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Bimodal Inference in Humans and Mice

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¹ 2 Abstract

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

¹⁴ 3 One sentence summary

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

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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 lapses and threshold, and no change in bias. In line with our prediction, we
²⁴⁹ found that internal mode processing was associated with a history-dependent
²⁵⁰ increase in bias and lapse as well as a history-independent increase in threshold
²⁵¹ (Supplemental Section 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 longer exposure to the experiments of the Confidence database, the frequency of
²⁵⁹ history-congruent choices increased over time, speaking against the proposition
²⁶⁰ that participants stereotypically repeat preceding choices when not yet familiar
²⁶¹ with the experimental task (Supplemental Section 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 task*²¹, 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 , p and ζ (see

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

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

414 Model M2 ($AIC_2 = 9.76 \times 10^4$ in humans and 4.91×10^4 in mice) and Model M3
415 ($AIC_3 = 1.19 \times 10^5$ in humans and 5.95×10^4 in mice) incorporated only oscillations
416 of either likelihood or prior precision. Model M4 ($AIC_4 = 1.69 \times 10^5$ in humans
417 and 9.12×10^4 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 ($AIC_4 = 2.01 \times 10^5$ in humans and 1.13×10^5 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 ($AIC_1 = 8.16 \times 10^4$ in humans and 4.24×10^4 in mice) and was clearly superior to
424 the normative Bayesian model of evidence accumulation ($\delta_{AIC} = -8.79 \times 10^4$ in
425 humans and -4.87×10^4 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 **We hypothesized that observers have certain hyperpriors that are apt for ac-**
543 **commodating fluctuations in the predictability of their environment, i.e., people**
544 **believe that their world is inherently volatile. To be Bayes optimal, it is therefore**
545 **necessary to periodically re-evaluate posterior beliefs about the parameters that**
546 **define an internal generative model of the external sensory environment. One**
547 **way to do this is to periodically suspend the precision of prior beliefs and increase**
548 **the precision afforded to sensory evidence, thus updating Bayesian beliefs about**
549 **model parameters.**

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

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

563 **6.2 Bimodal inference versus normative Bayesian evidence accu-**
564 **mulation**

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

581 While it is thus clear that the impact of perceptual history and sensory evidence
582 are anti-correlated *at each individual trial*, we here introduce anti-phase oscilla-

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

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

605 **6.3 Task engagement and residual motor activation as alternative
606 explanations for bimodal inference**

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

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

626 **Outside of the predictive processing field, attention is often understood in the**
627 **context of task engagement⁶³,** which varies according to the availability of cognitive
628 resources that are modulated by factors such as tonic arousal, familiarity with
629 the task, or fatigue⁶³. Our results suggest that internal mode processing cannot
630 be completely reduced to intervals of low task engagement: In addition to shorter

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

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

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

654 Residual activation of the motor system may provide another contribution to
655 serial biases in perceptual choices⁷². Such motor-driven priming may lead to
656 errors in randomized psychophysical designs, resembling the phenomenon that

657 we identify as internally-biased processing⁷³. Moreover, residual activation of the
658 motor system may lead to faster responses, and thus constitutes an alternative
659 explanation for the quadratic relationship of mode with RTs⁷². The observation
660 of elevated confidence for stronger biases toward internal mode speaks against
661 the proposition that residual activation of the motor system is the primary
662 driver of serial choice biases, since strong motor-driven priming should lead to
663 frequent lapses that are typically associated reduced confidence⁷⁴. Likewise,
664 perceptual history effects have repeatedly been replicated in experiments with
665 counter-balanced stimulus-response mappings³⁰: Feigin²⁰²¹.

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

672 6.4 Limitations and open questions

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

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

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

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

695 Second, our results point to an attraction of perception toward preceding choices.
696 Previous work has shown that perceptual decision-making is concurrently affected
697 by both attractive and repulsive serial biases that operate on distinct time-
698 scales and serve complementary functions for sensory processing^{27,75,76}: Short-
699 term attraction may serve the decoding of noisy sensory inputs and increase
700 the stability of perception, whereas long-term repulsion may enable efficient
701 encoding and sensitivity to change²⁷. In the data analyzed here, history biases
702 tended to be repetitive (Figure 2A, Figure 3A, Supplemental Figure S6 and
703 S7), and only 2 of the 66 experiments of the Confidence database²⁰ showed
704 significant alternating biases (Supplemental Figure S1). However, as we show in
705 Supplemental Figure S14, fluctuations in both alternating and repeating history
706 biases generate overlapping autocorrelation curves. Our analysis of between-
707 mode fluctuations is therefore not tied exclusively to repeating biases, but

708 accommodates alternating biases as well, such that both may lead to internally-
709 biased processing and reduced sensitivity to external sensory information. Future
710 work could apply our approach to paradigms that boost alternating as opposed
711 to repeating biases, as this would help to better understand how repetition
712 and alternation are linked in terms of their computational function and neural
713 implementation²⁷.

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

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

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

⁷³⁵ Establishing the neural correlates of externally- an internally-biased modes will enable exiting
⁷³⁶ opportunities to investigate their role for adaptive perception and decision-making: Causal
⁷³⁷ interventions via pharmacological challenges, optogenetic manipulations or (non-)invasive
⁷³⁸ brain stimulation will help to understand whether between-mode fluctuations are implicated
⁷³⁹ in resolving credit-assignment problems^{18,77} or in calibrating metacognition and reality
⁷⁴⁰ monitoring⁵⁹. Answers to these questions may provide new insights into the pathophysiology
⁷⁴¹ of hallucinations and delusions, which have been characterized by an imbalance in the impact
⁷⁴² of external versus internal information^{56,78,79} and are typically associated with metacognitive
⁷⁴³ failures and a departure from consensual reality⁷⁹.

⁷⁴⁴ **7 Methods**

⁷⁴⁵ **7.1 Resource availability**

⁷⁴⁶ **7.1.1 Lead contact**

⁷⁴⁷ Further information and requests for resources should be directed to and will be fulfilled by
⁷⁴⁸ the lead contact, Veith Weilnhammer (veith.weilnhammer@gmail.com).

⁷⁴⁹ **7.1.2 Materials availability**

⁷⁵⁰ This study did not generate new unique reagents.

⁷⁵¹ **7.1.3 Data and code availability**

⁷⁵² All custom code and behavioral data are available on <https://github.com/veithweilnhammer/>
⁷⁵³ Modes. This manuscript was created using the *R Markdown* framework, which integrates all
⁷⁵⁴ data-related computations and the formatted text within one document. With this, we wish
⁷⁵⁵ to make our approach fully transparent and reproducible for reviewers and future readers.

⁷⁵⁶ **7.2 Experimental model and subject details**

⁷⁵⁷ **7.2.1 Confidence database**

⁷⁵⁸ We downloaded the human data from the Confidence database²⁰ on 10/21/2020,
⁷⁵⁹ limiting our analyses to the category *perception*. Within this category, we
⁷⁶⁰ selected studies in which participants made binary perceptual decisions between
⁷⁶¹ two alternatives. We excluded two experiments in which the average perceptual
⁷⁶² accuracy fell below 50%. After excluding these experiments, our sample consisted
⁷⁶³ of 21.05 million trials obtained from 4317 human participants and 66 individual
⁷⁶⁴ experiments (Supplemental Table 1). Out of the 66 included experiments, 62
⁷⁶⁵ investigated visual, 1 auditory, 2 proprioceptive, and 1 multimodal perception.

⁷⁶⁶ **59 experiments were based on discrimination and 6 on detection, with one**
⁷⁶⁷ **investigating both.**

⁷⁶⁸ **7.2.2 IBL database**

⁷⁶⁹ We downloaded the data from the IBL database²¹ on 04/28/2021. We limited our analyses to
⁷⁷⁰ the *basic task*, during which mice responded to gratings that appeared with equal probability
⁷⁷¹ in the left or right hemifield. Within each mouse, we excluded sessions in which perceptual
⁷⁷² accuracy was below 80% for stimuli presented at a contrast $\geq 50\%$. After exclusion, our
⁷⁷³ sample consisted of 1.46 million trials obtained from $N = 165$ mice.

⁷⁷⁴ **7.3 Method details**

⁷⁷⁵ **7.3.1 Variables of interest**

⁷⁷⁶ **Primary variables of interest:** We extracted trial-wise data on the presented stimulus and
⁷⁷⁷ the associated perceptual decision. Stimulus-congruent choices were defined by perceptual
⁷⁷⁸ decisions that matched the presented stimuli. History-congruent choices were defined by
⁷⁷⁹ perceptual choices that matched the perceptual choice at the immediately preceding trial.
⁷⁸⁰ The dynamic probabilities of stimulus- and history-congruence were computed in sliding
⁷⁸¹ windows of ± 5 trials.

⁷⁸² The *mode* of sensory processing was derived by subtracting the dynamic probability of history-
⁷⁸³ congruence from the dynamic probability of stimulus-congruence, such that positive values
⁷⁸⁴ indicate externally-oriented processing, whereas negative values indicate internally-oriented
⁷⁸⁵ processing. When visualizing the relation of the mode of sensory processing to confidence,
⁷⁸⁶ RTs or trial duration (see below), we binned the mode variable in 10% intervals. We excluded
⁷⁸⁷ bins that contained less than 0.5% of the total number of available data-points.

⁷⁸⁸ **Secondary variables of interest:** From the Confidence Database²⁰, we furthermore
⁷⁸⁹ extracted trial-wise confidence reports and RTs. **Out of the 58 experiments that provide**

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

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

805 7.3.2 Control variables

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

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

819 **7.3.3 Autocorrelations**

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

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

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

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

845 **7.3.4 Spectral analysis**

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

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

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

863 **7.4 Quantification and statistical procedures**

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

866 **7.4.1 Mixed effects modeling**

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

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

884 **7.4.2 Psychometric function**

885 We obtained psychometric curves by fitting the following error function to the behavioral
886 data:

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

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

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

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

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

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

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

7.4.3 Computational modeling

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

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

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

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

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

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

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

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

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

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

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

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

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

924 To allow for long-range autocorrelation in stimulus- and history-congruence (Figure 2B and
 925 3B), our modeling approach differed from Glaze et al.⁵¹ in that it allowed for systematic
 926 fluctuation in the impact of sensory information (i.e., LLR) and the prior probability
 927 of choices ψ on the posterior probability L . This was achieved by multiplying the log
 928 likelihood ratio and the log prior ratio with coherent anti-phase fluctuations according to
 929 $\omega_{LLR} = a_{LLR} * \sin(f * t + phase) + 1$ and $\omega_\psi = a_\psi * \sin(f * t + phase + \pi) + 1$.

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

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

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

943 (lower bound = 1, upper bound = 10; human posterior = $4.63 \pm 1.95 \times 10^{-4}$; mouse posterior
944 = $4.82 \pm 3.03 \times 10^{-3}$) using maximum likelihood estimation with the Broyden–Fletcher–
945 Goldfarb–Shanno algorithm as implemented in the R-function *optimx*⁸⁰ (see Supplemental
946 **Table T2** for a description of our model parameters).

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

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

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

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

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

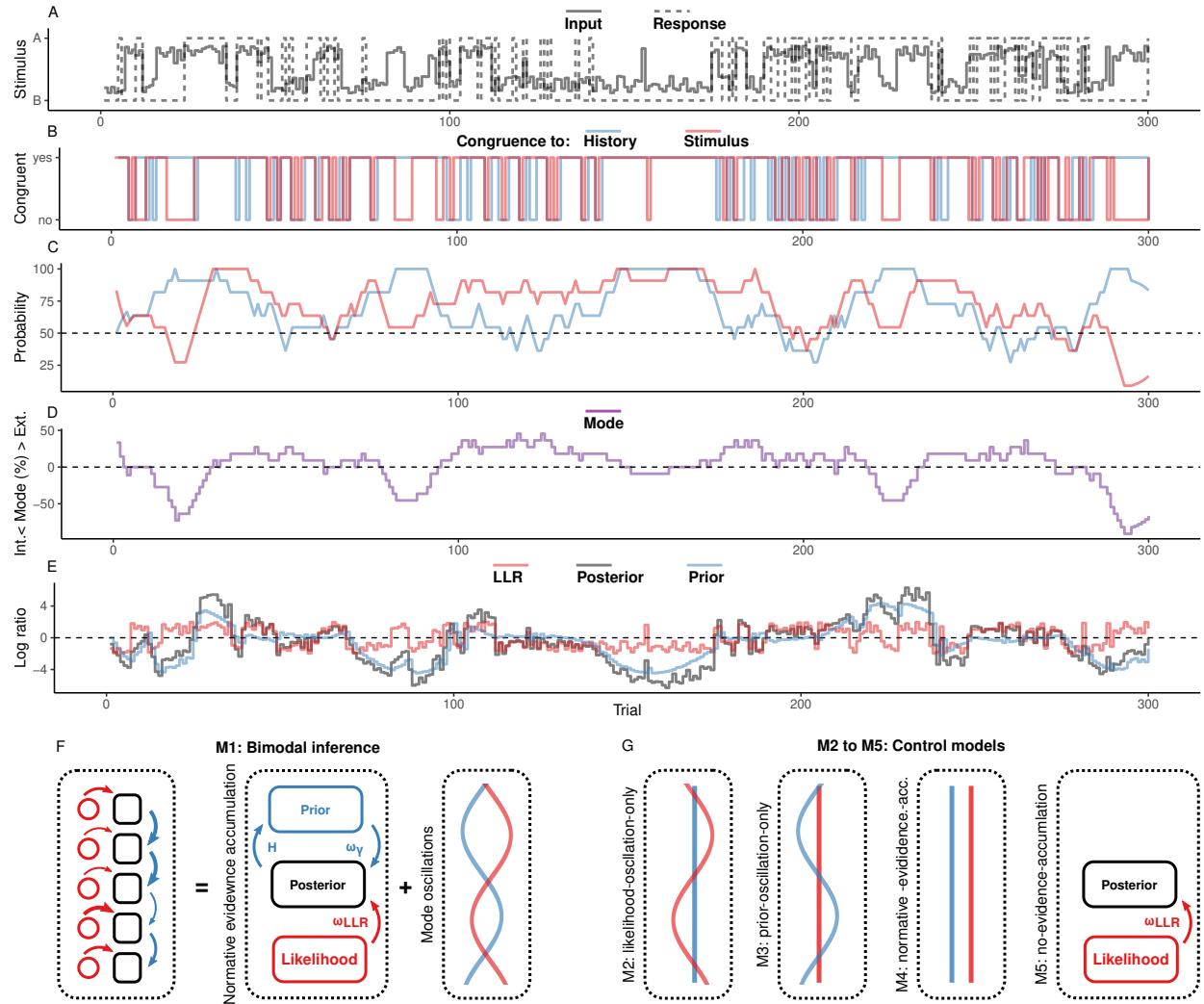
985 Prediction of within-training and out-of-training variables. To validate our model,
986 we correlated individual posterior parameter estimates with the respective con-
987 ventional variables. As a sanity check, we tested (i), whether the estimated hazard
988 rate H correlated negatively with the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

