/N_{trials}$ and
2177 $0.11 \pm 1.63 \times 10^{-4} 1/N_{trials}$ in mice.

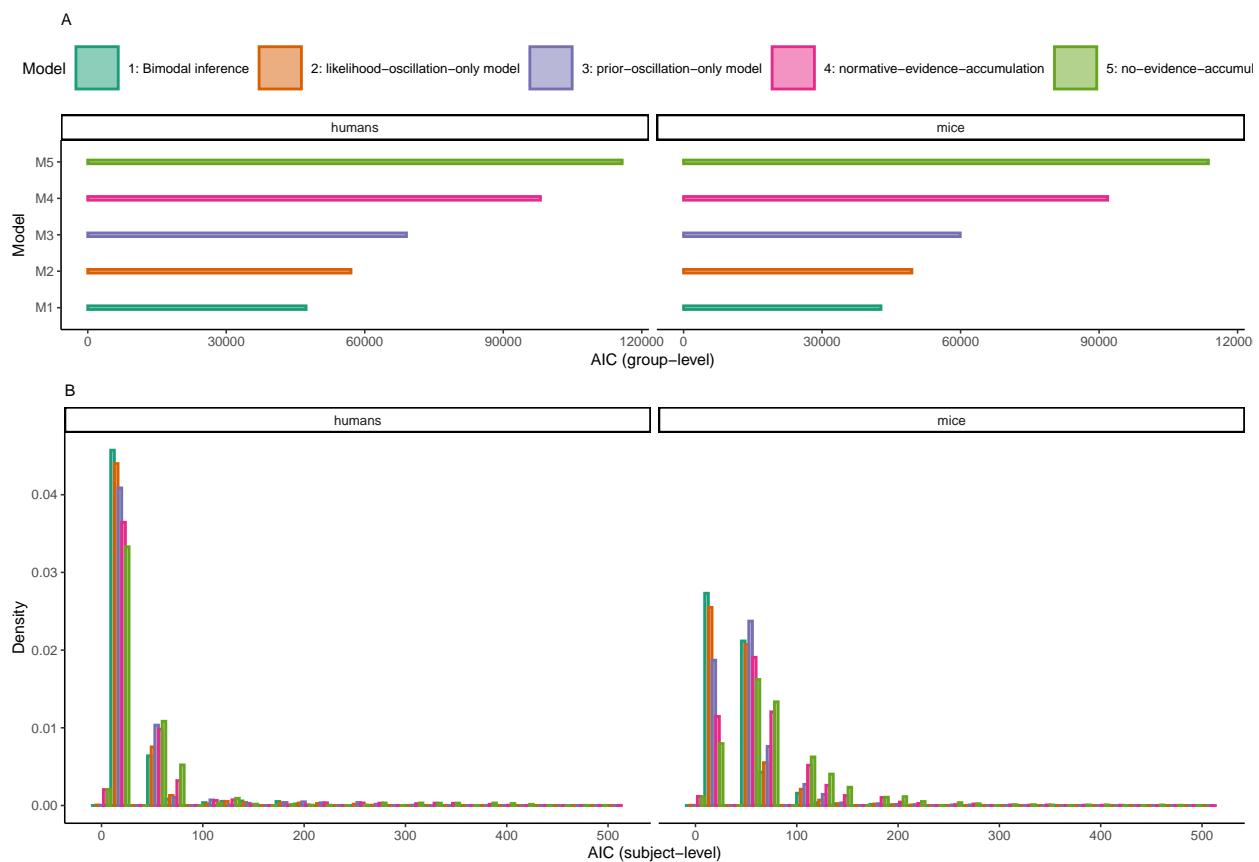
- 2178 • As a sanity check for model fit, we tested whether the frequency of stimulus- and
2179 history-congruent trials in the Confidence database²⁰ and IBL database²¹ correlate with
2180 the estimated parameters α and H , respectively. As expected, the estimated sensitivity
2181 toward stimulus information α was positively correlated with the frequency of stimulus-
2182 congruent perceptual choices (humans: $\beta = 8.4 \pm 0.26$, $T(4.31 \times 10^3) = 32.87$, $p =$
2183 1.3×10^{-211} ; mice: $\beta = 1.93 \pm 0.12$, $T(2.07 \times 10^3) = 16.21$, $p = 9.37 \times 10^{-56}$). Likewise,
2184 H was negatively correlated with the frequency of history-congruent perceptual choices
2185 (humans: $\beta = -11.84 \pm 0.5$, $T(4.29 \times 10^3) = -23.5$, $p = 5.16 \times 10^{-115}$; mice: $\beta = -6.18$
2186 ± 0.66 , $T(2.08 \times 10^3) = -9.37$, $p = 1.85 \times 10^{-20}$).
- 2187 • Our behavioral analyses reveal that humans and mice show significant effects of perceptual
2188 history that impaired performance in randomized psychophysical experiments^{24,28,30,31,43}
2189 (Figure 2A and 3A). We therefore expected that humans and mice underestimated the
2190 true hazard rate \hat{H} of the experimental environments (Confidence database²⁰: \hat{H}_{Humans}
2191 $= 0.5 \pm 1.58 \times 10^{-5}$; IBL database²¹: $\hat{H}_{Mice} = 0.49 \pm 6.47 \times 10^{-5}$). Indeed, when
2192 fitting the bimodal inference model to the trial-wise perceptual choices, we found that
2193 the estimated (i.e., subjective) hazard rate H was lower than \hat{H} for both humans (β
2194 $= -6.87 \pm 0.94$, $T(61.87) = -7.33$, $p = 5.76 \times 10^{-10}$) and mice ($\beta = -2.91 \pm 0.34$,
2195 $T(112.57) = -8.51$, $p = 8.65 \times 10^{-14}$).
- 2196 • To further probe the validity of the bimodal inference model, we tested whether posterior

model quantities could explain aspects of the behavioral data that the model was not fitted to. We predicted that the posterior decision variable L_t not only encodes perceptual choices (i.e., the variable used for model estimation), but should also predict the speed of response and subjective confidence^{30,44}. Indeed, the estimated trial-wise posterior decision certainty $|L_t|$ correlated negatively with RTs in humans ($\beta = -4.36 \times 10^{-3} \pm 4.64 \times 10^{-4}$, $T(1.98 \times 10^6) = -9.41$, $p = 5.19 \times 10^{-21}$) and TDs mice ($\beta = -35.45 \pm 0.86$, $T(1.28 \times 10^6) = -41.13$, $p < 2.2 \times 10^{-308}$). Likewise, subjective confidence reports were positively correlated with the estimated posterior decision certainty in humans ($\beta = 7.63 \times 10^{-3} \pm 8.32 \times 10^{-4}$, $T(2.06 \times 10^6) = 9.18$, $p = 4.48 \times 10^{-20}$).

- The dynamic accumulation of information inherent to our model entails that biases toward perceptual history are stronger when the posterior decision certainty at the preceding trial is high^{30,31,51}. Due to the link between posterior decision certainty and confidence, we reasoned that confident perceptual choices should be more likely to induce history-congruent perception at the subsequent trial^{30,31}. Indeed, logistic regression indicated that history-congruence was predicted by the posterior decision certainty $|L_{t-1}|$ (humans: $\beta = 8.22 \times 10^{-3} \pm 1.94 \times 10^{-3}$, $z = 4.25$, $p = 2.17 \times 10^{-5}$; mice: $\beta = -3.72 \times 10^{-3} \pm 1.83 \times 10^{-3}$, $z = -2.03$, $p = 0.04$) and subjective confidence (humans: $\beta = 0.04 \pm 1.62 \times 10^{-3}$, $z = 27.21$, $p = 4.56 \times 10^{-163}$) at the preceding trial.
- As a third validation of the bimodal inference model, we used the posterior model parameters to simulate synthetic perceptual choices and repeated the behavioral analyses conducted for the empirical data. Simulations from the 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

2223 quadratic relationship to the mode of sensory processing (Figure 4H), mirroring the
 2224 relation of RTs and confidence reports to external and internal biases in perception
 2225 (Figure 2G-H and Figure 3G-H). Crucially, the overlap between empirical and simulated
 2226 data broke down when we removed the anti-phase oscillations or the accumulation of
 2227 evidence over time from the bimodal inference model (Supplemental Figure S10-13).

- 2228 • In sum, computational modeling suggested that between-mode fluctuations are best
 2229 explained by two interlinked processes (Figure 1E): (i), the dynamic accumulation of
 2230 information across successive trials mandated by normative Bayesians model of evidence
 2231 accumulation and, (ii), ongoing anti-phase oscillations in the impact of external and
 2232 internal information.



- 2233 • **Supplemental Figure S9.** Comparison of the bimodal inference model against reduced
 2234 control models.

2236 • A. Group-level AIC. The bimodal inference model (M1) achieved the lowest AIC across
2237 the full model space ($AIC_1 = 4.73 \times 10^4$ in humans and 4.28×10^4 in mice). Model M2
2238 ($AIC_2 = 5.7 \times 10^4$ in humans and 4.94×10^4 in mice) and Model M3 ($AIC_3 = 6.9 \times 10^4$
2239 in humans and 5.99×10^4 in mice) incorporated only oscillations of either likelihood or
2240 prior precision. Model M4 ($AIC_4 = 9.8 \times 10^4$ in humans and 9.19×10^4 in mice) lacked
2241 any oscillations of likelihood and prior precision and corresponded to the normative
2242 model proposed by Glaze et al.⁵¹. In model M5 ($AIC_4 = 1.16 \times 10^5$ in humans and
2243 1.14×10^5 in mice), we furthermore removed the integration of information across trials,
2244 such that perception depended only in incoming sensory information.

2245 • B. Subject-level AIC. Here, we show the distribution of AIC values at the subject-level.
2246 AIC for the bimodal inference model tended to be smaller than AIC for the comparator
2247 models (statistical comparison to the second-best model M2 in humans: $\beta = -1.81$
2248 ± 0.27 , $T(5.07 \times 10^3) = -6.82$, $p = 1.02 \times 10^{-11}$; mice: $T(1.5 \times 10^3) = -6.28$, $p =$
2249 4.38×10^{-10}).

2250 In light of our response to Comments 1 - 9 of Reviewer 1, we agree that a complete and
2251 extensive investigation of the relation between bimodal inference, learning about changes in
2252 the environment and the relation to metacognition may be beyond the scope of the current
2253 manuscript: Both Reviewer 1 and 3 (see below) have shared that the manuscript is too long
2254 and should be streamlined. Yet evaluating the full model space (e.g., comparing update rules
2255 for inferences about H and M , testing for an influence of beliefs about M on learning about H
2256 etc.) would make the manuscript even longer. We are therefore happy to follow Prof. Fristons
2257 suggestions to omit section 5.8. We have changed the manuscript in the following ways:

2258 When introducing ω_{LLR} , we identify it as the precision afforded to the likelihood, referring to
2259 the Bayesian framework, and refer to fluctuations in mode as a hyperprior.

2260 • To allow for *bimodal inference*, i.e., alternating periods of internally- and externally-
2261 biased modes of perceptual processing that occur irrespective of the sequence of preceding

experiences, we assumed that likelihood and prior vary in their influence on the perceptual decision according to fluctuations governed by ω_{LLR} and ω_ψ . These anti-phase sine functions (defined by amplitudes $a_{LLR/\psi}$, frequency f and phase p) determine the precision afforded to the likelihood and prior⁵³. The implicit anti-phase fluctuations are mandated by Bayes-optimal formulations in which inference depends only on the relative values of prior and likelihood precision (i.e., the Kalman gain⁵⁴). As such, ω_{LLR} and ω_ψ implement a hyperprior⁵⁵ in which the likelihood and prior precisions are shifted against each other at a dominant timescale defined by f .

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

- (...) Yet relying too strongly on serial dependencies may come at a cost: When accumulating over time, internal predictions may eventually override external information, leading to circular and false inferences about the state of the environment⁵⁷. Akin to the wake-sleep-algorithm in machine learning⁵⁸, bimodal inference may help to determine whether errors result from external input or from internally-stored predictions: During internal mode, sensory processing is more strongly constrained by predictive processes that auto-encode the agent's environment. Conversely, during external mode, the network is driven predominantly by sensory inputs¹⁸. Between-mode fluctuations may thus generate an unambiguous error signal that aligns internal predictions with the current state of the environment in iterative test-update-cycles⁵⁸. On a broader scale, between-mode fluctuations may thus regulate the balance between feedforward versus feedback contributions to perception and thereby play a adaptive role in metacognition and reality monitoring⁵⁹.
- From the perspective of the Bayesian brain hypothesis, we hypothesized that observers have certain hyperpriors that are apt for accommodating fluctuations in the predictability

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

- The empirical evidence above suggests that the timescale of this periodic scheduling of evidence accumulation may be scale-invariant. This means that there may exist a timescale of periodic fluctuations in precision over every window or length of perceptual decision-making. Bimodal inference predicts perceptual decisions under a generative model (based upon a hazard function to model serial dependencies between subsequent trials) with periodic fluctuations in the precision of sensory evidence relative to prior beliefs at a particular timescale. Remarkably, a systematic model comparison based on AIC indicated that a model with fluctuating precisions has much greater evidence, relative to a model in the absence of fluctuating precisions. This ad-hoc addition of oscillations to a normative Bayesian model of evidence accumulation⁵¹ allowed us to quantify the dominant timescale of periodic fluctuations mode at approximately $0.11 / N_{trials}$ in humans and mice that is appropriate for these kinds of paradigms.

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

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

2312 the autocorrelation of natural environments³⁴ and bias perception toward preceding
2313 experiences^{30,31,35}. Computational modeling indicated that ongoing changes in perceptual
2314 performance may be driven by systematic fluctuations between externally- and internally-
2315 oriented modes of sensory analysis. **We suggest that such *bimodal inference* may help
2316 to build stable internal representations of the sensory environment despite an ongoing
2317 stream of sensory information.

2318 **10.1.10 Comment 11**

2319 **This begs the question as to whether you want to pursue the 1/f story. You**
2320 **refer to this as “noise”. However, there is no noise in this setup. I think what**
2321 **you meant was that the fluctuations are scale free, because they evinced a power**
2322 **law. I am sure that there are scale free aspects of these kinds of hyperpriors;**
2323 **however, in the context of your paradigm I wonder whether you should just**
2324 **ignore the scale free aspect and focus on your estimated temporal scale implicit**
2325 **in f. This means you don’t have to hand wave about self-organized criticality in**
2326 **the discussion and focus upon your hypothesis.**

2327 We would like to thank the reviewer for this suggestion. We agree that the discussion
2328 of self-organized criticality is far from the data. We have omitted this section from the
2329 discussion. With respect to f , we have adapted the manuscript to make clear that it captures
2330 the dominant timescale of fluctuations in mode:

- 2331 • (...) This implements a hyperprior⁵⁵ in which the likelihood and prior precisions are
2332 shifted against each other at a dominant timescale defined by f : (...)
- 2333 • (...) The parameter f captured the dominant time scale at which likelihood and prior
2334 precision were shifted against each other and was estimated at $0.11 \text{ } 1/N_{trials}$ in both
2335 humans and mice.

2336 • Remarkably, a systematic model comparison based on AIC indicated that a model with
2337 fluctuating precisions has much greater evidence, relative to a model in the absence
2338 of fluctuating precisions. The ad-hoc addition of oscillations to a normative Bayesian
2339 model of evidence accumulation⁵¹ allowed us to quantify the dominant timescale of
2340 periodic fluctuations mode at approximately $0.11 \text{ } 1/N_{trials}$ in humans and mice that is
2341 appropriate for these kinds of paradigms.

2342 **10.1.11 Comment 12**

2343 **A final move—to make the paper more focused and digestible—would be to**
2344 **put a lot of your defensive analyses (e.g. about general arousal et cetera) in**
2345 **supplementary material. You have to be careful not to exhaust the reader by**
2346 **putting up a lot of auxiliary material before the important messages in your**
2347 **report.**

2348 We have followed this suggestion and move the following sections to the supplement: section
2349 5.3 (Internal and external modes of processing facilitate response behavior and enhance
2350 confidence in human perceptual decision-making), section 5.4 (Fluctuations between internal
2351 and external mode modulate perceptual performance beyond the effect of general response
2352 biases), section 5.5 (Internal mode is characterized by lower thresholds as well as by history-
2353 dependent changes in biases and lapses). We have also moved secondary statistics to the
2354 figure legends and to the Supplement.

2355 **Minor points**

2356 **10.1.12 Comment 13**

2357 **I cannot resist suggesting that you change your title to “Bimodal Inference in**
2358 **Mice and Men”**

2359 We thank you for this suggestion and have changed the title accordingly.

₂₃₆₀ **10.1.13 Comment 14**

₂₃₆₁ Please replace “infra-slow fluctuations” with “slow fluctuations”. Slow has some
₂₃₆₂ colloquial meaning in fMRI studies but not in any scale free context.

₂₃₆₃ Done.

₂₃₆₄ **10.1.14 Comment 15**

₂₃₆₅ Please replace “simulated data” with “simulations” in the abstract. Finally,
₂₃₆₆ please replace “robust learning and metacognition in volatile environments” with
₂₃₆₇ “enable optimal inference and learning in volatile environments.”

₂₃₆₈ Done. Since we have followed the suggestion to delete section 5.8, we have rephrased the last
₂₃₆₉ paragraph of the abstract into:

₂₃₇₀ • (...) We propose that between-mode fluctuations generate unambiguous error signals
₂₃₇₁ that enable optimal inference in volatile environments.

₂₃₇₂ **10.1.15 Comment 16**

₂₃₇₃ Line 50, please replace “about the degree of noise inherent in encoding of
₂₃₇₄ sensory information” with “the precision of sensory information relative to prior
₂₃₇₅ (Bayesian) beliefs.”

₂₃₇₆ Done.

₂₃₇₇ **10.1.16 Comment 17**

₂₃₇₈ Line 125: please replace “a source of error” with “a source of bias”

₂₃₇₉ Done.

2380 10.1.17 Comment 18

2381 Line 141: please replace “one 1/f noise” with a scale-invariant process with a 1/f
2382 power law” (here and throughout) this is not “noise” it is a particular kind of
2383 fluctuation.

2384 Done.

2385 10.1.18 Comment 19

2386 Line 178, when you say that the fluctuations may arise due to “changes in level of
2387 tonic arousal or on-task attention”, I think you need to qualify this. In predictive
2388 processing, on-task attention is exactly the modulation of sensory precision,
2389 relative to prior precision that you are characterizing here. Tonic arousal may be
2390 another thing may or may not confound your current results.

2391 Thank you very much for pointing this out. We have adapted the discussion to make the
2392 distinction between attention in the predictive processing sense and the broader issue of task
2393 engagement (reflecting fluctuations in arousal, fatigue etc.) clearer (see also our responses
2394 above):

- 2395 • As a functional explanation for bimodal inference, we propose that perception temporarily
2396 disengages from internal predictions to form stable inferences about the statistical
2397 properties of the sensory environment. Between-mode fluctuations may thus elude
2398 circular inferences that occur when both the causes and the encoding of sensory stimuli
2399 are volatile^{19,57}). By the same token, we suggest that fluctuations in mode occur at
2400 the level of perceptual processing^{26,30,46,47}, and are not a passive phenomenon that is
2401 primarily driven by factors situated up- or downstream of sensory analysis.
- 2402 • How does attention relate between-mode fluctuations? According to predictive processing,
2403 attention corresponds to the precision afforded to the probability distributions that

underlie perceptual inference⁵³. As outlined above, between-mode fluctuations can be understood as ongoing shifts in the precision afforded to likelihood (*external mode*) and prior (*internal mode*), respectively. When the precision afforded to prior or likelihood increases, posterior precision increases, which leads to faster RTs and higher confidence. When defined from the perspective of predictive processing as the precision afforded to likelihood and prior⁵³, fluctuations in attention may thus provide a plausible explanation for the quadratic relationship between mode and RTs and confidence (Figure 2H and J; Figure 3I; Figure 3J).