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

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

1012 **8 Figures**

1013 **8.1 Figure 1**



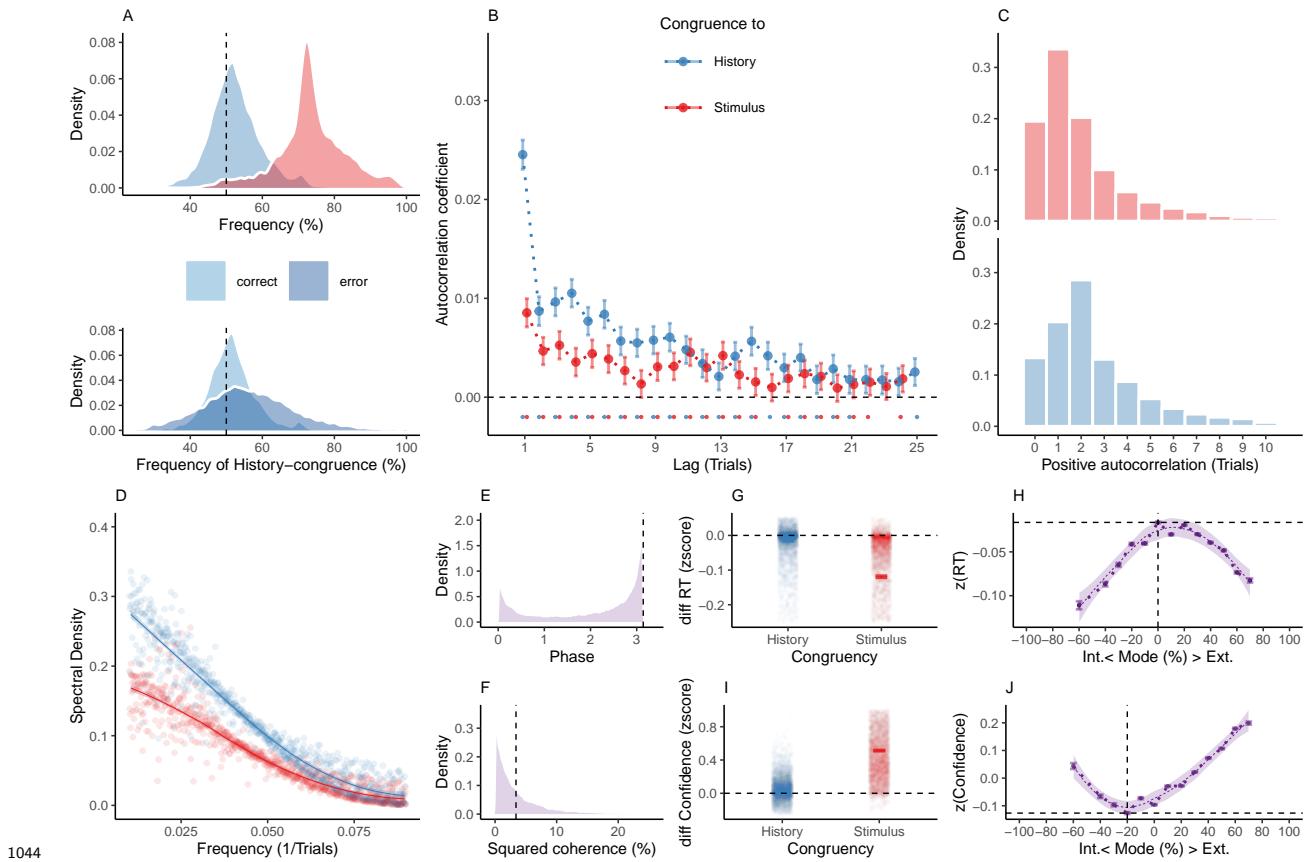
1014 **Figure 1. Concept.**

1015 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.

1016 B. When the response matches the external stimulus information (i.e., overlap between dotted 1017 and solid line in panel A), perceptual choices are *stimulus-congruent* (red line). When the 1018 response matches the response at the preceding trial, perceptual choices are *history-congruent*

- 1022 (blue line).
- 1023 C. The dynamic probabilities of stimulus- and history-congruence (i.e., computed in sliding
1024 windows of ± 5 trials) fluctuate over time.
- 1025 D. The *mode* of perceptual processing is derived by computing the difference between the
1026 dynamic probabilities of stimulus- and history-congruence. Values above 0% indicate a
1027 bias toward external information, whereas values below 0% indicate a bias toward internal
1028 information.
- 1029 E. In computational modeling, internal mode is caused by an enhanced impact of perceptual
1030 history. This causes the posterior (black line) to be close to the prior (blue line). Conversely,
1031 during external mode, the posterior is close to the sensory information (log likelihood ratio,
1032 red line).
- 1033 F. The bimodal inference model (M1) explains fluctuations between externally-
1034 and externally-biased modes (left panel) by two interacting factors: a normative
1035 accumulation of evidence according to parameters H (middle panel), and anti-
1036 phase oscillations in the precision terms ω_{LLR} and ω_ψ (right panel).
- 1037 G. The control models M2-M5 were constructed by successively removing the anti-
1038 phase oscillations and the integration of information from the bimodal inference
1039 model. Please note that the normative-evidence-accumulation-model (M4) corre-
1040 sponds to the model proposed by Glaze et al.⁵¹. In the no-evidence-accumulation
1041 model (M5), perceptual decisions depend only on likelihood information (flat
1042 priors).

1043 **8.2 Figure 2**



1044 **Figure 2. Internal and external modes in human perceptual decision-making.**

1045 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.

1046 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 $\gamma = -1.92 \times 10^{-3} \pm 4.5 \times 10^{-4}$ ($T(6.88 \times 10^4)$)

₁₀₅₇ $= -4.27$, $p = 1.98 \times 10^{-5}$) for stimulus-congruence and at a rate of $\gamma = -6.11 \times 10^{-3} \pm$
₁₀₅₈ 5.69×10^{-4} ($T(6.75 \times 10^4) = -10.74$, $p = 7.18 \times 10^{-27}$) for history-congruence.

₁₀₅₉ C. Here, we depict the number of consecutive trials at which autocorrelation coefficients
₁₀₆₀ exceeded the respective autocorrelation of randomly permuted data within individual partici-
₁₀₆₁ pants. For stimulus-congruence (upper panel), the lag of positive autocorrelation amounted
₁₀₆₂ to $3.24 \pm 2.39 \times 10^{-3}$ on average, showing a peak at trial $t+1$ after the index trial. For
₁₀₆₃ history-congruence (lower panel), the lag of positive autocorrelation amounted to $4.87 \pm$
₁₀₆₄ 3.36×10^{-3} on average, peaking at trial $t+2$ after the index trial.

₁₀₆₅ D. The smoothed probabilities of stimulus- and history-congruence (sliding windows of ± 5
₁₀₆₆ trials) fluctuated as a **scale-invariant process with a 1/f power law**, i.e., at power
₁₀₆₇ densities that were inversely proportional to the frequency.

₁₀₆₈ E. The distribution of phase shift between fluctuations in stimulus- and history-congruence
₁₀₆₉ peaked at half a cycle (π denoted by dotted line).

₁₀₇₀ F. The average squared coherence between fluctuations in stimulus- and history-congruence
₁₀₇₁ (black dotted line) amounted to $6.49 \pm 2.07 \times 10^{-3}\%$

₁₀₇₂ G. We observed faster RTs for both stimulus-congruence (as opposed to stimulus-incongruence,
₁₀₇₃ $\beta = -0.14 \pm 1.6 \times 10^{-3}$, $T(1.99 \times 10^6) = -85.84$, $p < 2.2 \times 10^{-308}$) and history-congruence
₁₀₇₄ ($\beta = -9.56 \times 10^{-3} \pm 1.37 \times 10^{-3}$, $T(1.98 \times 10^6) = -6.97$, $p = 3.15 \times 10^{-12}$).

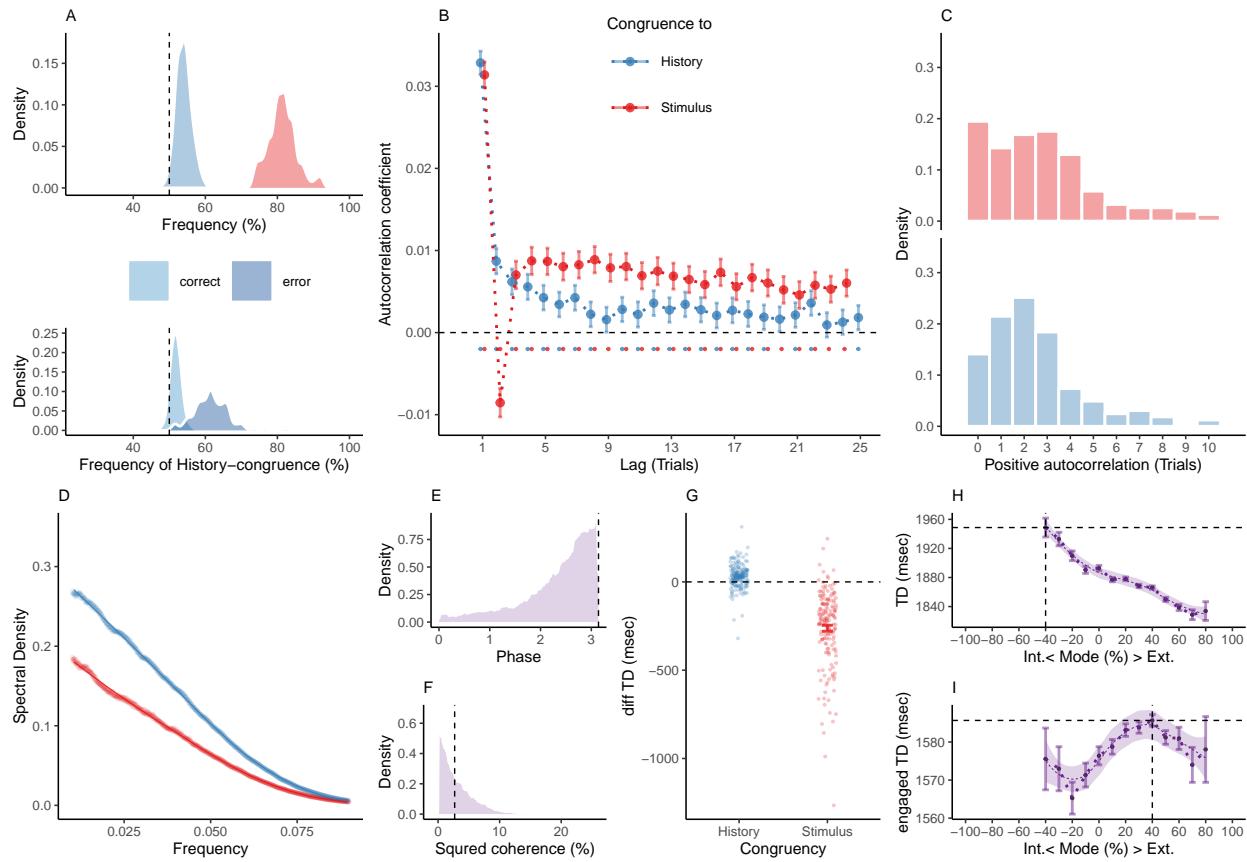
₁₀₇₅ H. The mode of perceptual processing (i.e., the difference between the smoothed probability
₁₀₇₆ of stimulus- vs. history-congruence) showed a quadratic relationship to RTs, with faster
₁₀₇₇ RTs for stronger biases toward both external sensory information and internal predictions
₁₀₇₈ provided by perceptual history ($\beta_2 = -19.86 \pm 0.52$, $T(1.98 \times 10^6) = -38.43$, $p = 5 \times 10^{-323}$).
₁₀₇₉ The horizontal and vertical dotted lines indicate maximum RT and the associated mode,
₁₀₈₀ respectively.

₁₀₈₁ I. Confidence was enhanced for both stimulus-congruence (as opposed to stimulus-

₁₀₈₂ 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
₁₀₈₃ history-congruence ($\beta = 0.04 \pm 1.18 \times 10^{-3}$, $T(2.06 \times 10^6) = 36.85$, $p = 3.25 \times 10^{-297}$).

₁₀₈₄ J. In analogy to RTs, we found a quadratic relationship between the mode of perceptual
₁₀₈₅ processing and confidence, which increased when both externally- and internally-biased modes
₁₀₈₆ 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
₁₀₈₇ and vertical dotted lines indicate minimum confidence and the associated mode, respectively.

1088 **8.3 Figure 3**



1089 **Figure 3. Internal and external modes in mouse perceptual decision-making.**

1090 A. In mice, $81.37\% \pm 0.3\%$ of trials were stimulus-congruent (in red) and $54.03\% \pm 0.17\%$ of trials were history-congruent (in blue; upper panel). History-congruent perceptual choices were not a consequence of the experimental design, but a source of error, as they were more frequent on stimulus-incongruent trials (lower panel).

1091 B. Relative to randomly permuted data, we found highly significant autocorrelations of stimulus-congruence and history-congruence (dots indicate intercepts $\neq 0$ in trial-wise linear mixed effects modeling at $p < 0.05$). Please note that the negative autocorrelation of stimulus-congruence at trial 2 was a consequence of the experimental design (Supplemental Figure 2D-F). As in humans, autocorrelation coefficients were best fit by an exponential function (adjusted R^2 for stimulus-congruence: 0.44; history-congruence: 0.52) as compared to a linear function (adjusted R^2 for stimulus-congruence: 3.16×10^{-3} ; history-congruence:

₁₁₀₂ 0.26), decaying at a rate of $\gamma = -6.2 \times 10^{-4} \pm 5.93 \times 10^{-4}$ ($T(3.55 \times 10^4) = -1.05$, $p = 0.3$)
₁₁₀₃ for stimulus-congruence and at a rate of $\gamma = -6.7 \times 10^{-3} \pm 5.94 \times 10^{-4}$ ($T(3.69 \times 10^4) =$
₁₁₀₄ -11.27 , $p = 2.07 \times 10^{-29}$) for history-congruence.

₁₁₀₅ C. For stimulus-congruence (upper panel), the lag of positive autocorrelation was longer in
₁₁₀₆ comparison to humans (4.59 ± 0.06 on average). For history-congruence (lower panel), the
₁₁₀₇ lag of positive autocorrelation was slightly shorter relative to humans (2.58 ± 0.01 on average,
₁₁₀₈ peaking at trial $t+2$ after the index trial).

₁₁₀₉ D. In mice, the dynamic probabilities of stimulus- and history-congruence (sliding windows
₁₁₁₀ of ± 5 trials) fluctuated as **a scale-invariant process with a 1/f power law**.

₁₁₁₁ E. The distribution of phase shift between fluctuations in stimulus- and history-congruence
₁₁₁₂ peaked at half a cycle (π denoted by dotted line).

₁₁₁₃ F. The average squared coherence between fluctuations in stimulus- and history-congruence
₁₁₁₄ (black dotted line) amounted to $3.45 \pm 0.01\%$.