- Outside of the predictive processing field, attention is often understood in the context of task engagement⁶³, which varies according to the availability of cognitive resources that are modulated by factors such as tonic arousal, familiarity with the task, or fatigue⁶³. Our results suggest that internal mode processing cannot be completely reduced to intervals of low task engagement: In addition to shorter RTs and elevated confidence, choices during internal mode were not random or globally biased, but driven by perceptual history (Supplemental Figures S6-7). Moreover, our computational model identified the dominant timescale of between-mode fluctuations at $0.11 \text{ } 1/N_{trials}$, which may be compatible with fluctuations in arousal⁶⁴, but is faster than to be expected for the development of task familiarity or fatigue.
- However, in interpreting the impact of between-mode fluctuations on perceptual accuracy, speed of response and confidence, it is important to consider that global modulators such as tonic arousal are known to have non-linear effects on task performance⁶⁵: In perceptual tasks, performance seems to be highest during mid-level arousal, whereas low- and high-level arousal lead to reduced accuracy and slower responses⁶⁵. This contrasts with the effects of bimodal inference, where accuracy increases linearly as one moves from internal to external mode, and responses become faster at both ends of the mode spectrum.

- 2430 • Of note, high phasic arousal has been shown to suppress multi-domain biases in decision-
 2431 making in humans and mice^{66–68}, including the biases toward perceptual history²⁸ that
 2432 we implicate in internal mode processing. The increase in response speed and history
 2433 congruence over time (Supplemental Section 9.4) may argue against insufficient training
 2434 as an alternative explanation for internal mode processing, but may also taken as a
 2435 sign of waning arousal. The multiple mechanistic mappings to RTs and confidence
 2436 therefore warrant more direct measures of arousal (such as pupil size^{28,65,66,68–70}, motor
 2437 behavior^{69,70}, or neural data⁷¹) to better delineate bimodal inference from fluctuations
 2438 in global modulators of task performance.

2439 **10.1.19 Comment 20**

2440 **When introducing Equation 2, please make it clear that the omega terms stand in**
 2441 **for the precisions afforded to the likelihood (omega_LL) and prior (omega_psi)**
 2442 **that constitute the log posterior.**

2443 We have modified the introduction of equation 2 as follows:

- 2444 • Following Bayes' theorem, we reasoned that binary perceptual decisions depend on the
 2445 log posterior ratio L of the two alternative states of the environment that participants
 2446 learn about via noisy sensory information⁵¹. We computed the posterior by combining
 2447 the sensory evidence available at time-point t (i.e., the log likelihood ratio LLR) with
 2448 the prior probability ψ^{**} , weighted by the respective precision terms ω_{LL} and ω_ψ :

2449 **You can then motivate Equation 6 and 7 as implementing the hyperprior in which**
 2450 **the sensory and prior precisions fluctuate at a particular time scale.**

2451 We would like to thank the reviewer for this suggestion, which we have added to the
 2452 introduction of equations (6) and (7):

2453 • To allow for *bimodal inference*, i.e., alternating periods of internally- and externally-
2454 biased modes of perceptual processing that occur irrespective of the sequence of preceding
2455 experiences, we assumed that likelihood and prior vary in their influence on the perceptual
2456 decision according to fluctuations governed by ω_{LLR} and ω_ψ . These anti-phase sine
2457 functions (defined by amplitudes $a_{LLR/\psi}$, frequency f and phase p) determine the
2458 precision afforded to the likelihood and prior⁵³. The implicit anti-phase fluctuations
2459 are mandated by Bayes-optimal formulations in which inference depends only on the
2460 relative values of prior and likelihood precision (i.e., the Kalman gain⁵⁴). As such, ω_{LLR}
2461 and ω_ψ implement a hyperprior⁵⁵ in which the likelihood and prior precisions are shifted
2462 against each other at a dominant timescale defined by f : (...)

2463 10.1.20 Comment 21

2464 You can also point out that the implicit anti-phase fluctuations are mandated by
2465 Bayes optimal formulations in which it is only the relative values of the prior
2466 and sensory precision that matter. Bayesian filters these precisions constitute
2467 the Kalman gain. You can find a derivation of why this in treatments of the
2468 hierarchical Gaussian filter is by Mathys et al.

2469 We would like to thank the reviewer for this suggestion. We added this information to the
2470 description of our model in the Results section (see comment above).

2471 10.1.21 Comment 22

2472 In your first model simulations, I would make it clear in the main text which
2473 parameters you are optimizing's; namely (H, alpha, a_likelihood, a_prior f).
2474 Perhaps a little table with a brief description of the meaning of these hyper
2475 parameters would be useful?

2476 We now identify the optimized parameters at the outset of the modeling section:

2477 • (...) We used a maximum likelihood procedure to fit the bimodal inference model
2478 (M1, Figure 1F) to the behavioral data from the Confidence database²⁰ and the IBL
2479 database²¹, optimizing the parameters α , H , amp_{LLR} , amp_ψ , f and p (see Methods for
2480 details and Supplemental Table T2 for a summary of the parameters of the bimodal
2481 inference model). We validated our model in three steps: (...).

2482 We furthermore included a table summarizing the model parameters in the Supplement:

2483 10.1.22 Comment 23

2484 Please remove Section 5.8. If you do not, you need to explain why — on line 586
2485 - setting $a = 0$ is appropriate when $a = 0$, the log posterior in Equation 2 is zero
2486 because the precisions (omegas) are zero (by Equations 6 and 7).

2487 We have removed the section 5.8. When setting the amplitude parameters to zero, ω_{LLR} and
2488 ω_ψ are constant at 1, creating a unimodal control model that corresponds to the normative
2489 Bayesian evidence accumulation model proposed by Glaze et al⁵¹.

2490 10.2 Reviewer 2

2491 The authors elucidate whether periodicities in the sensitivity to external informa-
2492 tion represent an epiphenomenon of limited processing capacity or, alternatively,
2493 result from a structured and adaptive mechanism of perceptual inference. Ana-
2494 lyzing large datasets of perceptual decision-making in humans and mice, they
2495 investigated whether the accuracy of visual perception is constant over time
2496 or whether it fluctuates. The authors found significant autocorrelations on the
2497 group level and on the level of individual participants, indicating that a stimulus-
2498 congruent response in a given trial increased the probability of stimulus-congruent
2499 responses in the future. Furthermore, the authors addressed whether observers
2500 cycle through periods of enhanced and reduced sensitivity to external information

2501 or whether observers rely on internal information in certain phases. This was
2502 quantified by whether a response at a given trial was correlated with responses
2503 in previous trials. The authors used computational modeling to infer the origin
2504 of the different modes (internal vs. external).

2505 **Evaluation**

2506 This is a very interesting and well-written manuscript, dealing with an important
2507 question. The findings are novel and provide an innovative account of interpreting
2508 visual perception. I am not an expert in modeling, so I will restrict my comments
2509 to theoretical framework and the experimental approach. I have a few minor
2510 questions that I would like the authors to answer or clarify.

2511 We would like to thank the reviewer for the evaluation of our manuscript. We have added
2512 the discussion of potential effects at the motor-level to our discussion.

2513 **Minor questions**

2514 **10.2.1 Comment 1**

2515 History congruent perception was defined on the basis of response repetitions.
2516 Are we really sure that responses are repeated due to some variant of a per-
2517 ceptual decision process (internal or external) or may arise on the motor-level -
2518 independent of a perceptual source? For instance, a response primed by residual
2519 activation in the motor system may represent a local effect independent from a
2520 general response bias. If indeed, a response repetition is initiated by whatever
2521 reasons (non-perceptual), wouldn't this imply that the repeated response is
2522 per se more related to previous than to current visual information and would
2523 hence signal a reduced sensitivity to current external information? The authors
2524 are discussing the option of stereotypically repeated responses in the context
2525 of alertness. However, a tendency to repeat responses may arise due to other

2526 **reasons. For instance, may the motor priming effects mentioned possibly explain**
2527 **faster RTs along with a stronger bias when in internal-mode.**

2528 Thanks a lot for pointing this out. In this manuscript, we attempt to characterize the
2529 phenomenon of bimodal inference at the level of behavior: The Confidence database consists
2530 only of behavioral data. At the time of publishing this paper as a preprint, the IBL database
2531 had also released only behavioral data.

2532 We realize that it is very difficult to preclude all influences from effects that occur at the
2533 level of behavior. Not all studies in the confidence database have used a counter-balanced
2534 mapping between the perceptual decision and the associated motor-response. In the IBL
2535 data, the mapping between the perceptual decision and the associated motor-response is
2536 fixed (turning a response wheel left or right depending on the perceived location of a grating).
2537 Confidence reports also provide only indirect information on motor- vs. perceptual effects.
2538 One may speculate that, if a response was driven by residual activity in the motor system, it
2539 may be more likely to be a lapse and be accompanied by reduced confidence. By contrast,
2540 we found that confidence was, on average, elevated for history-congruent choices.

2541 That being said, behavioral analyses alone are insufficient to rule out the contribution of
2542 motor-related effects to seriality in choices. This would require analyses of additional types
2543 of data, such as video tracking of the motor response or even neural data collected in brain
2544 areas directly related to motor behavior. While this analysis is beyond the scope of the
2545 present manuscript, we plan to carry out these analyses using the recent data publication of
2546 the IBL, that contains, among others, video tracking of the motor response (turning of the
2547 response wheel) and neuropixel recording across the whole brain, including premotor and
2548 motor cortex⁷¹.

2549 We have added these considerations to the discussion of potential confounds:

- 2550 • Residual activation of the motor system may provide another contribution to serial biases
2551 in perceptual choices⁷². Such motor-driven priming may lead to errors in randomized

psychophysical designs, resembling the phenomenon that we identify as internally-biased processing⁷³. Moreover, residual activation of the motor system may lead to faster responses, and thus constitutes an alternative explanation for the quadratic relationship of mode with RTs⁷². The observation of elevated confidence for stronger biases toward internal mode speaks against the proposition that residual activation of the motor system is the primary driver of serial choice biases, since strong motor-driven priming should lead to frequent lapses that are typically associated reduced confidence⁷⁴. Likewise, perceptual history effects have repeatedly been replicated in experiments with counter-balanced stimulus-response mappings⁸².

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

10.3 Reviewer 3

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

Overall, the authors make a very interesting proposal about what drives slow

2577 fluctuations in perceptual performance during randomized two-alternative choice
2578 tasks. This proposal relates changes in accuracy with changes in serial choice
2579 biases, which is a timely and synthesizing contribution. Furthermore, this proposal
2580 is backed by analyses over several human datasets and a large dataset in mice.

2581 Despite its strong empirical contribution, the paper seems limited by the fact
2582 that alternative computational hypotheses are not adequately considered (or at
2583 least considered in a systematic way). At the same time, and although the paper
2584 is well written, some parts are overly technical.

2585 We would like to thank the Reviewer for the very helpful comments on our manuscript.
2586 We fully agree that the previous version of our manuscript did not consider alternative
2587 computational hypotheses in a systematic and adequate way. As we outline in more detail in
2588 our point-by-point-responses below, we have addressed this issue by adding a formal model
2589 comparison of the bimodal inference model to reduced models, including a normative models
2590 of Bayesian evidence accumulation. We have added null-hypothesis-testing for enhanced
2591 history-congruence during internal mode. We have also moved a number of defensive analyses
2592 to the supplement.

2593 **Major comments:**

2594 **10.3.1 Comment 1**

2595 The authors collapse across various datasets in which different tasks were em-
2596 ployed. However, some details on the nature of these different tasks and a
2597 discussion on the rationale of collapsing behavioral metrics across them is miss-
2598 ing. The authors mention that all tasks involved binary perceptual decisions. In
2599 some parts of the manuscript the term “false alarms” is mentioned, indicating a
2600 detection protocol. Other terms in the methods section (e.g., “set size”) might
2601 need further clarification. Importantly, it is not clear how reaction times were

2602 calculated in the various tasks and whether some experiments involved free
2603 response paradigms while others interrogation/ cued paradigms (in which case
2604 RTs can be defined as the latency between the response cue and the response).

2605 We would like to thank the Reviewer for this important point. Regarding the rationale for
2606 collapsing across the studies in the Confidence database: Having found strong evidence of
2607 apparent between-mode fluctuations in a study on intermittent bistable perception¹⁹, our
2608 goal was to test whether between-mode fluctuations were a general phenomenon in perceptual
2609 decision-making. We thus had a lenient threshold for including studies from the Confidence
2610 database, i.e., all that addressed the domain of perception in 2AFC tasks. This has the
2611 advantage of looking at perceptual 2AFC decisions in general and indicated that history
2612 effects and bimodal inference are present in a wide variety of tasks.

2613 At the same time, collapsing across diverse set of experiments means that the stimuli, the
2614 timing and the way that responses were collected differed between them. To account for this
2615 variability, we included individual experiments as random factors in linear mixed modeling.
2616 We also made sure that perceptual performance is comparable across studies (Supplemental
2617 Figure S1A-B). While our analysis of the IBL database was mainly motivated by investigating
2618 bimodal inference across species, it also allowed us to replicate our results in a highly
2619 standardized task that was collected across many individual subjects²¹. We have added the
2620 rationale for collapsing across studies with its advantages and disadvantages to the *Open*
2621 *questions and limitations* subsection of the discussion:

- 2622 • Our results suggest bimodal inference as a pervasive aspect in perceptual decision-
2623 making in humans and mice. However, a number of limitations and open questions
2624 have to be considered: First, this work sought to understand whether fluctuations
2625 between internal and external mode, which we initially observed in an experiment on
2626 bistable perception in humans¹⁹, are general phenomenon that occurs across a diverse
2627 set of perceptual decision-making tasks. Our analysis of the Confidence database²⁰

2628 therefore collapsed across all available experiments on binary perceptual decision-making.
2629 Individual experiments differed with respect to the stimuli, the manipulation of difficulty,
2630 the timing of trials, and the way responses were collected, but were highly comparable
2631 with respect to the central variables of stimulus- and history-congruence (Supplemental
2632 Figure S1A-B).

- 2633 • The variability across experiments, which we considered as random effects in all statistical
2634 analyses, enabled us to assess whether bimodal inference represents a general phenomenon
2635 in perceptual decision-making, but limited the precision at which we were able to
2636 investigate the relation of mode to behavioral variables such as timing, task difficulty,
2637 RT or confidence. This issue is partially resolved by our analyses of the IBL database,
2638 which replicated our findings in an experiment that was highly standardized with respect
2639 to timing, task difficulty, and behavioral read-out²¹. It will be an important task for
2640 future research to validate our results on bimodal inference in a standardized dataset of
2641 comparable volume in humans, which is, to our knowledge, not yet available.

2642 We apologize for the lack of clarity regarding the way we queried the Confidence database.
2643 To select a broad variety of experiments on 2AFC perceptual decision-making, we queried
2644 the Confidence database for studies from the *perception* category (excluding studies from the
2645 categories *cognitive*, *motor*, *memory* and *mixed*) and selected studies with 2AFC responses.
2646 Our previous version of the manuscript had mentioned the variable names given to the
2647 difficulty variable in the individual experiments (i.e., the name of the column in the individual
2648 .txt files provided for every experiment in the Confidence database). The term *false alarm*
2649 turned up in the discussion of lapses of attention and arousal, which we have re-written in
2650 response to Comment 19 by Reviewer 1 and Comment 6 by Reviewer 3. We now provide
2651 more information on the experiments and variables selected in the Method section:

- 2652 • We downloaded the human data from the Confidence database²⁰ on 10/21/2020, limiting
2653 our analyses to the category *perception*. Within this 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, a 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.

2679 We would like to thank the reviewer for highlighting this important point. Following this
2680 suggestion, we have explicitly tested our main hypothesis ($H1$: periods of reduced stimulus-
2681 congruence are periods of enhanced reliance on history-congruence) against the following null
2682 hypotheses:

- 2683 • $H0_1$: Periods of reduced stimulus-congruence are periods of enhanced random choices
2684 • $H0_2$: Periods of reduced stimulus-congruence are periods of enhanced general bias

2685 We present three sets of statistical analyses to test $H1$ against $H0_{1/2}$:

2686 First, we used logistic regression to predict individual choices. Under $H1$, one would expect a
2687 significant effect of perceptual history in a logistic regression model that predicts individual
2688 choices from the external stimulus, perceptual history and general response bias. At the
2689 model level, one would expect higher AIC in a model without perceptual history as a predictor
2690 of individual choices, indicating that perceptual history influences choices beyond noise ($H0_1$)
2691 and general response bias ($H0_2$).

2692 In both humans and mice, we found a significant effect of perceptual history on choices
2693 while controlling for bias. When eliminating perceptual history as a predictor of individual
2694 choices, we found higher AIC (providing model-level evidence against $H0_1$ and $H0_2$). We
2695 complemented this analysis by computing AIC in individual observers (Supplemental Figure
2696 S4), and again found higher AIC in models from which perceptual history was eliminated.

2697 We have made the following changes to the main manuscript:

2698 Humans:

- 2699 • Subsection title: Fluctuations between internal and external mode cannot be reduced to
2700 general response biases or random choices
- 2701 • The core assumption of bimodal inference - that ongoing changes in the sensitivity to
2702 external information are driven by internal predictions induced via perceptual history

2703 - needs to be contrasted against two alternative hypotheses: When making errors,
2704 observers may not engage with the task and respond stereotypically, i.e., exhibit stronger
2705 general biases toward one of the two potential outcomes, or simply choose randomly.
2706 Logistic regression confirmed that perceptual history made a significant contribution to
2707 perception ($\beta = 0.11 \pm 5.79 \times 10^{-3}$, $z = 18.53$, $p = 1.1 \times 10^{-76}$) over and above the
2708 ongoing stream of external sensory information ($\beta = 2.2 \pm 5.87 \times 10^{-3}$, $z = 375.11$, $p <$
2709 2.2×10^{-308}) and general response biases toward ($\beta = 15.19 \pm 0.08$, $z = 184.98$, $p <$
2710 2.2×10^{-308}). When eliminating perceptual history as a predictor of individual choices
2711 at individual trials, AIC increased by $\delta_{AIC} = 1.64 \times 10^3$ (see Supplemental Figure S4A-B
2712 for parameter- and model-level inference at the level of individual observers).

2713 Mice:

2714 • In line with humans, mice were biased toward perceptual history in $54.03\% \pm 0.17\%$
2715 of trials ($T(163) = -7.52$, $p = 3.44 \times 10^{-12}$; Figure 4A and Supplemental Figure S1D).
2716 Perceptual history effects remained significant ($\beta = 0.51 \pm 4.49 \times 10^{-3}$, $z = 112.84$, $p <$
2717 2.2×10^{-308}) when controlling for external sensory information ($\beta = 2.96 \pm 4.58 \times 10^{-3}$,
2718 $z = 646.1$, $p < 2.2 \times 10^{-308}$) and general response biases toward one of the two potential
2719 outcomes ($\beta = -1.78 \pm 0.02$, $z = -80.64$, $p < 2.2 \times 10^{-308}$). When eliminating perceptual
2720 history as a predictor of individual choices, AIC increased by $\delta_{AIC} = 1.48 \times 10^4$, arguing
2721 against the notion that choice randomness and general response bias are the only
2722 determinants of perceptual performance (see Supplemental Figure S4C-D for parameter-
2723 and model-level inference within individual mice).

2724 Second, we analyzed dynamic changes in history- and stimulus-congruence (i.e., smoothed
2725 probabilities for stimulus-congruence, history-congruence and general response bias in sliding
2726 10 trial time-windows). Under H1, one would expect a significant negative correlation between
2727 the dynamic probability of stimulus- and history-congruence. At the model level, one would

2728 expect higher AIC in a model without history-congruence as a predictor of stimulus-congruence,
2729 indicating that changes in the probability of history-congruence influence stimulus-congruence
2730 beyond noise ($H0_1$) and general response bias ($H0_2$).