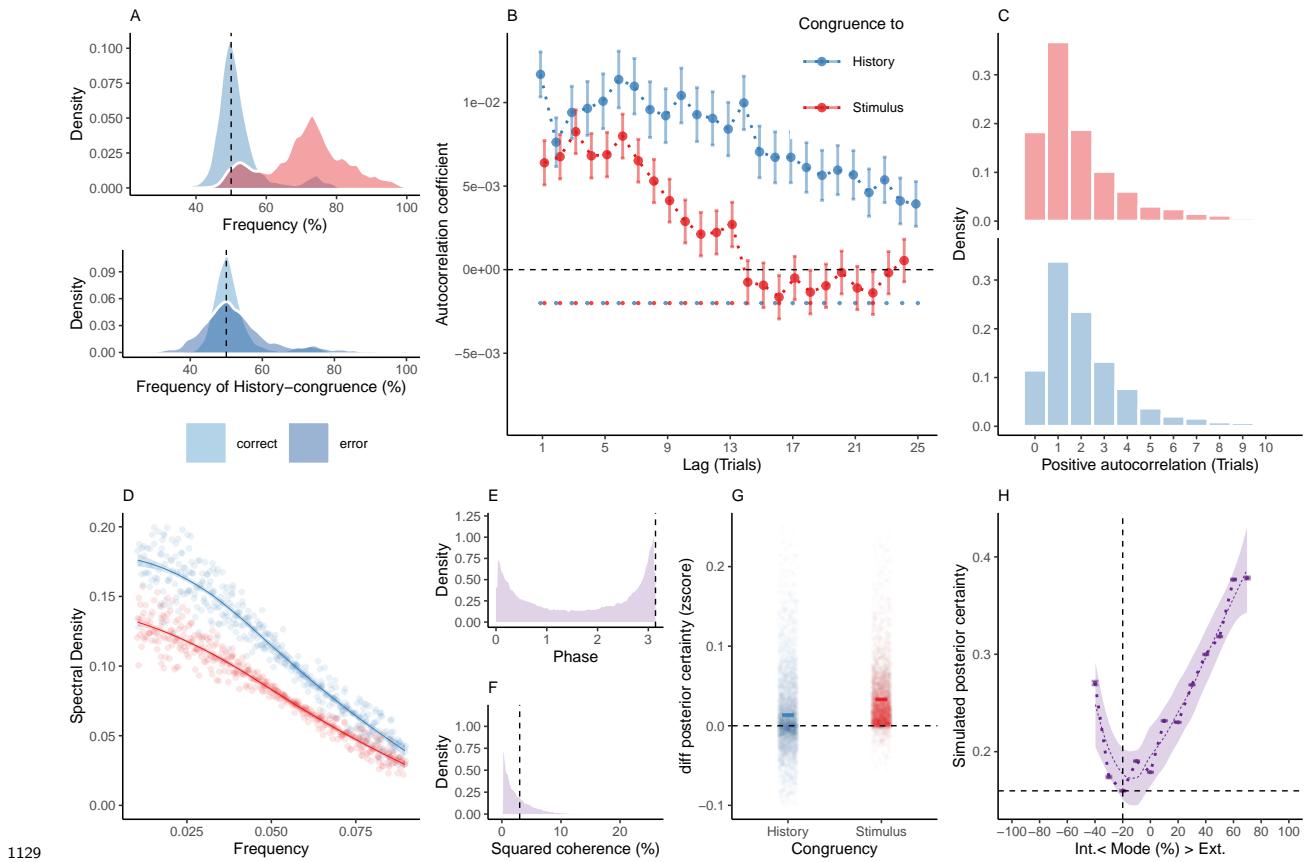
₁₁₁₅ G. We observed shorter trial durations (TDs) for stimulus-congruence (as opposed to stimulus-
₁₁₁₆ incongruence, $\beta = -1.12 \pm 8.53 \times 10^{-3}$, $T(1.34 \times 10^6) = -131.78$, $p < 2.2 \times 10^{-308}$), but
₁₁₁₇ longer TDs for history-congruence ($\beta = 0.06 \pm 6.76 \times 10^{-3}$, $T(1.34 \times 10^6) = 8.52$, $p =$
₁₁₁₈ 1.58×10^{-17}).

₁₁₁₉ H. TDs decreased monotonically for stronger biases toward external mode ($\beta_1 = -4.16 \times 10^4$
₁₁₂₀ $\pm 1.29 \times 10^3$, $T(1.35 \times 10^6) = -32.31$, $p = 6.03 \times 10^{-229}$). The horizontal and vertical dotted
₁₁₂₁ lines indicate maximum TD and the associated mode, respectively.

₁₁₂₂ I. For TDs that differed from the median TD by no more than $1.5 \times \text{MAD}$ (median absolute
₁₁₂₃ distance⁴⁹), mice exhibited a quadratic component in the relationship between the mode of
₁₁₂₄ sensory processing and TDs ($\beta_2 = -1.97 \times 10^3 \pm 843.74$, $T(1.19 \times 10^6) = -2.34$, $p = 0.02$).
₁₁₂₅ This explorative post-hoc analysis focuses on trials at which mice engage more swiftly with
₁₁₂₆ the experimental task. The horizontal and vertical dotted lines indicate maximum TD and

₁₁₂₇ the associated mode, respectively.

1128 **8.4 Figure 4**



1129 **Figure 4. Internal and external modes in simulated perceptual decision-making.**

1130 A. Simulated perceptual choices were stimulus-congruent in $71.36\% \pm 0.17\%$ (in red) and
 1131 history-congruent in $51.99\% \pm 0.11\%$ of trials (in blue; $T(4.32 \times 10^3) = 17.42$, $p = 9.89 \times 10^{-66}$;
 1132 upper panel). Due to the competition between stimulus- and history-congruence, history-
 1133 congruent perceptual choices were more frequent when perception was stimulus-incongruent
 1134 (i.e., on *error* trials; $T(4.32 \times 10^3) = 11.19$, $p = 1.17 \times 10^{-28}$; lower panel) and thus impaired
 1135 performance in the randomized psychophysical design simulated here.

1136
 1137 B. At the simulated group level, we found significant autocorrelations in both stimulus-
 1138 congruence (13 consecutive trials) and history-congruence (30 consecutive trials).

1139 C. On the level of individual simulated participants, autocorrelation coefficients exceeded the
 1140 autocorrelation coefficients of randomly permuted data within a lag of $2.46 \pm 1.17 \times 10^{-3}$

₁₁₄₁ trials for stimulus-congruence and $4.24 \pm 1.85 \times 10^{-3}$ trials for history-congruence.

₁₁₄₂ D. The smoothed probabilities of stimulus- and history-congruence (sliding windows of ± 5
₁₁₄₃ trials) fluctuated as a **scale-invariant process with a $1/f$ power law**, i.e., at power
₁₁₄₄ densities that were inversely proportional to the frequency (power $\sim 1/f^\beta$; stimulus-congruence:
₁₁₄₅ $\beta = -0.81 \pm 1.18 \times 10^{-3}$, $T(1.92 \times 10^5) = -687.58$, $p < 2.2 \times 10^{-308}$; history-congruence: β
₁₁₄₆ $= -0.83 \pm 1.27 \times 10^{-3}$, $T(1.92 \times 10^5) = -652.11$, $p < 2.2 \times 10^{-308}$).

₁₁₄₇ E. The distribution of phase shift between fluctuations in simulated stimulus- and history-
₁₁₄₈ congruence peaked at half a cycle (π denoted by dotted line). The dynamic probabilities of
₁₁₄₉ simulated stimulus- and history-congruence were therefore were strongly anti-correlated ($\beta =$
₁₁₅₀ $-0.03 \pm 8.22 \times 10^{-4}$, $T(2.12 \times 10^6) = -40.52$, $p < 2.2 \times 10^{-308}$).

₁₁₅₁ F. The average squared coherence between fluctuations in simulated stimulus- and history-
₁₁₅₂ congruence (black dotted line) amounted to $6.49 \pm 2.07 \times 10^{-3}\%$.

₁₁₅₃ G. Simulated confidence was enhanced for stimulus-congruence ($\beta = 0.03 \pm 1.71 \times 10^{-4}$,
₁₁₅₄ $T(2.03 \times 10^6) = 178.39$, $p < 2.2 \times 10^{-308}$) and history-congruence ($\beta = 0.01 \pm 1.5 \times 10^{-4}$,
₁₁₅₅ $T(2.03 \times 10^6) = 74.18$, $p < 2.2 \times 10^{-308}$).

₁₁₅₆ H. In analogy to humans, the simulated data showed a quadratic relationship between the
₁₁₅₇ mode of perceptual processing and posterior certainty, which increased for stronger external
₁₁₅₈ and internal biases ($\beta_2 = 31.03 \pm 0.15$, $T(2.04 \times 10^6) = 205.95$, $p < 2.2 \times 10^{-308}$). The
₁₁₅₉ horizontal and vertical dotted lines indicate minimum posterior certainty and the associated
₁₁₆₀ mode, respectively.

1161 **9 Supplemental Items**

1162 **9.1 Internal mode processing is driven by choice history as opposed
1163 to stimulus history**

1164 The main manuscript reports the effects of perceptual history, which we defined
1165 as the impact of the choice at the preceding trial on the choice at the current trial
1166 (henceforth *choice history*). *Stimulus history*, which is defined as the impact of
1167 the stimulus presented at the preceding trial on the choice at the present trial,
1168 represents an alternative approach to this. Here, we compare the effects of choice
1169 history to the effects of stimulus history.

1170 We observed a significant bias toward stimulus history (humans: $49.76\% \pm 0.1\%$
1171 of trials, $\beta = 1.26 \pm 0.94$, $T(373.62) = 1.34$, $p = 0.18$; mice: $51.11\% \pm 0.08\%$ of
1172 trials, $T(164) = 13.4$, $p = 3.86 \times 10^{-28}$). The bias toward stimulus history was
1173 smaller than the bias toward choice history (humans: $\beta = -3.53 \pm 0.5$, $T(66.53)$
1174 $= -7.01$, $p = 1.48 \times 10^{-9}$; mice: $T(164) = -17.21$, $p = 1.43 \times 10^{-38}$).

1175 The attraction of choices toward both preceding choices and stimuli is expected,
1176 as perception was *stimulus-congruent* on approximately 75% of trials, causing
1177 choices and stimuli to be highly correlated. We therefore compared the effects
1178 of choice history and stimulus history after *stimulus-incongruent* (i.e., *error*)
1179 trials, since those trials lead to opposite predictions regarding the perceptual
1180 choice at the subsequent trial.

1181 As expected from the findings presented in the main manuscript, perceptual
1182 choices were attracted toward perceptual choices when the inducing trial was
1183 stimulus-incongruent (i.e., a positive effect of choice history; humans: $\beta = 0.19 \pm$
1184 1.4×10^{-4} , $z = 1.36 \times 10^3$, $p < 2.2 \times 10^{-308}$; mice: $\beta = 0.92 \pm 0.01$, $z = 88.82$, $p <$
1185 2.2×10^{-308}). By contrast, perceptual choices tended to be repelled away from

1186 the stimulus presented at preceding stimulus-incongruent trial (i.e., a negative
1187 effect of stimulus history; humans: $\beta = -0.19 \pm 0.01$, $z = -16.47$, $p = 5.99 \times 10^{-61}$:
1188 mice: $\beta = -0.92 \pm 0.01$, $z = -88.76$, $p < 2.2 \times 10^{-308}$). This repulsion of choices
1189 away from stimuli presented at stimulus-incongruent trials confirmed that choices
1190 (which are anti-correlated to stimuli at stimulus-incongruent trials) were the
1191 primary driver of attracting serial effects in perception.

1192 In sum, the above results suggest that, in both humans and mice, serial depen-
1193 dencies were better explained by the effects of choice history as opposed to the
1194 effects of stimulus history. This aligns with a result recently published for the
1195 IBL database, where mice were shown to follow an *action-kernel* as opposed to a
1196 *stimulus-kernel* model when integrating information across trials⁸¹.

1197 9.2 Fluctuations between internal and external mode modulate 1198 perceptual performance beyond the effect of general response 1199 biases

1200 The hypothesis that perception cycles through opposing internally- and externally-biased
1201 modes is motivated by the assumption that recurring intervals of stronger perceptual history
1202 temporally reduce the participants' sensitivity to external information. Importantly, the
1203 history-dependent biases that characterize internal mode processing must be differentiated
1204 from general response biases. In binary perceptual decision-making, general response biases
1205 are defined by a propensity to choose one of the two outcomes more often than the alternative.
1206 Indeed, human participants selected the more frequent of the two possible outcomes in 58.71%
1207 $\pm 0.22\%$ of trials, and mice selected the more frequent of the two possible outcomes in 54.6%
1208 $\pm 0.3\%$ of trials.

1209 Two caveats have to be considered to make sure that the effect of history-congruence is
1210 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

1237 that, in both humans and mice, the observed influence of preceding choices on perceptual
1238 decision-making cannot be reduced to general response biases.

1239 **9.3 Internal mode is characterized by lower thresholds as well as**
1240 **by history-dependent changes in biases and lapses**

1241 Random or stereotypical responses may provide an alternative explanation for the reduced
1242 sensitivity to external sensory information that we attribute to internal mode processing. To
1243 test this hypothesis, we asked whether history-independent changes in biases and lapses may
1244 provide an alternative explanation of the reduced sensitivity during internal mode.

1245 To this end, we estimated full and history-conditioned psychometric curves to investigate how
1246 internal and external mode relate to biases (i.e., the horizontal position of the psychometric
1247 curve), lapses (i.e., the asymptotes of the psychometric curve) and thresholds (i.e., 1/sensitivity,
1248 estimated from the slope of the psychometric curve). We used a maximum likelihood procedure
1249 to predict trial-wise choices y ($y = 0$ and $y = 1$ for outcomes A and B respectively) from
1250 the choice probabilities y_p . y_p was computed from the difficulty-weighted inputs s_w via a
1251 parametric error function defined by the parameters γ (lower lapse), δ (upper lapse), μ (bias)
1252 and t (threshold; see Methods for details):

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

1253 Under our main hypothesis that periodic reductions in sensitivity to external information
1254 are driven by increases in the impact of perceptual history, one would expect (i) a history-
1255 dependent increase in biases and lapses (effects of perceptual history), and (ii), a history-
1256 independent increase in threshold (reduced sensitivity to external information). Conversely,
1257 if what we identified as internal mode processing was in fact driven by random choices, one
1258 would expect (i), a history-independent increase in lapses (choice randomness), (ii), no change

1259 in bias (no effect of perceptual history), and (iii), reduced thresholds (reduced sensitivity to
1260 external information).

1261 **9.3.1 Humans**

1262 Across all data provided by the Confidence database²⁰ (i.e., irrespective of the preceding
1263 perceptual choice y_{t-1}), biases μ were distributed around zero (-0.05 ± 0.03 ; $\beta_0 = 7.37 \times 10^{-3}$
1264 ± 0.09 , $T(36.8) = 0.08$, $p = 0.94$; Supplemental Figure 6A-B, upper panel). When conditioned
1265 on perceptual history, biases μ varied according to the preceding perceptual choice, with
1266 negative biases for $y_{t-1} = 0$ (-0.22 ± 0.04 ; $\beta_0 = 0.56 \pm 0.12$, $T(43.39) = 4.6$, $p = 3.64 \times 10^{-5}$;
1267 Supplemental Figure 6A-B, upper panel) and positive biases for $y_{t-1} = 1$ (0.29 ± 0.03 ; β_0
1268 $= 0.56 \pm 0.12$, $T(43.39) = 4.6$, $p = 3.64 \times 10^{-5}$; Supplemental Figure 6A-B, lower panel).
1269 Absolute biases $|\mu|$ were larger in internal mode (1.84 ± 0.03) as compared to external
1270 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
1271 differences in lapses and thresholds).