2731 In both humans and mice, we found a significant negative correlation between history-
2732 congruence and stimulus-congruence while controlling for general response bias. When elimi-
2733 nating the dynamic probability of history-congruence as a predictor of stimulus-congruence,
2734 we found higher AIC (providing model-level evidence against $H0_1$ and $H0_2$). The section
2735 5.4 or our original manuscript (*Fluctuations between internal and external mode modulate*
2736 *perceptual performance beyond the effect of general response biases*) complements these control
2737 analyses and has been moved to the supplement to stream-line the manuscript (following the
2738 Comment 12 by Reviewer 1 and Comment 9 by Reviewer 3). We have modified the main
2739 manuscript in the following way:

2740 Humans:

2741 • Finally, we ensured that fluctuations in stimulus- and history-congruence are linked to
2742 each other, while controlling for fluctuations in the strength of general response biases.

2743 When perceptual choices were less biased toward external information, participants
2744 relied more strongly on internal information acquired from perceptual history (and vice
2745 versa, $\beta = -0.05 \pm 5.63 \times 10^{-4}$, $T(2.1 \times 10^6) = -84.21$, $p < 2.2 \times 10^{-308}$), controlling
2746 for fluctuations in the strength of general response biases ($\beta = -0.06 \pm 5.82 \times 10^{-4}$,
2747 $T(2.1 \times 10^6) = -103.51$, $p < 2.2 \times 10^{-308}$).

2748 • (...) Likewise, eliminating the dynamic fluctuations in history-congruence as a predictor
2749 of fluctuations in stimulus-congruence yielded an increase in AIC by $\delta_{AIC} = 7.06 \times 10^3$.
2750 These results provided model-level evidence against the null hypotheses that fluctuations
2751 in stimulus-congruence are driven exclusively by choice randomness or general response
2752 bias (see Supplemental Section 9.2 for an in-depth assessment of general response bias).

2753 Mice:

- 2754 • As in humans, fluctuations in the strength of history-congruent biases had a significant
2755 effect on stimulus-congruence ($\beta_1 = -0.12 \pm 7.17 \times 10^{-4}$, $T(1.34 \times 10^6) = -168.39$, $p <$
2756 2.2×10^{-308}) beyond the effect of ongoing changes in general response biases ($\beta_2 = -0.03$
2757 $\pm 6.94 \times 10^{-4}$, $T(1.34 \times 10^6) = -48.14$, $p < 2.2 \times 10^{-308}$). Eliminating the dynamic
2758 fluctuations in history-congruence as a predictor of fluctuations in stimulus-congruence
2759 resulted in an increase in AIC by $\delta_{AIC} = 2.8 \times 10^4$. This confirmed that, in both humans
2760 and mice, perceptual performance is modulated by systematic fluctuations between
2761 externally- and internally-oriented modes of sensory processing that exist beyond general
2762 response bias (see Supplemental Section 9.2 for an in-depth assessment of general
2763 response bias).

2764 Third, we analyzed full and history-conditioned psychometric curves in external and internal
2765 mode as well as across modes. Under our main hypothesis that periodic reductions in
2766 sensitivity to external information are driven by increases in the impact of perceptual history,
2767 one would expect (i) a history-dependent increase in biases and lapses (effects of perceptual
2768 history), and (ii), a history-independent increase in threshold (reduced sensitivity to external
2769 information). Conversely, if what we identified as internal mode processing was in fact driven
2770 by random choices, one would expect (i), a history-independent increase in lapse (choice
2771 randomness), (ii), no change in bias (no effect of perceptual history), and (iii), reduced
2772 thresholds (reduced sensitivity to external information). In both humans and mice, we
2773 observed the pattern predicted by H1. In response to the comments by Reviewer 1 and 3,
2774 we have significantly streamlined the manuscript and moved our assessment of psychometric
2775 functions to the supplement. We now provide a summary of our results in the main manuscript
2776 to make our reasoning with respect to $H0_1$ and $H1$ more explicit:

2777 Humans:

2778 • To confirm that changes in the sensitivity to external information are indicative of
2779 internal mode processing, we estimated full and history-dependent psychometric curves
2800 during internal, external, and across modes. If, as we hypothesized, internal mode
2801 processing reflects an enhanced impact of perceptual history, one would expect a history-
2802 dependent increase in biases and lapses as well as a history-independent increase in
2803 threshold. Conversely, if internal mode processing were driven by random choices, one
2804 would expect a history-independent increase in biases and threshold, and no change in
2805 bias. In line with our prediction, we found that internal mode processing was associated
2806 with a history-dependent increase in bias and lapse as well as a history-independent
2807 increase in threshold (Supplemental Section 9.3.1 and Supplemental Figure S6). This
2808 confirms that internal mode processing is indeed driven by an enhanced impact of
2809 perceptual history.

2790 Mice:

2791 • When fitting full and history-conditioned psychometric curves to the data from the IBL
2792 database, we observed that internal mode processing was associated with a history-
2793 dependent increase in bias and lapse as well as a history-independent increase in threshold
2794 (Supplemental Section 9.3.2 and Supplemental Figure S7). This provided further evidence
2795 for the hypothesis that internal mode processing is driven by an enhanced impact of
2796 perceptual history, as opposed to increased choice randomness.

2797 **10.3.3 Comment 3**

2798 **From a mechanistic (sequential sampling) perspective, several previous papers**
2799 **have examined whether choice history biases influence the starting point or the**
2800 **drift rate of the evidence accumulation process. Under the former formulation,**
2801 **reliance on the evidence vs. reliance on the previous choice will be naturally**
2802 **anti-correlated (the less weight you place on the evidence the more impactful the**

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

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

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

2829 We validated our model in three steps: First, to show that bimodal inference does not
2830 emerge spontaneously in normative Bayesian models of evidence accumulation, but
2831 requires the ad-hoc addition of anti-phase oscillations in prior and likelihood precision,
2832 we compared the bimodal inference model to four control models (M2-5, Figure 1G).
2833 In these models, we successively removed the anti-phase oscillations (M2-M4) and the
2834 integration of information across trials (M5) from the bimodal inference model and
2835 performed a model comparison based on AIC.

- 2836 • Model M2 ($AIC_2 = 5.7 \times 10^4$ in humans and 4.94×10^4 in mice) and Model M3 (AIC_3
2837 $= 6.9 \times 10^4$ in humans and 5.99×10^4 in mice) incorporated only oscillations of either
2838 likelihood or prior precision. Model M4 ($AIC_4 = 9.8 \times 10^4$ in humans and 9.19×10^4 in
2839 mice) lacked any oscillations of likelihood and prior precision and corresponded to the
2840 normative model proposed by Glaze et al.⁵¹. In model M5 ($AIC_4 = 1.16 \times 10^5$ in humans
2841 and 1.14×10^5 in mice), we furthermore removed the integration of information across
2842 trials, such that perception depended only in incoming sensory information (Figure 1G).
- 2843 • The bimodal inference model achieved the lowest AIC across the full model space (AIC_1
2844 $= 4.73 \times 10^4$ in humans and 4.28×10^4 in mice) and was clearly superior to the normative
2845 Bayesian model of evidence accumulation ($\delta_{AIC} = -5.08 \times 10^4$ in humans and -4.91×10^4
2846 in mice; Supplemental Figure S9).
- 2847 • In sum, computational modeling suggested that between-mode fluctuations are best
2848 explained by two interlinked processes (Figure 1E): (i), the dynamic accumulation of
2849 information across successive trials mandated by normative Bayesian models of evidence
2850 accumulation and, (ii), ongoing anti-phase oscillations in the impact of external and
2851 internal information.
- 2852 • Could bimodal inference emerge spontaneously in normative models of perceptual
2853 decision-making? In predictive processing, the relative precision of prior and likelihood
2854 determines their integration into the posterior that determines the content of perception.

2855 At the level of individual trials, the perceptual impact of internal predictions generated
2856 from perceptual history (prior precision) and external sensory information (likelihood
2857 precision) are thus necessarily anti-correlated. The same holds for mechanistic models of
2858 drift diffusion, which understand choice history biases as driven by changes in the starting
2859 point⁵¹ or the drift rate of evidence accumulation³². Under the former formulation,
2860 perceptual history is bound to have a stronger influence on perception when less weight
2861 is given to incoming sensory evidence, assuming that the last choice is represented as a
2862 starting point bias. The effects of choice history in normative Bayesian and mechanistic
2863 drift diffusion models can be mapped onto one another via the Bayesian formulation
2864 of drift diffusion⁶⁰, where the inverse of likelihood precision determines the amount of
2865 noise in the accumulation of new evidence, and prior precision determines the absolute
2866 shift in its starting point⁶⁰.

- 2867 • While it is thus clear that the impact of perceptual history and sensory evidence are anti-
2868 correlated *at each individual trial*, we here introduce anti-phase oscillations as an ad-hoc
2869 modification to model slow fluctuations in prior and likelihood precision that evolve *over*
2870 *many consecutive trials* and are not mandated by normative Bayesian or mechanistic
2871 drift diffusion models. The bimodal inference model provides a reasonable explanation
2872 of the linked autocorrelations in stimulus- and history-congruence, as evidenced by
2873 formal model comparison, successful prediction of RTs and confidence as out-of-training
2874 variables, and a qualitative reproduction of our empirical data from posterior model
2875 parameter as evidence against over- or under-fitting.
- 2876 • Of note, similar non-stationarities have been observed in descriptive models that assume
2877 continuous⁶¹ or discrete¹² changes in the latent states that modulate perceptual decision-
2878 making at slow timescales. A recent computational study⁶² has used a Hidden Markov
2879 model to investigate perceptual decision-making in the IBL database²¹. In analogy
2880 to our findings, the authors observed that mice switch between temporally extended

2881 *strategies* that last for more than 100 trials: During *engaged* states, perception was highly
2882 sensitive to external sensory information. During *disengaged* states, in turn, choice
2883 behavior was prone to errors due to enhanced biases toward one of the two perceptual
2884 outcomes⁶². Despite the conceptual differences to our approach (discrete states in a
2885 Hidden Markov model that correspond to switches between distinct decision-making
2886 strategies⁶² vs. gradual changes in mode that emerge from sequential Bayesian inference
2887 and ongoing fluctuations in the impact of external relative to internal information), it is
2888 tempting to speculate that engaged/disengaged states and between-mode fluctuations
2889 might tap into the same underlying phenomenon.