1272 Lower and upper lapses amounted to $\gamma = 0.13 \pm 2.83 \times 10^{-3}$ and $\delta = 0.1 \pm 2.45 \times 10^{-3}$
1273 (Supplemental Figure 6A, C and D). Lapses were larger in internal mode ($\gamma = 0.17 \pm$
1274 3.52×10^{-3} , $\delta = 0.14 \pm 3.18 \times 10^{-3}$) as compared to external mode ($\gamma = 0.1 \pm 2.2 \times 10^{-3}$, $\delta =$
1275 $0.08 \pm 2 \times 10^{-3}$; $\beta_0 = -0.05 \pm 5.73 \times 10^{-3}$, $T(47.03) = -9.11$, $p = 5.94 \times 10^{-12}$; controlling
1276 for differences in biases and thresholds).

1277 Conditioning on the previous perceptual choice revealed that the between-mode difference in
1278 lapse was not general, but depended on perceptual history: For $y_{t-1} = 0$, only higher lapses δ
1279 differed between internal and external mode ($\beta_0 = -0.1 \pm 9.58 \times 10^{-3}$, $T(36.87) = -10.16$, p
1280 $= 3.06 \times 10^{-12}$), whereas lower lapses γ did not ($\beta_0 = 0.01 \pm 7.77 \times 10^{-3}$, $T(33.1) = 1.61$, p
1281 $= 0.12$). Vice versa, for $y_{t-1} = 1$, lower lapses γ differed between internal and external mode
1282 ($\beta_0 = -0.11 \pm 0.01$, $T(40.11) = -9.59$, $p = 6.14 \times 10^{-12}$), whereas higher lapses δ did not
1283 ($\beta_0 = 0.01 \pm 7.74 \times 10^{-3}$, $T(33.66) = 1.58$, $p = 0.12$).

1284 Thresholds t were estimated at 3 ± 0.06 (Supplemental Figure 6A and E). Thresholds t were
1285 larger in internal mode (3.66 ± 0.09) as compared to external mode (2.02 ± 0.03 ; $\beta_0 = -1.77$
1286 ± 0.25 , $T(50.45) = -7.14$, $p = 3.48 \times 10^{-9}$; controlling for differences in biases and lapses).
1287 In contrast to the bias μ and the lapse rates γ and δ , thresholds t were not modulated by
1288 perceptual history ($\beta_0 = 0.04 \pm 0.06$, $T(2.97 \times 10^3) = 0.73$, $p = 0.47$).

1289 **9.3.2 Mice**

1290 When estimated based on the full dataset provided in the IBL database²¹ (i.e., irrespective
1291 of the preceding perceptual choice y_{t-1}), biases μ were distributed around zero (3.87×10^{-3}
1292 $\pm 9.81 \times 10^{-3}$; $T(164) = 0.39$, $p = 0.69$; Supplemental Figure 7A-B, upper panel). When
1293 conditioned on the preceding perceptual choice, biases were negative for $y_{t-1} = 0$ (-0.02
1294 $\pm 8.7 \times 10^{-3}$; $T(164) = -1.99$, $p = 0.05$; Supplemental Figure 7A-B, middle panel) and
1295 positive for $y_{t-1} = 1$ ($0.02 \pm 9.63 \times 10^{-3}$; $T(164) = 1.91$, $p = 0.06$; Supplemental Figure
1296 7A-B, lower panel). As in humans, mice showed larger biases during internal mode (0.14
1297 $\pm 7.96 \times 10^{-3}$) as compared to external mode ($0.07 \pm 8.7 \times 10^{-3}$; $\beta_0 = -0.18 \pm 0.03$, $T =$
1298 -6.38 , $p = 1.77 \times 10^{-9}$; controlling for differences in lapses and thresholds).

1299 Lower and upper lapses amounted to $\gamma = 0.1 \pm 4.35 \times 10^{-3}$ and $\delta = 0.11 \pm 4.65 \times 10^{-3}$
1300 (Supplemental Figure 7A, C and D). Lapse rates were higher in internal mode ($\gamma = 0.15 \pm$
1301 5.14×10^{-3} , $\delta = 0.16 \pm 5.79 \times 10^{-3}$) as compared to external mode ($\gamma = 0.06 \pm 3.11 \times 10^{-3}$,
1302 $\delta = 0.07 \pm 3.34 \times 10^{-3}$; $\beta_0 = -0.11 \pm 4.39 \times 10^{-3}$, $T = -24.8$, $p = 4.91 \times 10^{-57}$; controlling
1303 for differences in biases and thresholds).

1304 For $y_{t-1} = 0$, the difference between internal and external mode was more pronounced for
1305 higher lapses δ ($T(164) = 21.44$, $p = 1.93 \times 10^{-49}$). Conversely, for $y_{t-1} = 1$, the difference
1306 between internal and external mode was more pronounced for lower lapses γ ($T(164) =$
1307 -18.24 , $p = 2.68 \times 10^{-41}$). In contrast to the human data, higher lapses δ and lower lapses
1308 γ were significantly elevated during internal mode irrespective of the preceding perceptual
1309 choice (higher lapses δ for $y_{t-1} = 1$: $T(164) = -2.65$, $p = 8.91 \times 10^{-3}$; higher lapses δ for

₁₃₁₀ $y_{t-1} = 0$: $T(164) = -28.29$, $p = 5.62 \times 10^{-65}$; lower lapses γ for $y_{t-1} = 1$: $T(164) = -32.44$, p
₁₃₁₁ $= 2.92 \times 10^{-73}$; lower lapses γ for $y_{t-1} = 0$: $T(164) = -2.5$, $p = 0.01$.

₁₃₁₂ In mice, thresholds t amounted to $0.15 \pm 6.52 \times 10^{-3}$ (Supplemental Figure 7A and E) and
₁₃₁₃ were higher in internal mode (0.27 ± 0.01) as compared to external mode ($0.09 \pm 4.44 \times 10^{-3}$;
₁₃₁₄ $\beta_0 = -0.28 \pm 0.04$, $T = -7.26$, $p = 1.53 \times 10^{-11}$; controlling for differences in biases and
₁₃₁₅ lapses). Thresholds t were not modulated by perceptual history ($T(164) = 0.94$, $p = 0.35$).

₁₃₁₆ In sum, the above analyses showed that, in both humans and mice, internal and external
₁₃₁₇ mode differ with respect to biases, lapses and thresholds. Internally-biased processing was
₁₃₁₈ characterized by higher thresholds, indicating a reduced sensitivity to sensory information,
₁₃₁₉ as well as by larger biases and lapses. Importantly, between-mode differences in biases and
₁₃₂₀ lapses strongly depended on perceptual history. This confirmed that internal mode processing
₁₃₂₁ cannot be explained solely on the ground of a general (i.e., history-independent) increase in
₁₃₂₂ lapses or bias indicative of random or stereotypical responses.

₁₃₂₃ **9.4 Internal mode processing can not be reduced to insufficient 1324 task familiarity**

₁₃₂₅ It may be assumed that participants tend to repeat preceding choices when they are not yet
₁₃₂₆ familiar with the experimental task, leading to history-congruent choices that are caused by
₁₃₂₇ insufficient training. To assess this alternative explanation, we contrasted the correlates of
₁₃₂₈ bimodal inference with training effects in humans and mice.

₁₃₂₉ **9.4.1 Humans**

₁₃₃₀ In the Confidence database²⁰, training effects were visible from RTs that were shortened by
₁₃₃₁ 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
₁₃₃₂ $< 2.2 \times 10^{-308}$). Intriguingly, however, history-congruent choices became more frequent with
₁₃₃₃ increased exposure to the task ($\beta = 3.6 \times 10^{-5} \pm 2.54 \times 10^{-6}$, $z = 14.19$, $p = 10^{-45}$), speaking

¹³³⁴ against the proposition that insufficient training induces seriality in response behavior.

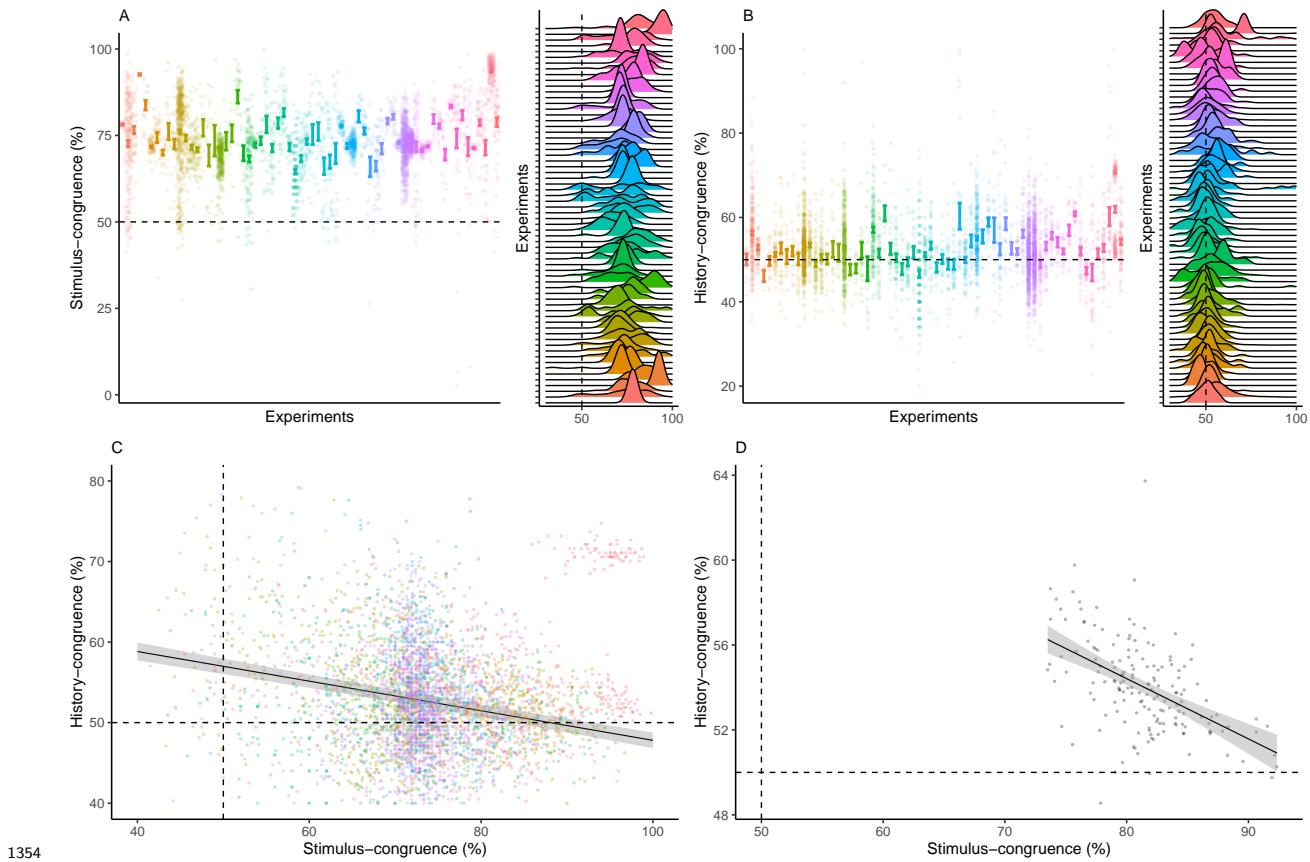
¹³³⁵ **9.4.2 Mice**

¹³³⁶ As in humans, it is an important caveat to consider whether the observed serial dependencies
¹³³⁷ in mice reflect a phenomenon of perceptual inference, or, alternatively, an unspecific strategy
¹³³⁸ that occurs at the level of reporting behavior. We reasoned that, if mice indeed tended to
¹³³⁹ repeat previous choices as a general response pattern, history effects should decrease during
¹³⁴⁰ training of the perceptual task. We therefore analyzed how stimulus- and history-congruent
¹³⁴¹ perceptual choices evolved across sessions in mice that, by the end of training, achieved
¹³⁴² proficiency (i.e., stimulus-congruence $\geq 80\%$) in the *basic* task of the IBL dataset²¹.

¹³⁴³ Across sessions, we found that stimulus-congruent perceptual choices became more frequent
¹³⁴⁴ ($\beta = 0.34 \pm 7.13 \times 10^{-3}$, $T(8.51 \times 10^3) = 47.66$, $p < 2.2 \times 10^{-308}$) and TDs were progressively
¹³⁴⁵ shortened ($\beta = -22.14 \pm 17.06$, $T(1.14 \times 10^3) = -1.3$, $p < 2.2 \times 10^{-308}$). Crucially, the
¹³⁴⁶ frequency of history-congruent perceptual choices also increased during training ($\beta = 0.13 \pm$
¹³⁴⁷ 4.67×10^{-3} , $T(8.4 \times 10^3) = 27.04$, $p = 1.96 \times 10^{-154}$; Supplemental Figure S8).

¹³⁴⁸ Within individual session, longer task exposure was associated with an increase in history-
¹³⁴⁹ 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
¹³⁵⁰ $= -0.1 \pm 3.96 \times 10^{-3}$, $T(1.34 \times 10^6) = -24.99$, $p = 9.45 \times 10^{-138}$). In sum, these findings
¹³⁵¹ strongly argue against the proposition that mice show biases toward perceptual history due
¹³⁵² to an unspecific response strategy.

1353 **9.5 Supplemental Figure S1**



1355 **Supplemental Figure S1. Stimulus- and history-congruence.**

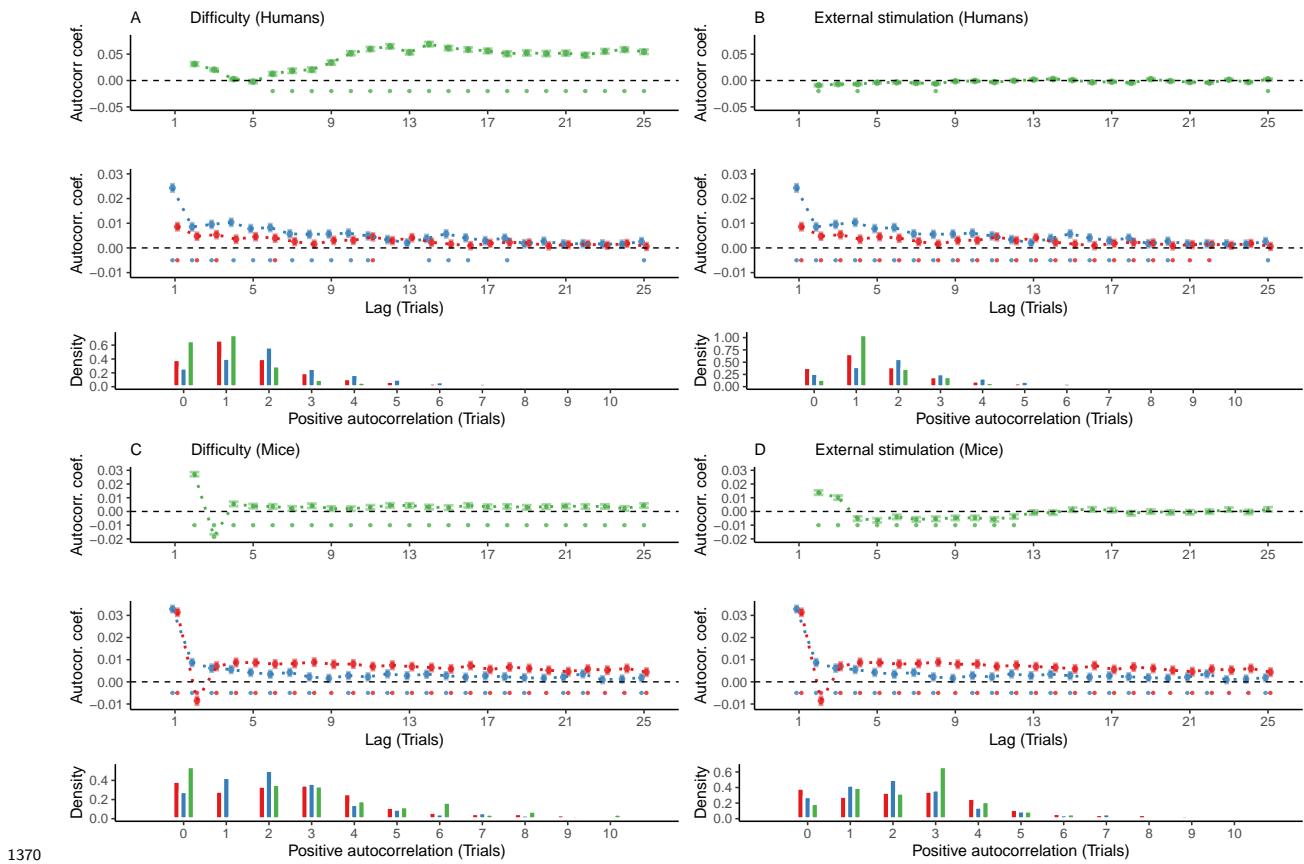
1356 A. Stimulus-congruent choices in humans amounted to $73.46\% \pm 0.15\%$ of trials and were
1357 highly consistent across the experiments selected from the Confidence Database.

1358 B. History-congruent choices in humans amounted to $52.7\% \pm 0.12\%$ of trials. In analogy
1359 to stimulus-congruence, the prevalence of history-congruence was highly consistent across
1360 the experiments selected from the Confidence Database. 48.48% of experiments showed
1361 significant ($p < 0.05$) biases toward preceding choices, whereas 2 of the 66 of the included
1362 experiments showed significant repelling biases.

1363 C. In humans, we found an enhanced impact of perceptual history in participants who were
1364 less sensitive to external sensory information ($T(4.3 \times 10^3) = -14.27$, $p = 3.78 \times 10^{-45}$),
1365 suggesting that perception results from the competition of external with internal information.

₁₃₆₆ D. In analogy to humans, mice that were less sensitive to external sensory information
₁₃₆₇ showed stronger biases toward perceptual history ($T(163) = -7.52$, $p = 3.44 \times 10^{-12}$, Pearson
₁₃₆₈ correlation).

1369 **9.6 Supplemental Figure S2**



1370

1371 **Supplemental Figure S2. Controlling for task difficulty and external stimulation.**

1372 In this study, we found highly significant autocorrelations of stimulus- and history-congruence
 1373 in humans as well as in mice, while controlling for task difficulty and the sequence of external
 1374 stimulation. **Here, we confirm that the autocorrelations of stimulus- and history-**
 1375 **congruence were not a trivial consequence of the experimental design or the**
 1376 **addition of task difficulty and external stimulation as control variables in the**
 1377 **computation of group-level autocorrelations.**

1378 A. In humans, task difficulty (in green) showed a significant autocorrelation starting at the
 1379 5th trial (upper panel, dots at the bottom indicate intercepts $\neq 0$ in trial-wise linear mixed
 1380 effects modeling at $p < 0.05$). When controlling for task difficulty only, linear mixed effects
 1381 modeling indicated a significant autocorrelation of stimulus-congruence (in red) for the first 3
 1382 consecutive trials (middle panel). 20% of trials within the displayed time window remained

1383 significantly autocorrelated. The autocorrelation of history-congruence (in blue) remained
1384 significant for the first 11 consecutive trials (64% significantly autocorrelated trials within
1385 the displayed time window). At the level of individual participants, the autocorrelation of
1386 task difficulty exceeded the respective autocorrelation of randomly permuted within a lag of
1387 $21.66 \pm 8.37 \times 10^{-3}$ trials (lower panel).

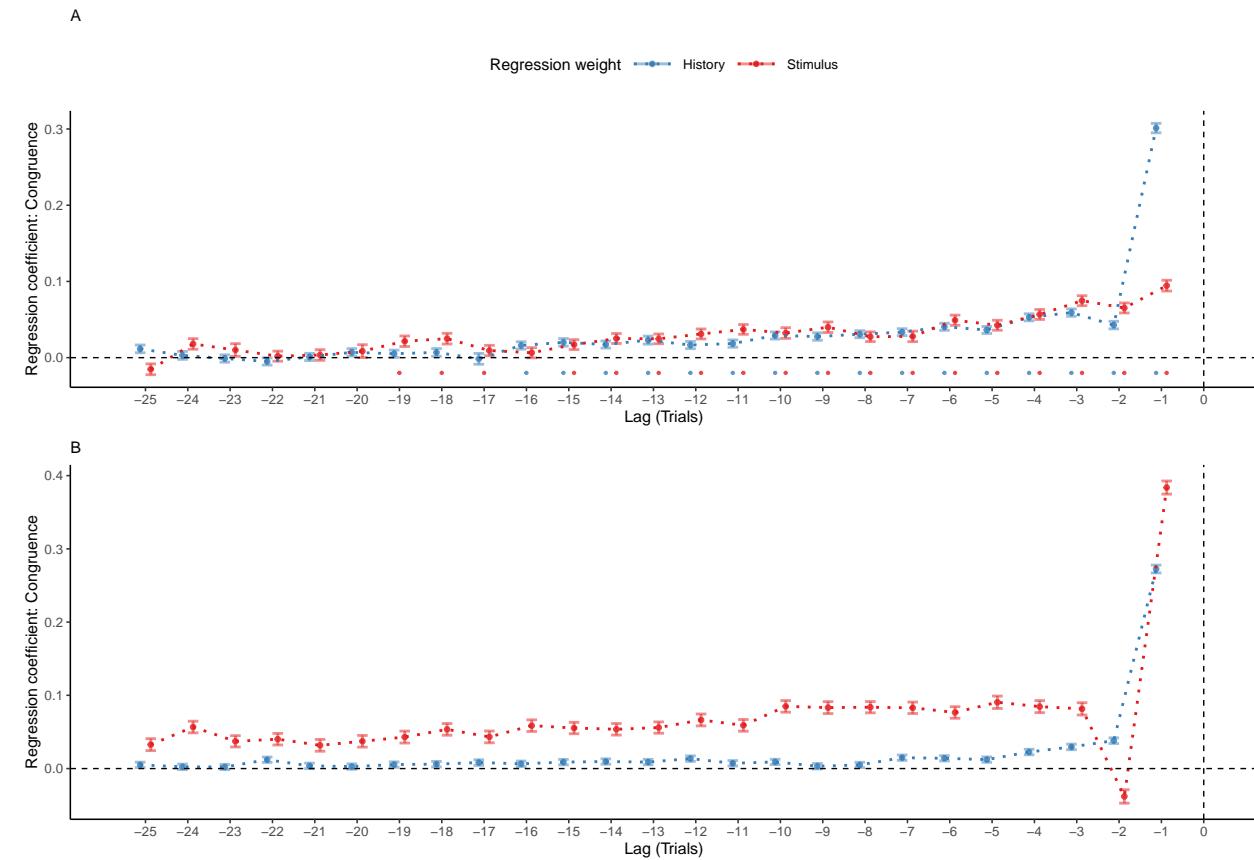
1388 B. In humans, the sequence of external stimulation (i.e., which of the two binary outcomes
1389 was supported by the presented stimuli; depicted in green) was negatively autocorrelated
1390 for 1 trial. When controlling for the autocorrelation of external stimulation only, stimulus-
1391 congruence remained significantly autocorrelated for 22 consecutive trials (88% of trials
1392 within the displayed time window; lower panel) and history-congruence remained significantly
1393 autocorrelated for 20 consecutive trials (84% of trials within the displayed time window). At
1394 the level of individual participants, the autocorrelation of external stimulation exceeded the
1395 respective autocorrelation of randomly permuted within a lag of $2.94 \pm 4.4 \times 10^{-3}$ consecutive
1396 trials (lower panel).

1397 C. In mice, task difficulty showed a significant autocorrelated for the first 25 consecutive trials
1398 (upper panel). When controlling only for task difficulty only, linear mixed effects modeling
1399 indicated a significant autocorrelation of stimulus-congruence for the first 36 consecutive trials
1400 (middle panel). In total, 100% of trials within the displayed time window remained significantly
1401 autocorrelated. The autocorrelation of history-congruence remained significant for the first
1402 8 consecutive trials, with 84% significantly autocorrelated trials within the displayed time
1403 window. At the level of individual mice, autocorrelation coefficients for difficulty were elevated
1404 above randomly permuted data within a lag of 15.13 ± 0.19 consecutive trials (lower panel).

1405 D. In mice, the sequence of external stimulation (i.e., which of the two binary outcomes was
1406 supported by the presented stimuli) was negatively autocorrelated for 11 consecutive trials
1407 (upper panel). When controlling only for the autocorrelation of external stimulation, stimulus-
1408 congruence remained significantly autocorrelated for 86 consecutive trials (100% of trials

¹⁴⁰⁹ within the displayed time window; middle) and history-congruence remained significantly
¹⁴¹⁰ autocorrelated for 8 consecutive trials (84% of trials within the displayed time window). At
¹⁴¹¹ the level of individual mice, autocorrelation coefficients for external stimulation were elevated
¹⁴¹² above randomly permuted data within a lag of $2.53 \pm 9.8 \times 10^{-3}$ consecutive trials (lower
¹⁴¹³ panel).

1414 **9.7 Supplemental Figure S3**



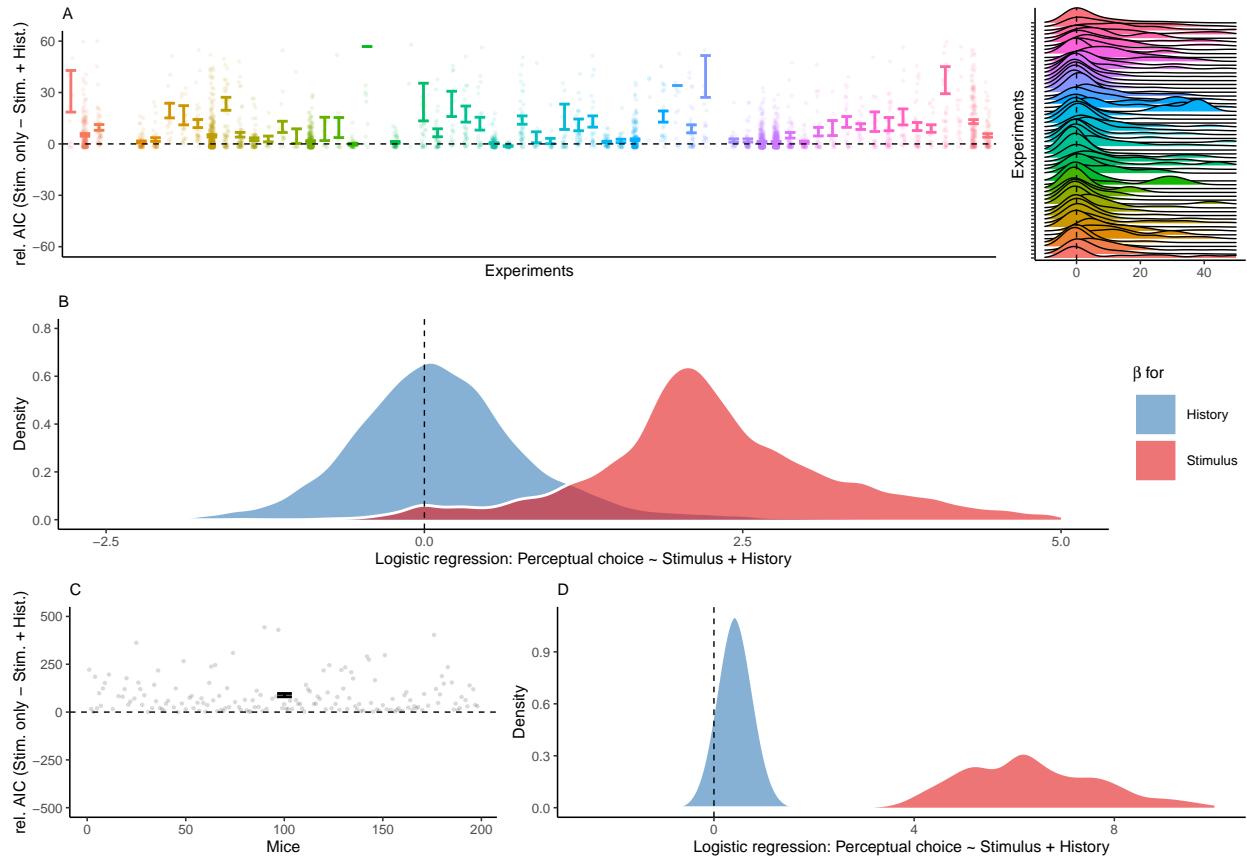
1416 **Supplemental Figure S3. Reproducing group-level autocorrelations using logistic
1417 regression.**

1418 A. As an alternative to group-level autocorrelation coefficients, we used trial-wise logistic
1419 regression to quantify serial dependencies in stimulus- and history-congruence. This analysis
1420 predicted stimulus- and history-congruence at the index trial (trial $t = 0$, vertical line) based
1421 on stimulus- and history-congruence at the 100 preceding trials. Mirroring the shape of the
1422 group-level autocorrelations, trial-wise regression coefficients (depicted as mean \pm SEM, dots
1423 mark trials with regression weights significantly greater than zero at $p < 0.05$) increased
1424 toward the index trial $t = 0$ for the human data.

1425 B. Following our results in human data, regression coefficients that predicted history-
1426 congruence at the index trial (trial $t = 0$, vertical line) increased exponentially for trials
1427 closer to the index trial in mice. In contrast to history-congruence, stimulus-congruence

¹⁴²⁸ showed a negative regression weight (or autocorrelation coefficient; Figure 3B) at trial -2.
¹⁴²⁹ This was due to the experimental design (see also the autocorrelations of difficulty and
¹⁴³⁰ external stimulation in Supplemental Figure S2C and D): When mice made errors at easy
¹⁴³¹ trials (contrast $\geq 50\%$), the upcoming stimulus was shown at the same spatial location and at
¹⁴³² high contrast. This increased the probability of stimulus-congruent perceptual choices after
¹⁴³³ stimulus-incongruent perceptual choices at easy trials, thereby creating a negative regression
¹⁴³⁴ weight (or autocorrelation coefficient) of stimulus-congruence at trial -2.