- 2890 • A third open question concerns the computational underpinnings of bimodal inference.
2891 The addition of slow anti-phase oscillations to the integration of prior and likelihood rep-
2892 resents an ad-hoc modification of a normative Bayesian model of evidence accumulation⁵¹.
2893 While the bimodal inference model is supported by formal model comparison, the suc-
2894 cessful prediction of out-of-training variables and the qualitative reproduction of our
2895 empirical data in simulations from posterior model parameters, it is an important task for
2896 future research to test whether between-mode fluctuations can emerge spontaneously in
2897 hierarchical models of Bayesian inference, whether modes are continuous¹⁹ or discrete⁶²,
2898 and whether bimodal inference can be causally manipulated by experimental variables.
2899 We speculate that between-mode fluctuations may separate the perceptual contribu-
2900 tion of internal predictions and external sensory data in time, creating unambiguous
2901 learning signals that benefit inference about the precision of prior and likelihood, re-
2902 spectively. This proposition should be tested empirically by relating the phenomenon of
2903 bimodal inference to performance in, e.g., reversal learning, probabilistic reasoning, or
2904 metacognition.

2905 **10.3.4 Comment 4**

2906 The authors need to unpack their definition of history biases since in previous
2907 work biases due to the response or the identity of the stimulus at the previous
2908 trial are treated differently. Here, the authors focus on response biases but it
2909 is not clear whether they could examine also stimulus-driven history biases (in
2910 paradigms where stimulus-response is remapped on each trial).

2911 We would like to thank the reviewer for raising this important point. We defined the
2912 history-biases reported in our main manuscript by comparing the *response about the perceived*
2913 stimulus category (A vs. B) at the current and at the preceding trial (choice history). An
2914 alternative would have been to define history biases by comparing the choice at the current
2915 trial to the stimulus category *presented* at the preceding trial (stimulus history). As we show
2916 below, perceptual responses tended to be biased not only toward choice history, but also (but
2917 to a lesser degree) to stimulus history. This is expected, as perception was *stimulus-congruent*
2918 on approximately 75% of trials, causing the effects of the preceding response and the preceding
2919 stimulus to be highly correlated. We therefore compared the effects on choice history and
2920 stimulus history induced by trials at which perception was *stimulus-incongruent*, since those
2921 trials lead to opposite predictions regarding the perceptual choice at the subsequent trial.

2922 As expected, perceptual choices were attracted toward perceptual choices at preceding
2923 stimulus-incongruent trials (i.e., a positive effect of choice history). By contrast, perceptual
2924 choices tended to be repelled away from the stimulus presented the preceding trial. This
2925 repulsion of choices away from stimuli presented at stimulus-incongruent trials confirms
2926 that the choices at stimulus-incongruent trials were the primary driver of serial effects in
2927 perception in both humans and mice.

2928 We now refer to our analysis on stimulus history as an additional confound, which we present
2929 in detail in the Supplement 9.1 of our manuscript:

- 2930 • (...) These serial biases were effects of choice history, i.e., driven by the experiences
2931 reported at the preceding trial, and could not be attributed to stimulus history, i.e., to
2932 effects of the stimuli presented at the preceding trial (Supplemental Section 9.1).

2933 Supplement:

- 2934 • The main manuscript reports the effects of perceptual history, which we defined as the
2935 impact of the choice at the preceding trial on the choice at the current trial (henceforth
2936 *choice history*). *Stimulus history*, which is defined as the impact of the stimulus presented
2937 at the preceding trial on the choice at the present trial, represents an alternative approach
2938 to this. Here, we compare the effects of choice history to the effects of stimulus history.
- 2939 • We observed a significant bias toward stimulus history (humans: $49.76\% \pm 0.1\%$ of trials,
2940 $\beta = 1.26 \pm 0.94$, $T(373.62) = 1.34$, $p = 0.18$; mice: $51.11\% \pm 0.08\%$ of trials, $T(164)$
2941 $= 13.4$, $p = 3.86 \times 10^{-28}$). The bias toward stimulus history was smaller than the bias
2942 toward choice history (humans: $\beta = -3.53 \pm 0.5$, $T(66.53) = -7.01$, $p = 1.48 \times 10^{-9}$;
2943 mice: $T(164) = -17.21$, $p = 1.43 \times 10^{-38}$).
- 2944 • The attraction of choices toward both preceding choices and stimuli is expected, as
2945 perception was *stimulus-congruent* on approximately 75% of trials, causing choices and
2946 stimuli to be highly correlated. We therefore compared the effects of choice history and
2947 stimulus history after *stimulus-incongruent* (i.e., *error*) trials, since those trials lead to
2948 opposite predictions regarding the perceptual choice at the subsequent trial.
- 2949 • As expected from the findings presented in the main manuscript, perceptual choices were
2950 attracted toward perceptual choices when the inducing trial was stimulus-incongruent
2951 (i.e., a positive effect of choice history; humans: $\beta = 0.19 \pm 1.4 \times 10^{-4}$, $z = 1.36 \times 10^3$, $p <$
2952 2.2×10^{-308} ; mice: $\beta = 0.92 \pm 0.01$, $z = 88.82$, $p < 2.2 \times 10^{-308}$). By contrast, perceptual
2953 choices tended to be repelled away from the stimulus presented at preceding stimulus-
2954 incongruent trial (i.e., a negative effect of stimulus history; humans: $\beta = -0.19 \pm 0.01$,

2955 $z = -16.47$, $p = 5.99 \times 10^{-61}$: mice: $\beta = -0.92 \pm 0.01$, $z = -88.76$, $p < 2.2 \times 10^{-308}$).

2956 This repulsion of choices away from stimuli presented at stimulus-incongruent trials
2957 confirmed that choices (which are anti-correlated to stimuli at stimulus-incongruent
2958 trials) were the primary driver of attracting serial effects in perception.

- 2959 • In sum, the above results suggest that, in both humans and mice, serial dependencies
2960 were better explained by the effects of choice history as opposed to the effects of stimulus
2961 history. This aligns with a result recently published for the IBL database, where mice
2962 were shown to follow an *action-kernel* as opposed to a *stimulus-kernel* model when
2963 integrating information across trials⁸¹.

2964 **10.3.5 Comment 5**

2965 Previous work, which the authors acknowledges in their Discussion (6.5), distin-
2966 guishes repetitive history biases from alternating biases. For instance, in Braun,
2967 Urai & Donner (2018, JoN) participants are split into repetitive or alternating.
2968 Shouldn't the authors define the history bias in a similar fashion? The authors
2969 point out that attracting and repelling biases operate simultaneously across
2970 different timescales. However, this is not warranted given Braun et. al and other
2971 similar papers. It is not clear how this more nuanced definition of history bias
2972 would alter the conclusions.

2973 Our empirical results show that, on average, history biases tend to be repetitive (Figure 2A,
2974 Figure 3A, and the biases in the psychometric functions in the Supplemental Figure S6-7).
2975 In fact, only 2 of the 66 experiments we included from the Confidence database²⁰ showed
2976 significant alternating biases (Supplemental Figure S1, please note that history-congruence
2977 was not used in the inclusion algorithm). However, this does not rule out the possibility that
2978 there are periods of alternating biases in the other experiments with net repeating effects.

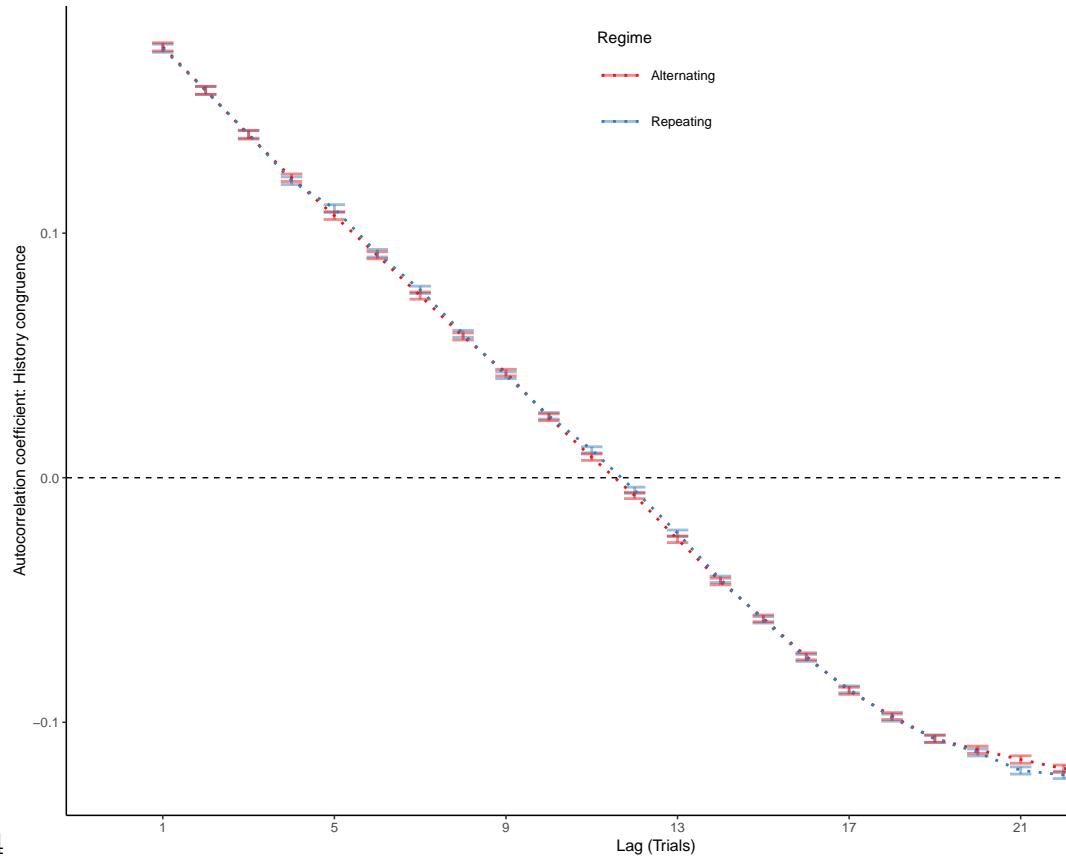
2979 Importantly, our central finding of autocorrelation in history-congruence does not distinguish

2980 between alternating and repetitive history biases. In the plot below, we show autocorrelation
2981 curves for fluctuations history-congruence for both alternation (hazard = 0.8) and repetition
2982 (hazard = 0.2). Both were simulated for 10 blocks of a random duration between 15
2983 and 30 trials, interleaved with 10 blocks with no history biases (hazard = 0.5). This
2984 simulation illustrates that the autocorrelation of alternating and repeating biases is identical
2985 for symmetric pairs of hazard rates. The autocorrelation of history-congruence and the
2986 associated internal mode processing is therefore not tied to repeating biases, but accommodates
2987 alternating biases as well (which seem to be, on average and in our data, less frequent). We
2988 therefore did not separate alternating from repeating biases in our analysis of mode.

2989 We apologize for not having recognized this aspect in the previous version of the discussion.
2990 We have rewritten the paragraph on alternating and repeating biases in the discussion,
2991 referring to the plot below, which we have added to the Supplemental Materials.

- 2992 • Second, our results point to an attraction of perception toward preceding choices.
2993 Previous work has shown that perceptual decision-making is concurrently affected by
2994 both attractive and repulsive serial biases that operate on distinct time-scales and
2995 serve complementary functions for sensory processing^{27,75,76}: Short-term attraction may
2996 serve the decoding of noisy sensory inputs and increase the stability of perception,
2997 whereas long-term repulsion may enable efficient encoding and sensitivity to change²⁷.
2998 In the data analyzed here, history biases tended to be repetitive (Figure 2A, Figure
2999 3A, Supplemental Figure S6 and S7), as only 2 of the 66 experiments of the Confidence
3000 database²⁰ showed significant alternating biases (Supplemental Figure S1). However,
3001 as we show in Supplemental Figure S14, fluctuations in both alternating and repeating
3002 history biases generate overlapping autocorrelation curves. Our analysis of between-mode
3003 fluctuations is therefore not tied exclusively to repeating biases, but accommodates
3004 alternating biases as well, such that both may lead to internally-biased processing
3005 and reduced sensitivity to external sensory information. Future work could apply our

3006 approach to paradigms that boost alternating as opposed to repeating biases, as this
3007 would help to better understand how repetition and alternation are linked in terms of
3008 their computational function and neural implementation²⁷.



3009 **Supplemental Figure S14**

- 3010 • **Supplemental Figure S14.** Autocorrelation of history-congruence of alternating and
3011 repeating biases. Here, we simulate the autocorrelation of history-congruence in 10^3
3012 synthetic participants. In the repeating regime (blue), history-congruence fluctuated
3013 between 50% and 80% (blue) in interleaved blocks (10 blocks per condition with a
3014 random duration between 15 and 30 trials). In the alternation regime (red), history-
3015 congruence fluctuated between 50% and 20%. The resulting autocorrelation curves for
3016 history-congruence overlap, indicating that our analysis is able to accommodate both
3017 repeating and alternating biases.

3018 10.3.6 Comment 6

3019 The arousal hypothesis seems to be ruled out too easily, merely in the presence
3020 of a non-monotonic “state” vs. RT pattern. Arousal can have an inverted U-
3021 shaped effect on behavioral performance and recent paper has demonstrated
3022 a non-monotonic effect of tonic arousal (baseline pupil) on RTs and accuracy
3023 (<https://www.biorxiv.org/content/10.1101/2023.07.28.550956.abstract>). More
3024 generally, the RT and confidence analyses need to be complemented, perhaps by
3025 computational modeling using sequential sampling models, as these behavioral
3026 metrics have multiple mechanistic mappings (e.g., a fast RT might correspond to
3027 high SNR or an impulsive decisions driven by a starting point bias).

3028 We would like to thank the reviewer for this important point. Considering this Comment
3029 and the Comment 3 by Reviewer 1, we realize that the quadratic relationships between
3030 mode and RTs/confidence do not represent a convincing defensive analysis against the
3031 potential contributions of arousal to the phenomenon that we have identified as between-
3032 mode fluctuations. Rather, we now interpret the fluctuations of RTs/confidence with mode
3033 as indicative of a scenario in which between-mode fluctuations modulate a decision-variable
3034 that determines not only the perceptual choices, but also the speed and confidence at which
3035 they are made.

3036 Therefore, as a first response to this comment, we have re-phrased our assessment of RT and
3037 confidence in the following way:

3038 Humans:

- 3039 • The above results point to systematic fluctuations in the *decision variable*⁴⁴ that deter-
3040 mines perceptual choices, causing enhanced sensitivity to external stimulus information
3041 during external mode and increased biases toward preceding choices during internal
3042 mode. As such, fluctuations in mode should influence downstream aspects of behavior

3043 and cognition that operate on the perceptual decision variable⁴⁴. To test this hypothesis
3044 with respect to motor behavior and metacognition, we asked how bimodal inference
3045 relates to response times (RTs) and confidence reports. (...).

- 3046 • (...) In sum, the above results indicate that reporting behavior and metacognition do
3047 not map linearly onto the mode of sensory processing. Rather, they suggest that slow
3048 fluctuations in the respective impact of external and internal information are most likely
3049 to affect perception at an early level of sensory analysis^{46,47}. Such low-level processing
3050 may thus integrate perceptual history with external inputs into a decision variable⁴⁴
3051 that influences not only perceptual choices, but also the speed and confidence at which
3052 they are made.
- 3053 • In what follows, we probe alternative explanations for between-mode fluctuations, test
3054 for the existence of modes in mice, and propose a predictive processing model that
3055 explains fluctuations in mode ongoing shifts in the precision afforded to external sensory
3056 information relative to internal predictions driven by perceptual history.

3057 Mice:

- 3058 • The above results confirm that fluctuations between internally- and externally-biased
3059 modes generalize to perceptual decision-making in mice. As in humans, we hypothesized
3060 that bimodal inference modulates the decision variable⁴⁴ that determines not only
3061 perceptual choices, but also downstream aspects of mouse behavior⁴⁴. (...). When
3062 fitting full and history-conditioned psychometric curves to the data from the IBL
3063 database, we observed that internal mode processing was associated with a history-
3064 dependent increase in bias and lapse as well as a history-independent increase in threshold
3065 (Supplemental Section 9.3.2 and Supplemental Figure S7). Over time, the frequency of
3066 history-congruent choices increased alongside stimulus-congruence and speed of response
3067 as mice were exposed to the experiment, arguing against the proposition that biases

3068 toward perceptual history reflected an unspecific response strategy in mice who were
3069 not sufficiently trained on the IBL task.

3070 Second, we have re-structured the section of defensive analyses, where we contrast the
3071 phenomenon that we identify as fluctuating modes in perception with stereotypical or random
3072 responses as evidence of low task engagement, and not specifically with attention or arousal,
3073 which we discuss below. To streamline the manuscript, we report those analyses in detail in
3074 the Supplement (see Comments 12 by Reviewer 1 and Comment 9 by Reviewer 3).

3075 • The core assumption of bimodal inference - that ongoing changes in the sensitivity to
3076 external information are driven by internal predictions induced via perceptual history
3077 - needs to be contrasted against two alternative hypotheses: When making errors,
3078 observers may not engage with the task and respond stereotypically, i.e., exhibit stronger
3079 general biases toward one of the two potential outcomes, or simply choose randomly.
3080 Logistic regression confirmed that perceptual history made a significant contribution to
3081 perception ($\beta = 0.11 \pm 5.79 \times 10^{-3}$, $z = 18.53$, $p = 1.1 \times 10^{-76}$) over and above the
3082 ongoing stream of external sensory information ($\beta = 2.2 \pm 5.87 \times 10^{-3}$, $z = 375.11$, $p <$
3083 2.2×10^{-308}) and general response biases toward ($\beta = 15.19 \pm 0.08$, $z = 184.98$, $p <$
3084 2.2×10^{-308}).

3085 • When eliminating perceptual history as a predictor of individual choices at individual
3086 trials, AIC increased by $\delta_{AIC} = 1.64 \times 10^3$ (see Supplemental Figure S4A-B for parameter-
3087 and model-level inference at the level of individual observers). Likewise, when eliminating
3088 slow fluctuations in history-congruence as a predictor of slow fluctuations in stimulus-
3089 congruence across trials, we observed an increase in AIC by $\delta_{AIC} = 7.06 \times 10^3$. These
3090 results provided model-level evidence against the null hypotheses that fluctuations in
3091 stimulus-congruence are driven exclusively by choice randomness or general response
3092 bias (see Supplemental Section 9.2 for an in-depth assessment of general response bias).

3093 • To confirm that changes in the sensitivity to external information are indicative of
3094 internal mode processing, we estimated full and history-dependent psychometric curves
3095 during internal, external, and across modes. If, as we hypothesized, internal mode
3096 processing reflects an enhanced impact of perceptual history, one would expect a history-
3097 dependent increase in biases and lapses as well as a history-independent increase in
3098 threshold. Conversely, if internal mode processing were driven by random choices, one
3099 would expect a history-independent increase in biases and threshold, and no change in
3100 bias. In line with our prediction, we found that internal mode processing was associated
3101 with a history-dependent increase in bias and lapse as well as a history-independent
3102 increase in threshold (Supplemental Section 9.3 and Supplemental Figure S6-7). This
3103 confirmed that internal mode processing is indeed driven by an enhanced impact of
3104 perceptual history.