1435 **9.8 Supplemental Figure S4**



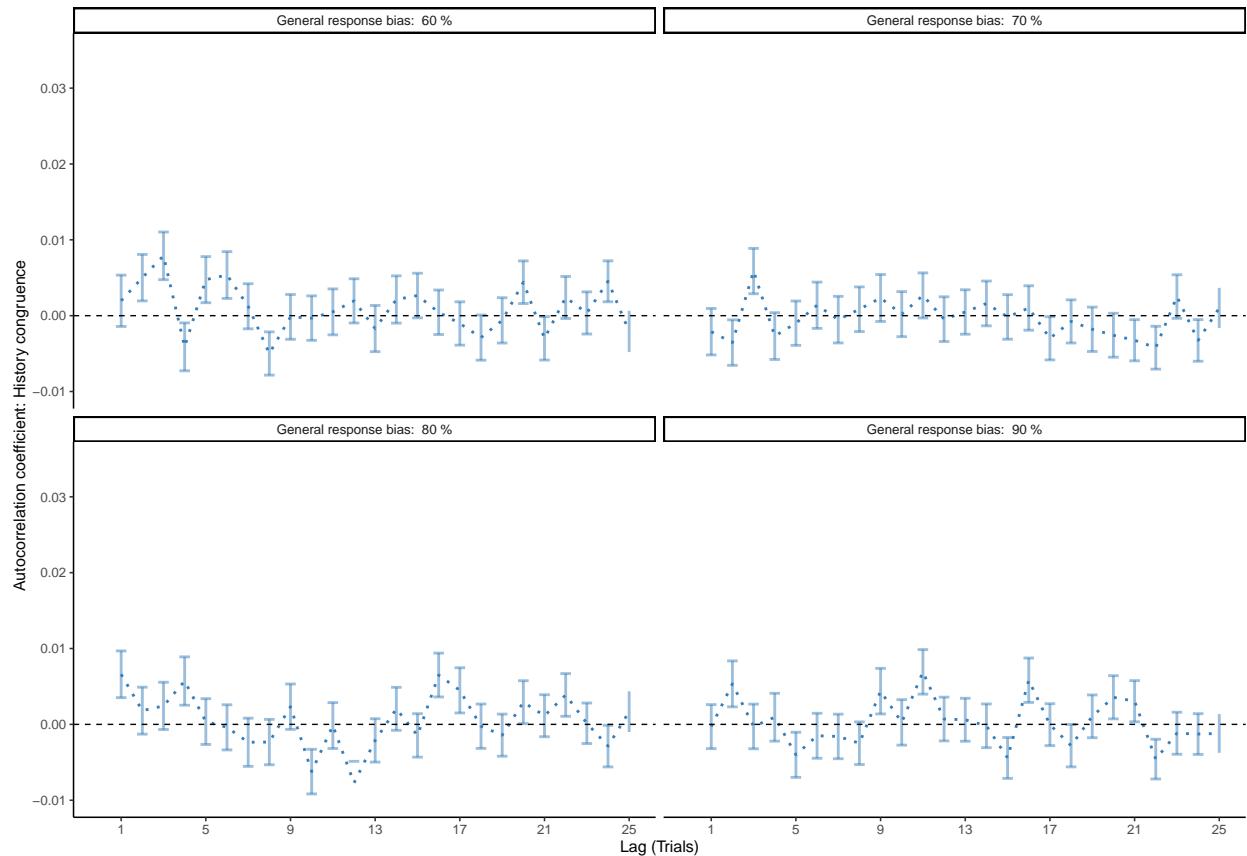
1436 **1437 Supplemental Figure S4. History-congruence in logistic regression.**

1438 A. To ensure that perceptual history played a significant role in perception despite the ongoing
 1439 stream of external information, we tested whether human perceptual decision-making was
 1440 better explained by the combination of external and internal information or, alternatively,
 1441 by external information alone. To this end, we compared AIC between logistic regression
 1442 models that predicted trial-wise perceptual responses either by both current external sensory
 1443 information and the preceding percept, or by external sensory information alone (values above
 1444 zero indicate a superiority of the full model). With high consistency across the experiments
 1445 selected from the Confidence Database, this model-comparison confirmed that perceptual
 1446 history contributed significantly to perception (difference in AIC = 8.07 ± 0.53 , T(57.22) =
 1447 4.1, $p = 1.31 \times 10^{-4}$).

1448 B. Participant-wise regression coefficients amount to 0.18 ± 0.02 for the effect of perceptual

- ₁₄₄₉ history and 2.51 ± 0.03 for external sensory stimulation.
- ₁₄₅₀ C. In mice, an AIC-based model comparison indicated that perception was better explained
₁₄₅₁ by logistic regression models that predicted trial-wise perceptual responses based on both
₁₄₅₂ current external sensory information and the preceding percept (difference in AIC = $88.62 \pm$
₁₄₅₃ 8.57 , $T(164) = -10.34$, $p = 1.29 \times 10^{-19}$).
- ₁₄₅₄ D. In mice, individual regression coefficients amounted to 0.42 ± 0.02 for the effect of
₁₄₅₅ perceptual history and 6.91 ± 0.21 for external sensory stimulation.

1456 **9.9 Supplemental Figure S5**



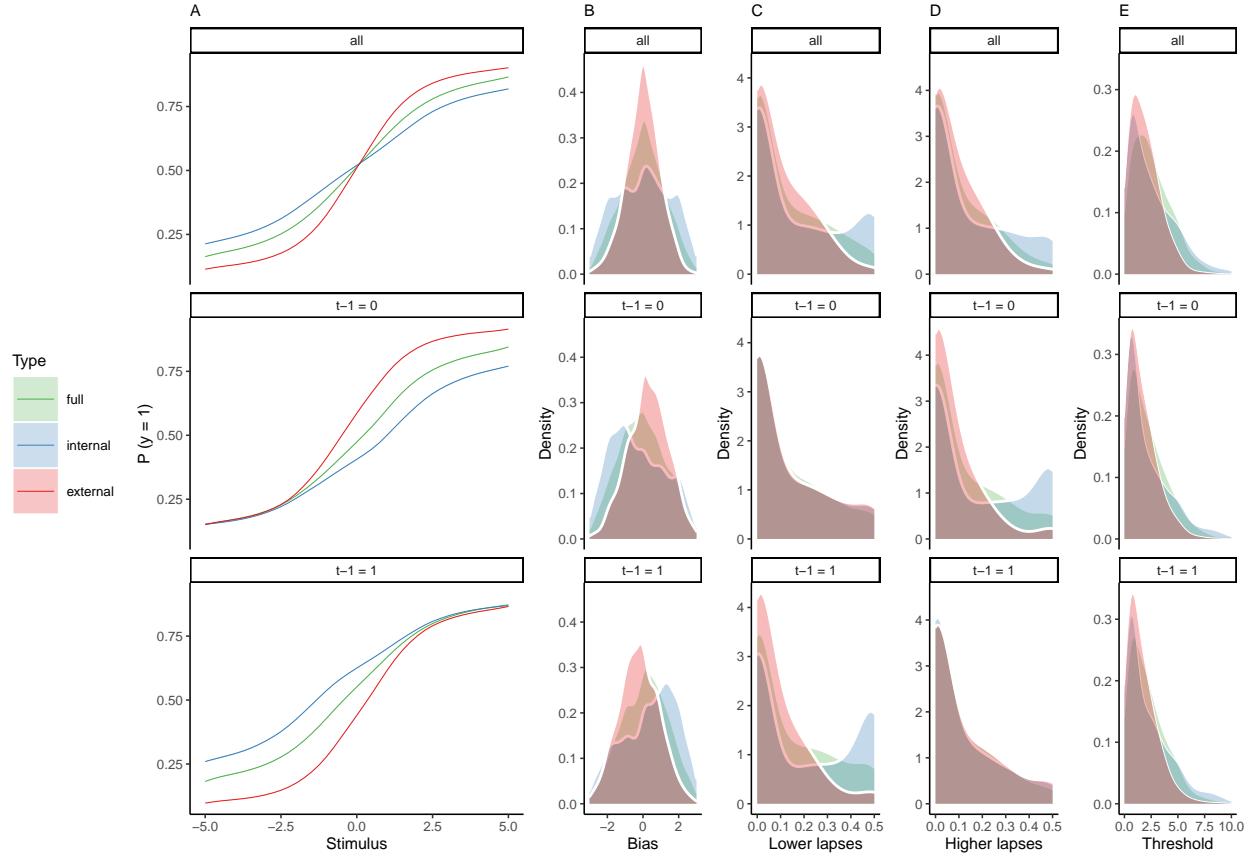
1457 **Supplemental Figure S5. Correcting for general response biases.**

1458 Here, we ask whether the autocorrelation of history-congruence (as shown in Figure 2-3C)
1459 may be driven by general response biases (i.e., a general propensity to choose one of the two
1460 possible outcomes more frequently than the alternative). To this end, we generated sequences
1461 of 100 perceptual choices with general response biases ranging from 60 to 90% for 1000
1462 simulated participants each. We then computed the autocorrelation of history-congruence
1463 for these simulated data. Crucially, we used the correction procedure that is applied to the
1464 autocorrelation curves shown in this manuscript: All reported autocorrelation coefficients are
1465 computed relative to the average autocorrelation coefficients obtained for 100 iterations of
1466 randomly permuted trial sequences. The above simulation show that this correction procedure
1467 removes any potential contribution of general response biases to the autocorrelation of history-
1468 congruence. This indicates that the autocorrelation of history-congruence (as shown in Figure
1469

₁₄₇₀ 2-3C) is not driven by general response biases that were present in the empirical data at a

₁₄₇₁ level of $58.71\% \pm 0.22\%$ in humans and $54.6\% \pm 0.3\%$ in mice.

1472 **9.10 Supplemental Figure S6**



1473

1474 **Supplemental Figure S6. Full and history-conditioned psychometric functions**
1475 **across modes in humans.**

1476 A. Here, we show average psychometric functions for the full dataset (upper panel) and
1477 conditioned on perceptual history ($y_{t-1} = 1$ and $y_{t-1} = 0$; middle and lower panel) across
1478 modes (green line) and for internal mode (blue line) and external mode (red line) separately.

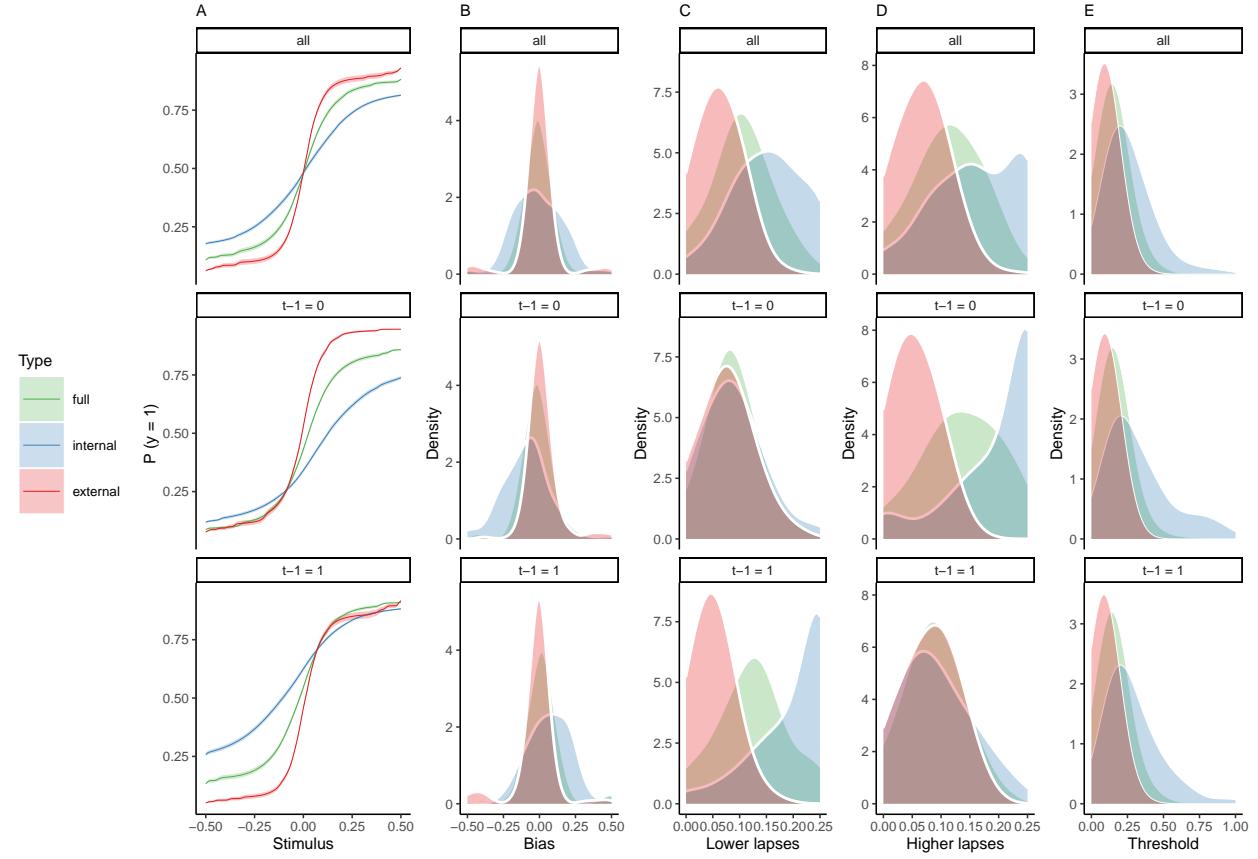
1479 B. Across the full dataset, biases μ were distributed around zero ($\beta_0 = 7.37 \times 10^{-3} \pm 0.09$,
1480 $T(36.8) = 0.08$, $p = 0.94$; upper panel), with larger absolute biases $|\mu|$ for internal as compared
1481 to external mode ($\beta_0 = -0.62 \pm 0.07$, $T(45.62) = -8.38$, $p = 8.59 \times 10^{-11}$; controlling for
1482 differences in lapses and thresholds). When conditioned on perceptual history, we observed
1483 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
1484 panel) and positive biases for $y_{t-1} = 1$ ($\beta_0 = 0.56 \pm 0.12$, $T(43.39) = 4.6$, $p = 3.64 \times 10^{-5}$;
1485 lower panel).

₁₄₈₆ C. Lapse rates were higher in internal mode as compared to external mode ($\beta_0 = -0.05 \pm$
₁₄₈₇ 5.73×10^{-3} , $T(47.03) = -9.11$, $p = 5.94 \times 10^{-12}$; controlling for differences in biases and
₁₄₈₈ thresholds; see upper panel and subplot D). Importantly, the between-mode difference in
₁₄₈₉ lapses depended on perceptual history: We found no significant difference in lower lapses
₁₄₉₀ 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
₁₄₉₁ significant difference for $y_{t-1} = 1$ ($\beta_0 = -0.11 \pm 0.01$, $T(40.11) = -9.59$, $p = 6.14 \times 10^{-12}$;
₁₄₉₂ lower panel).

₁₄₉₃ D. Conversely, higher lapses δ were significantly increased for $y_{t-1} = 0$ ($\beta_0 = -0.1 \pm$
₁₄₉₄ 9.58×10^{-3} , $T(36.87) = -10.16$, $p = 3.06 \times 10^{-12}$; middle panel), but not for $y_{t-1} = 1$ ($\beta_0 =$
₁₄₉₅ $0.01 \pm 7.74 \times 10^{-3}$, $T(33.66) = 1.58$, $p = 0.12$; lower panel).

₁₄₉₆ E. The thresholds t were larger in internal as compared to external mode ($\beta_0 = -1.77 \pm 0.25$,
₁₄₉₇ $T(50.45) = -7.14$, $p = 3.48 \times 10^{-9}$; controlling for differences in biases and lapses) and were
₁₄₉₈ not modulated by perceptual history ($\beta_0 = 0.04 \pm 0.06$, $T(2.97 \times 10^3) = 0.73$, $p = 0.47$).