- 3105 • In line with this, the quadratic relationship between mode and confidence (Figure
3106 2J) suggested that biases toward internal information do not reflect a post-perceptual
3107 strategy or repeating preceding choices when the subjective confidence in the perceptual
3108 decision is low. Moreover, while responses became faster with increased exposure
3109 to the experiments of the Confidence database, the frequency of history-congruent
3110 choices increased over time, speaking against the proposition that participants may
3111 stereotypically repeat preceding choices when not yet familiar with the experimental
3112 task (see Supplemental Section).
- 3113 • Taken together, our results thus argue against recurring intervals of low task engagement,
3114 which may be signaled by stereotypical or random responses, as an alternative explanation
3115 for the phenomenon that we identify as bimodal inference.

3116 Third, in response the Comment 3 by Reviewer 1, we now interpret the quadratic relationship
3117 of mode to RTs/confidence in the context of predictive processing views on attention⁵³. Based
3118 on the Bayesian formulation of drift diffusion⁶⁰, we propose that the effects of likelihood on

3119 prior precision on the decision variable and, consequently, on confidence and RTs can be
3120 translated into the mechanistic framework of drift diffusion. Specifically, Bitzer et al. relate
3121 likelihood precision to noise in the accumulation process, and prior precision to the amount
3122 of shift in the starting point⁶⁰. As a third response to this comment, we have re-written
3123 our discussion of the quadratic relationship of mode to RTs and Confidence, focusing on
3124 predictive coding models attention, which we relate to mechanistic drift diffusion models:

- 3125 • How does attention relate between-mode fluctuations? According to predictive processing,
3126 attention corresponds to the precision afforded to the probability distributions that
3127 underlie perceptual inference⁵³. As outlined above, between-mode fluctuations can be
3128 understood as ongoing shifts in the precision afforded to likelihood (*external mode*) and
3129 prior (*internal mode*), respectively. When the precision afforded to prior or likelihood
3130 increases, posterior precision increases, which leads to faster RTs and higher confidence.
3131 When defined from the perspective of predictive processing as the precision afforded to
3132 likelihood and prior⁵³, fluctuations in attention may thus provide a plausible explanation
3133 for the quadratic relationship of mode to RTs and confidence (Figure 2H and J; Figure
3134 3I; Figure 4I). Such effects of attention in the predictive processing sense can be directly
3135 related to mechanistic drift diffusion models⁶⁰, where both larger shifts in starting point
3136 (related to increased prior precision in internal mode) and lower noise in the accumulation
3137 of evidence (related to increased likelihood precision in external mode) may explain
3138 faster and more confident responses.

3139 Given the correspondence between normative Bayesian and mechanistic drift diffusion
3140 models⁶⁰, we believe that we would not gain additional insights into the role of arousal
3141 and additional potential confounds or causes of between-mode fluctuations by fitting drift
3142 diffusion models as an alternative class of behavioral models to our data. To understand the
3143 relation of arousal to the bimodal inference, we think that it is necessary to look at data
3144 beyond behavior, such as pupillometry, video tracking of response behavior, or neural data.

3145 While this is beyond the scope of the current manuscript, we plan to do these analyses in
3146 a follow-up paper, using data published by the IBL after this paper was submitted. The
3147 IBL data now contains eye tracking, video tracking of response behavior, and neuropixel
3148 recordings across the whole mouse brain⁷¹. As a fourth response to this comment, we have
3149 re-written our discussion of attention and arousal:

- 3150 • Outside of the predictive processing field, attention is often understood in the context of
3151 task engagement⁶³, which varies according to the availability of cognitive resources that
3152 are modulated by factors such as tonic arousal, familiarity with the task, or fatigue⁶³. Our
3153 results suggest that internal mode processing cannot be completely reduced to intervals
3154 of low task engagement: In addition to shorter RTs and elevated confidence, choices
3155 during internal mode were not random or globally biased, but driven by perceptual
3156 history (Supplemental Figures S6-7). Moreover, our computational model identified
3157 the dominant timescale of between-mode fluctuations at $0.11\sqrt{1/N_{trials}}$, which may be
3158 compatible with fluctuations in arousal⁶⁴, but is faster than to be expected for the
3159 development of task familiarity or fatigue.
- 3160 • However, in interpreting the impact of between-mode fluctuations on perceptual accuracy,
3161 speed of response and confidence, it is important to consider that global modulators
3162 such as tonic arousal are known to have non-linear effects on task performance⁶⁵: In
3163 perceptual tasks, performance seems to be highest during mid-level arousal, whereas low-
3164 and high-level arousal lead to reduced accuracy and slower responses⁶⁵. This contrasts
3165 with the effects of bimodal inference, where accuracy increases linearly as one moves
3166 from internal to external mode, and responses become faster at both ends of the mode
3167 spectrum.
- 3168 • Of note, high phasic arousal has been shown to suppress multi-domain biases in decision-
3169 making in humans and mice⁶⁶⁻⁶⁸, including the biases toward perceptual history²⁸ that
3170 we implicate in internal mode processing. The increase in response speed and history

3171 congruence over time (Supplemental Section 9.4) may argue against insufficient training
3172 as an alternative explanation for internal mode processing, but may also taken as a
3173 sign of waning arousal. The multiple mechanistic mappings to RTs and confidence
3174 therefore warrant more direct measures of arousal (such as pupil size^{28,65,66,68–70}, motor
3175 behavior^{69,70}, or neural data⁷¹) to better delineate bimodal inference from fluctuations
3176 in global modulators of task performance.

3177 **10.3.7 Comment 7**

3178 **In several analysis the authors present an effect and then show that this effects**
3179 **persists when key variables/ design aspects are also taken into account (see an**
3180 **example at around line 70). It makes more sense to present only one single**
3181 **analysis in which these key variables are controlled for. Results cannot be**
3182 **interpreted if they are spurious factors driving them so it is not clear why some**
3183 **of the results are presented in two versions (“uncontrolled” and “controlled”**
3184 **analyses).**

3185 We apologize for this. We have updated our manuscript accordingly and have omitted,
3186 whenever possible, reports of uncontrolled analyses (highlighted in the main text). The most
3187 significant changes are summarized here:

- 3188 • Group-level autocorrelation curves in humans: In line with previous work⁸, we found that
3189 the probability of stimulus-congruence was not independent across successive trials: At
3190 the group level, stimulus-congruent perceptual choices were significantly autocorrelated
3191 for up to 15 trials (Figure 2B), controlling for task difficulty and the sequence of presented
3192 stimuli (Supplemental Figure 2A-B). (...) In close analogy to stimulus-congruence, we
3193 found history-congruence to be significantly autocorrelated for up to 21 trials (Figure 2B),
3194 while controlling for task difficulty and the sequence of presented stimuli (Supplemental
3195 Figure 2A-B).

- 3196 • Group-level autocorrelation curves in mice: At the group level, we found significant auto-
 3197 correlations in both stimulus-congruence (42 consecutive trials) and history-congruence
 3198 (8 consecutive trials (Figure 3B), while controlling for the respective autocorrelation of
 3199 task difficulty and external stimulation (Supplemental Figure 2C-D).
- 3200 • Correlation between stimulus- and history-congruence in humans: When perceptual
 3201 choices were less biased toward external information, participants relied more strongly
 3202 on internal information acquired from perceptual history (and vice versa, $\beta = -0.05 \pm$
 3203 5.63×10^{-4} , $T(2.1 \times 10^6) = -84.21$, $p < 2.2 \times 10^{-308}$, **controlling for fluctuations in**
 3204 **general response biases**; Supplemental Section 9.2).
- 3205 • Correlation between stimulus- and history-congruence in mice: Fluctuations in the
 3206 strength of history-congruent biases had a significant effect on stimulus-congruence (β_1
 3207 $= -0.12 \pm 7.17 \times 10^{-4}$, $T(1.34 \times 10^6) = -168.39$, $p < 2.2 \times 10^{-308}$) beyond the effect
 3208 of ongoing changes in general response biases ($\beta_2 = -0.03 \pm 6.94 \times 10^{-4}$, $T(1.34 \times 10^6)$
 3209 $= -48.14$, $p < 2.2 \times 10^{-308}$).

3210 10.3.8 Comment 8

3211 The central empirical finding is potentially important but is currently shadowed by more
 3212 speculative sections/ discussions. For instance, the section on the adaptive merits of the
 3213 computational model is relatively weaker compared to the empirical results. In particular,
 3214 the model is simulated without feedback (whereas most experiments employ trial by trial
 3215 feedback) and does not outperform the baseline model in accuracy but in other secondary
 3216 metrics.

3217 **We agree with the Reviewer (see also a similar suggestion by Reviewer 1 in**
 3218 **Comment 9). We have removed the section 5.8 and the associated subsection of**
 3219 **the discussion from our manuscript. We will develop a model on the potential**
 3220 **function of between-mode fluctuations in a separate publication.**

3221 **Minor comments:**

3222 **10.3.9 Comment 9**

3223 **The amount of statistical analysis and results is often overwhelming. The authors
3224 could streamline the presentation better such that the main result is brought to
3225 the foreground. Currently the manuscript resembles a technical report.**

3226 We apologize for this. From the Results, we have moved a number of sections to the
3227 Supplemental Materials to stream-line the manuscript (i.e., our analysis of general response
3228 biases [former section 5.4], the analysis of psychometric functions [former section 5.5], and
3229 the respective paragraphs on the IBL database). From the Discussion, we have removed the
3230 section on self-organized criticality (also following the suggestion of Reviewer 1). We have
3231 also moved more peripheral statistical results to the figure legends and the method section:

3232 • We have moved the statistics on exponential decay in the autocorrelation to the figure
3233 legends of Figure 2B and 3B.

3234 • We have shortened the description of logistic regression models that predict the stimulus-
3235 and history-congruence at the index trial from the stimulus- and history-congruence at
3236 the preceding trials.

3237 • The section on mouse behavior now matches the logic and presentation of results in the
3238 human section.

3239 We hope that these changes will increase the readability of our manuscript.

3240 **10.3.10 Comment 10**

3241 **Some typos or omissions may alter the meaning in various places. Indicatively,
3242 in lines 273, 439, 649.**

3243 Thanks a lot, we have corrected these typos.

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