1499 **9.11 Supplemental Figure S7**



1500 **Supplemental Figure S7. Full and history-conditioned psychometric functions**
1501 **across modes in mice.**

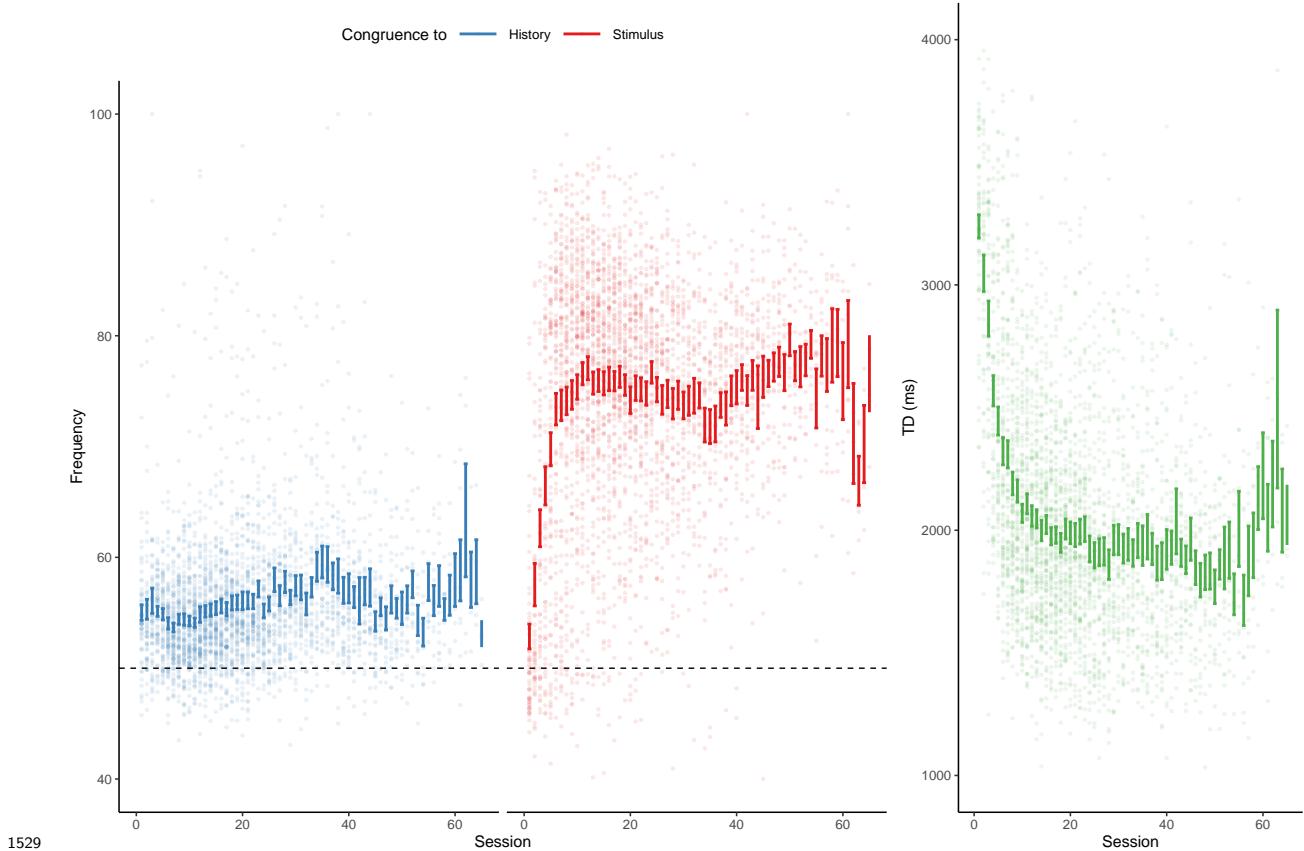
1502 A. Here, we show average psychometric functions for the full IBL dataset (upper panel) and
1503 conditioned on perceptual history ($y_{t-1} = 1$ and $y_{t-1} = 0$; middle and lower panel) across
1504 modes (green line) and for internal mode (blue line) and external mode (red line) separately.
1505
1506 B. Across the full dataset, biases μ were distributed around zero ($T(164) = 0.39$, $p = 0.69$;
1507 upper panel), with larger absolute biases $|\mu|$ for internal as compared to external mode ($\beta_0 =$
1508 -0.18 ± 0.03 , $T = -6.38$, $p = 1.77 \times 10^{-9}$; controlling for differences in lapses and thresholds).
1509 When conditioned on perceptual history, we observed negative biases for $y_{t-1} = 0$ ($T(164)$
1510 $= -1.99$, $p = 0.05$; middle panel) and positive biases for $y_{t-1} = 1$ ($T(164) = 1.91$, $p = 0.06$;
1511 lower panel).

1512 C. Lapse rates were higher in internal as compared to external mode ($\beta_0 = -0.11 \pm 4.39 \times 10^{-3}$,
1513 $T = -24.8$, $p = 4.91 \times 10^{-57}$; controlling for differences in biases and thresholds; upper
1514 panel, see subplot D). For $y_{t-1} = 1$, the difference between internal and external mode was
1515 more pronounced for lower lapses γ ($T(164) = -18.24$, $p = 2.68 \times 10^{-41}$) as compared to
1516 higher lapses δ (see subplot D). In mice, lower lapses γ were significantly elevated during
1517 internal mode irrespective of the preceding perceptual choice (middle panel: lower lapses γ
1518 for $y_{t-1} = 0$; $T(164) = -2.5$, $p = 0.01$, lower panel: lower lapses γ for $y_{t-1} = 1$; $T(164) =$
1519 -32.44 , $p = 2.92 \times 10^{-73}$).

1520 D. For $y_{t-1} = 0$, the difference between internal and external mode was more pronounced
1521 for higher lapses δ ($T(164) = 21.44$, $p = 1.93 \times 10^{-49}$, see subplot C). Higher lapses were
1522 significantly elevated during internal mode irrespective of the preceding perceptual choice
1523 (middle panel: higher lapses δ for $y_{t-1} = 0$; $T(164) = -28.29$, $p = 5.62 \times 10^{-65}$ lower panel:
1524 higher lapses δ for $y_{t-1} = 1$; $T(164) = -2.65$, $p = 8.91 \times 10^{-3}$;).

1525 E. Thresholds t were higher in internal as compared to external mode ($\beta_0 = -0.28 \pm 0.04$,
1526 $T = -7.26$, $p = 1.53 \times 10^{-11}$; controlling for differences in biases and lapses) and were not
1527 modulated by perceptual history ($T(164) = 0.94$, $p = 0.35$).

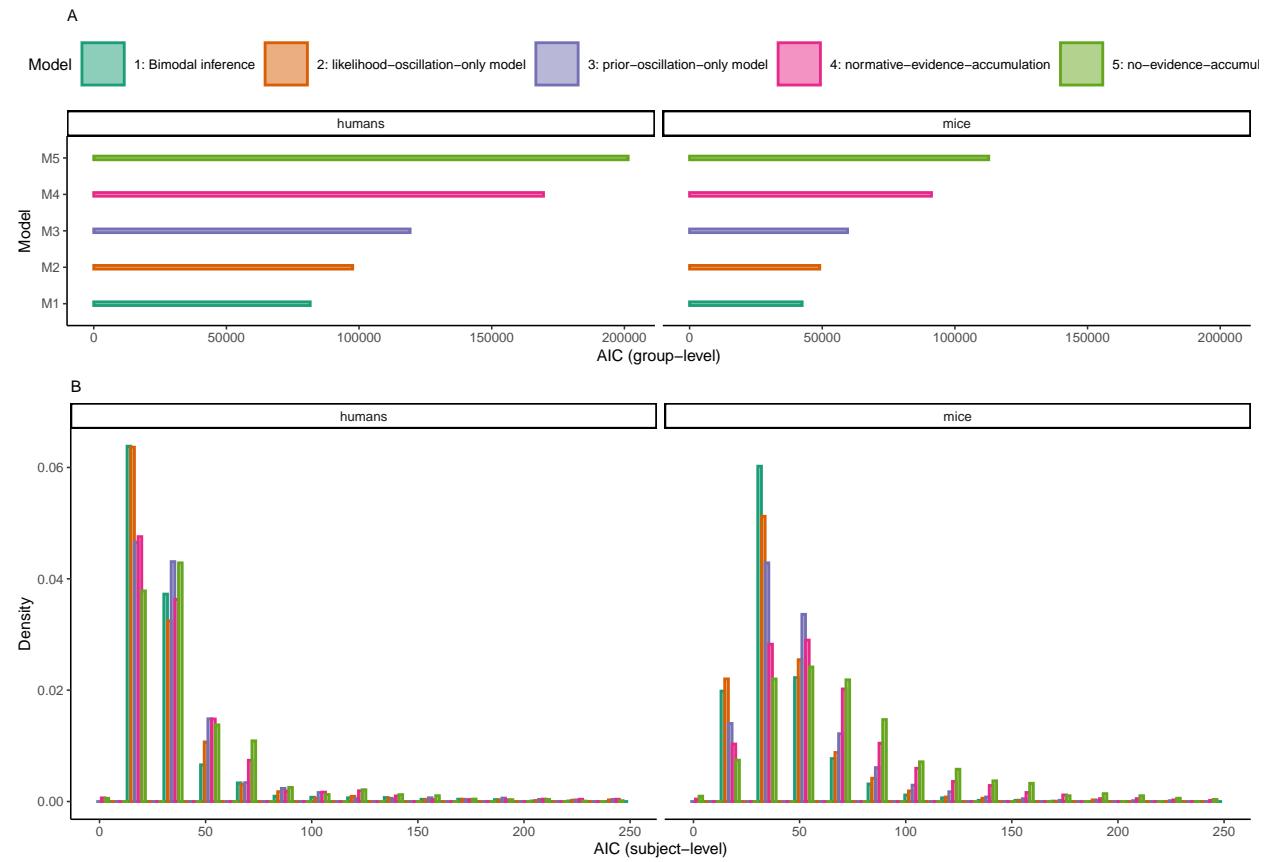
1528 **9.12 Supplemental Figure S8**



1530 **Supplemental Figure S8. History-/stimulus-congruence and TDs during training
1531 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 , $T(1.14 \times 10^3) = -1.3$, $p < 2.2 \times 10^{-308}$).

1540 **9.13 Supplemental Figure S9**



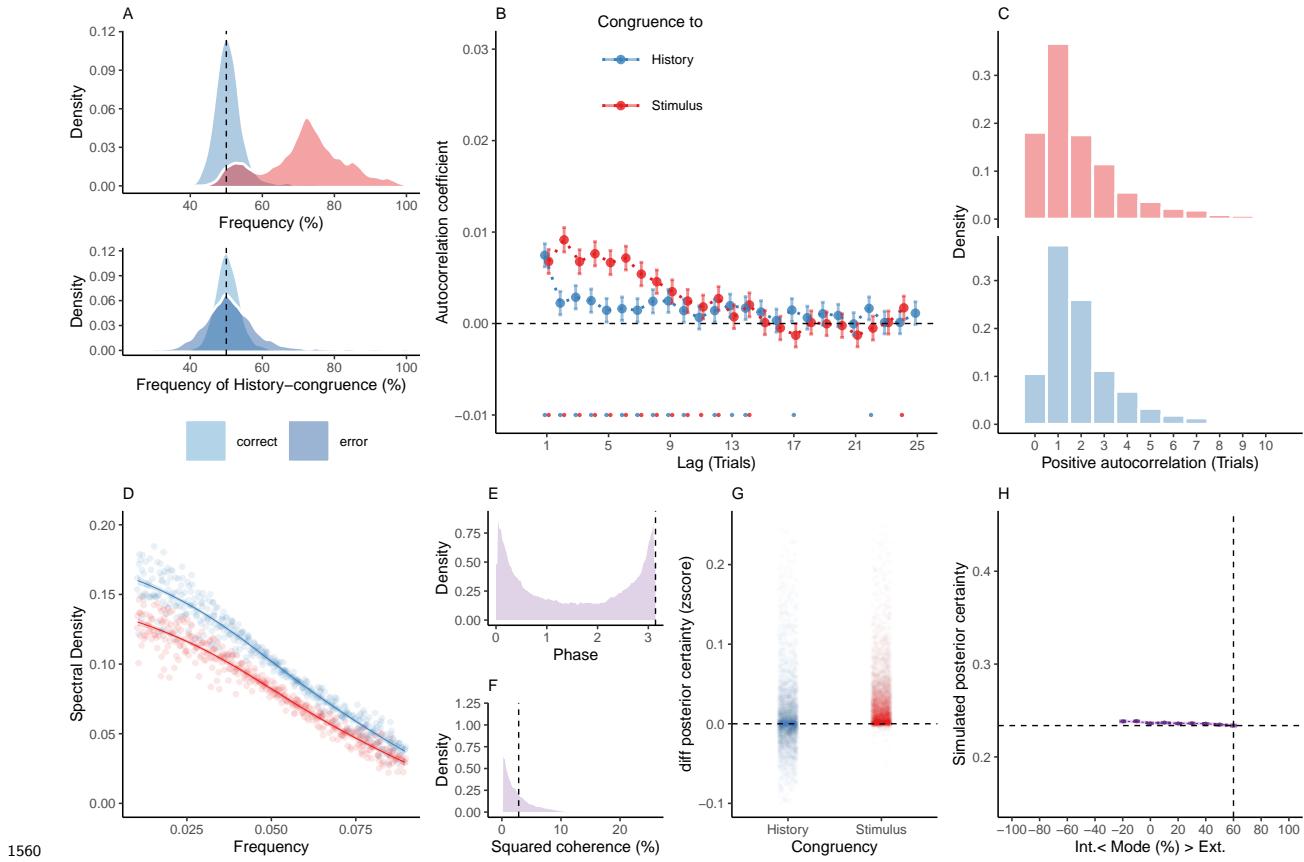
1541

1542 **Supplemental Figure S9. Comparison of the bimodal inference model against**
1543 **reduced control models.**

1544 **A. Group-level AIC.** The bimodal inference model (M1) achieved the lowest AIC
1545 across the full model space ($AIC_1 = 8.16 \times 10^4$ in humans and 4.24×10^4 in mice).
1546 Model M2 ($AIC_2 = 9.76 \times 10^4$ in humans and 4.91×10^4 in mice) and Model M3
1547 ($AIC_3 = 1.19 \times 10^5$ in humans and 5.95×10^4 in mice) incorporated only oscillations
1548 of either likelihood or prior precision. Model M4 ($AIC_4 = 1.69 \times 10^5$ in humans
1549 and 9.12×10^4 in mice) lacked any oscillations of likelihood and prior precision
1550 and corresponded to the normative model proposed by Glaze et al.⁵¹. In model
1551 M5 ($AIC_5 = 2.01 \times 10^5$ in humans and 1.13×10^5 in mice), we furthermore removed
1552 the integration of information across trials, such that perception depended only
1553 in incoming sensory information.

1554 **B. Subject-level AIC.** Here, we show the distribution of AIC values at the subject-
1555 level. AIC for the bimodal inference model tended to be smaller than AIC for
1556 the comparator models (statistical comparison to the second-best model M2 in
1557 humans: $\beta = -1.71 \pm 0.19$, $T(8.57 \times 10^3) = -8.85$, $p = 1.06 \times 10^{-18}$; mice: $T(1.57 \times 10^3)$
1558 = **-3.08**, $p = 2.12 \times 10^{-3}$).

1559 **9.14 Supplemental Figure S10**



1560 **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 .

1561 A. Similar to the full model M1 (Figure 1F and Figure 4), simulated perceptual choices
 1562 were stimulus-congruent in $71.97\% \pm 0.17\%$ of trials (in red). History-congruent amounted
 1563 to $50.76\% \pm 0.07\%$ of trials (in blue). As in the full model, the likelihood-oscillation-only
 1564 model showed a significant bias toward perceptual history $T(4.32 \times 10^3) = 10.29$, $p =$
 1565 1.54×10^{-24} ; upper panel). Similarly, history-congruent choices were more frequent at error
 1566 trials ($T(4.32 \times 10^3) = 9.71$, $p = 4.6 \times 10^{-22}$; lower panel).

1567 B. In the likelihood-oscillation-only model, we observed that the autocorrelation coefficients for

1573 history-congruence were reduced below the autocorrelation coefficients of stimulus-congruence.

1574 This is an approximately five-fold reduction relative to the empirical results observed in humans

1575 (Figure 2B), where the autocorrelation of history-congruence was above the autocorrelation of

1576 stimulus-congruence. Moreover, in the reduced model shown here, the number of consecutive

1577 trials that showed significant autocorrelation of history-congruence was reduced to 11.

1578 C. In the likelihood-oscillation-only model, the number of consecutive trials at which true

1579 autocorrelation coefficients exceeded the autocorrelation coefficients for randomly permuted

1580 data did not differ with respect to stimulus-congruence ($2.62 \pm 1.39 \times 10^{-3}$ trials; $T(4.32 \times 10^3)$

1581 = 1.85, $p = 0.06$), but decreased with respect to history-congruence ($2.4 \pm 8.45 \times 10^{-4}$ trials;

1582 $T(4.32 \times 10^3) = -15.26$, $p = 3.11 \times 10^{-51}$) relative to the full model.

1583 D. In the likelihood-oscillation-only model, the smoothed probabilities of stimulus- and

1584 history-congruence (sliding windows of ± 5 trials) fluctuated as **a scale-invariant process**

1585 **with a 1/f power law**, i.e., at power densities that were inversely proportional to the

1586 frequency (power $\sim 1/f^\beta$; stimulus-congruence: $\beta = -0.81 \pm 1.17 \times 10^{-3}$, $T(1.92 \times 10^5) =$

1587 -688.65 , $p < 2.2 \times 10^{-308}$; history-congruence: $\beta = -0.79 \pm 1.14 \times 10^{-3}$, $T(1.92 \times 10^5) =$

1588 -698.13 , $p < 2.2 \times 10^{-308}$).

1589 E. In the likelihood-oscillation-only model, the distribution of phase shift between fluctuations

1590 in simulated stimulus- and history-congruence peaked at half a cycle (π denoted by dotted

1591 line). In contrast to the full model, the dynamic probabilities of simulated stimulus- and

1592 history-congruence were positively correlated ($\beta = 2.7 \times 10^{-3} \pm 7.6 \times 10^{-4}$, $T(2.02 \times 10^6) =$

1593 3.55 , $p = 3.8 \times 10^{-4}$).

1594 F. In the likelihood-oscillation-only model, the average squared coherence between fluctuations

1595 in simulated stimulus- and history-congruence (black dotted line) was reduced in comparison

1596 to the full model ($T(3.51 \times 10^3) = -4.56$, $p = 5.27 \times 10^{-6}$) and amounted to $3.43 \pm 1.02 \times 10^{-3}\%$.

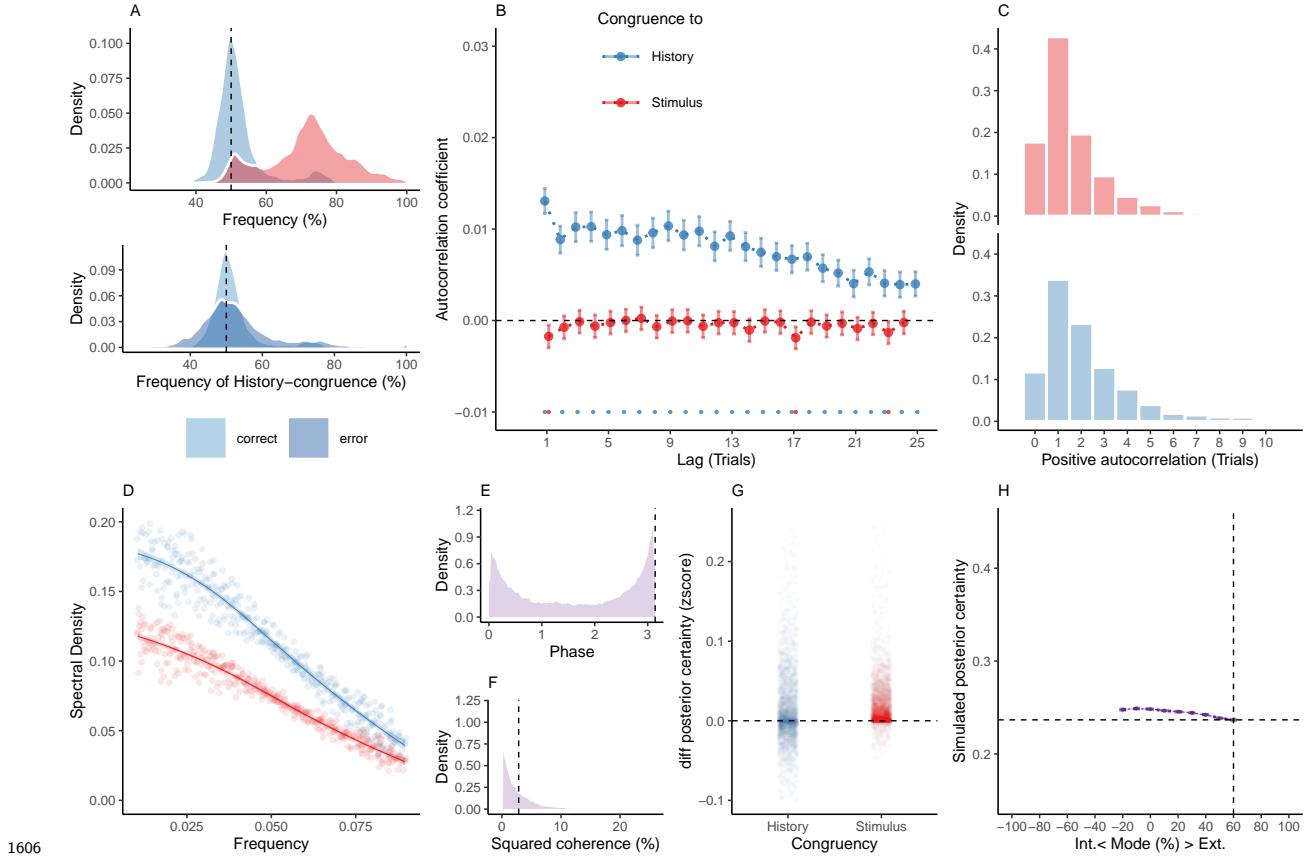
1597 G. Similar to the full bimodal inference model, confidence simulated from the likelihood-

1598 oscillation-only model was enhanced for stimulus-congruent choices ($\beta = 0.03 \pm 1.42 \times 10^{-4}$,

₁₅₉₉ $T(2.1 \times 10^6) = 191.78$, $p < 2.2 \times 10^{-308}$) and history-congruent choices ($\beta = 9.1 \times 10^{-3} \pm$
₁₆₀₀ 1.25×10^{-4} , $T(2.1 \times 10^6) = 72.51$, $p < 2.2 \times 10^{-308}$).

₁₆₀₁ H. In the likelihood-oscillation-only model, the positive quadratic relationship between the
₁₆₀₂ mode of perceptual processing and confidence was markedly reduced in comparison to the full
₁₆₀₃ 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
₁₆₀₄ dotted lines indicate minimum posterior certainty and the associated mode, respectively.

1605 **9.15 Supplemental Figure S11**



1606 **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 .

1612 A. Similar to the full model (Figure 1F and Figure 4), simulated perceptual choices were
 1613 stimulus-congruent in $71.97\% \pm 0.17\%$ of trials (in red). History-congruent amounted to
 1614 $52.1\% \pm 0.11\%$ of trials (in blue). As in the full model, the prior-oscillation-only showed a
 1615 significant bias toward perceptual history $T(4.32 \times 10^3) = 18.34$, $p = 1.98 \times 10^{-72}$; upper
 1616 panel). Similarly, history-congruent choices were more frequent at error trials ($T(4.31 \times 10^3)$
 1617 $= 12.35$, $p = 1.88 \times 10^{-34}$; lower panel).

1618 B. In the prior-oscillation-only model, we did not observe any significant positive autocor-

₁₆₁₉ relation of stimulus-congruence , whereas the autocorrelation of history-congruence was
₁₆₂₀ preserved.

₁₆₂₁ C. In the prior-oscillation-only model, the number of consecutive trials at which true au-
₁₆₂₂ tocorrelation coefficients exceeded the autocorrelation coefficients for randomly permuted
₁₆₂₃ data did was decreased with respect to stimulus-congruence relative to the full model ($1.8 \pm$
₁₆₂₄ 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
₁₆₂₅ model with respect to history-congruence ($4.25 \pm 1.84 \times 10^{-3}$ trials; $T(4.32 \times 10^3) = 0.07$, p
₁₆₂₆ = 0.95).

₁₆₂₇ D. In the prior-oscillation-only model, the smoothed probabilities of stimulus- and history-
₁₆₂₈ congruence (sliding windows of ± 5 trials) fluctuated as **a scale-invariant process with a**
₁₆₂₉ **1/f power law**, i.e., at power densities that were inversely proportional to the frequency
₁₆₃₀ (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
₁₆₃₁ $< 2.2 \times 10^{-308}$; history-congruence: $\beta = -0.83 \pm 1.27 \times 10^{-3}$, $T(1.92 \times 10^5) = -651.6$, $p <$
₁₆₃₂ 2.2×10^{-308}).

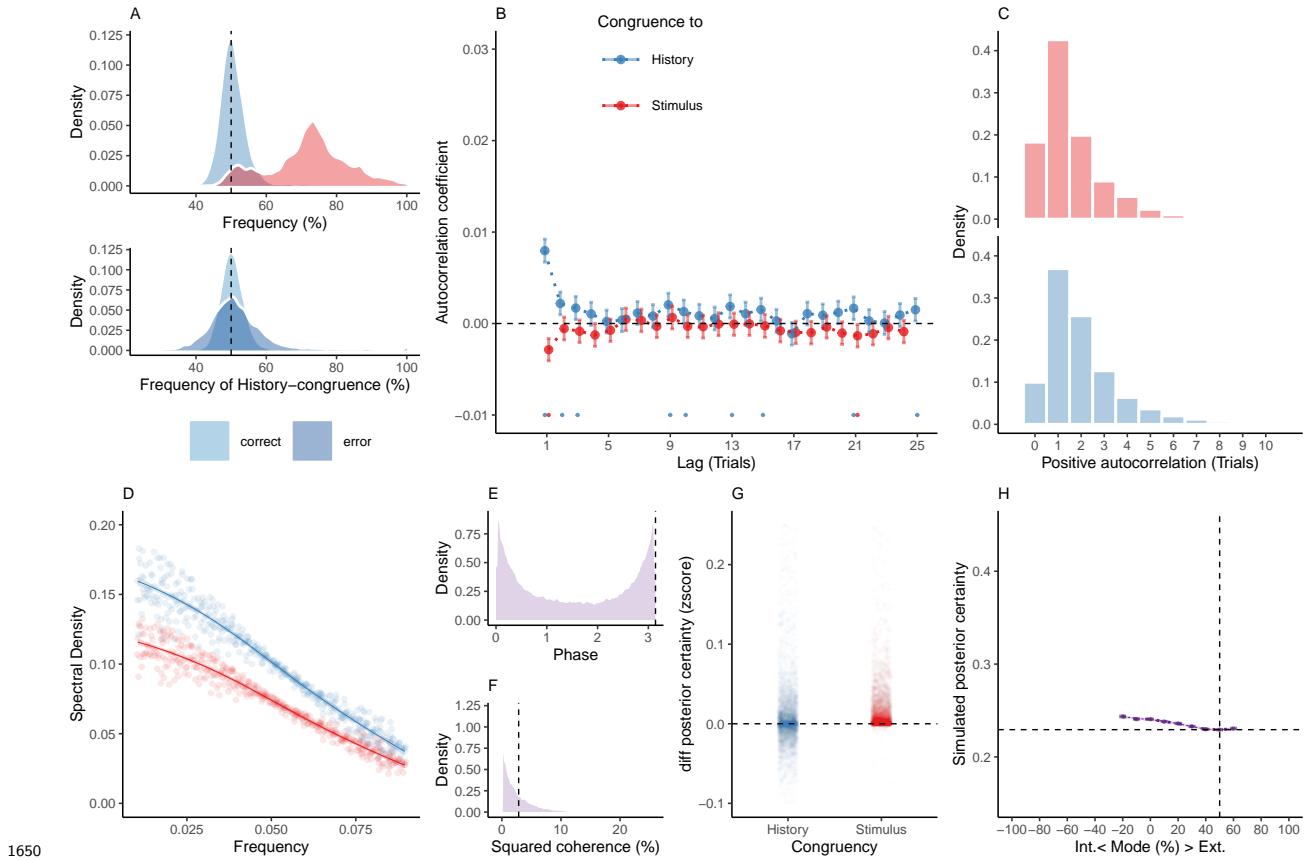
₁₆₃₃ E. In the prior-oscillation-only model, the distribution of phase shift between fluctuations
₁₆₃₄ in simulated stimulus- and history-congruence peaked at half a cycle (π denoted by dotted
₁₆₃₅ line). Similar to the full model, the dynamic probabilities of simulated stimulus- and history-
₁₆₃₆ congruence were anti-correlated ($\beta = -0.03 \pm 8.61 \times 10^{-4}$, $T(2.12 \times 10^6) = -34.03$, $p =$
₁₆₃₇ 8.17×10^{-254}).

₁₆₃₈ F. In the prior-oscillation-only model, the average squared coherence between fluctuations in
₁₆₃₉ simulated stimulus- and history-congruence (black dotted line) was reduced in comparison to
₁₆₄₀ the full model ($T(3.54 \times 10^3) = -3.22$, $p = 1.28 \times 10^{-3}$) and amounted to $3.52 \pm 1.04 \times 10^{-3}\%$.

₁₆₄₁ G. Similar to the full bimodal inference model, confidence simulated from the prior-oscillation-
₁₆₄₂ only model was enhanced for stimulus-congruent choices ($\beta = 0.02 \pm 1.44 \times 10^{-4}$, $T(2.03 \times 10^6)$
₁₆₄₃ = 128.53, $p < 2.2 \times 10^{-308}$) and history-congruent choices ($\beta = 0.01 \pm 1.26 \times 10^{-4}$, $T(2.03 \times 10^6)$
₁₆₄₄ = 88.24, $p < 2.2 \times 10^{-308}$).

₁₆₄₅ H. In contrast to the full bimodal inference model, the prior-oscillation-only model did
₁₆₄₆ not yield a positive quadratic relationship between the mode of perceptual processing and
₁₆₄₇ confidence ($\beta_2 = -0.17 \pm 0.1$, $T(2.04 \times 10^6) = -1.66$, $p = 0.1$). The horizontal and vertical
₁₆₄₈ dotted lines indicate minimum posterior certainty and the associated mode, respectively.

1649 **9.16 Supplemental Figure S12**



1650 **1651 Supplemental Figure S12. Reduced Control Model M4: Normative evidence**

1652 **accumulation.** When simulating data for the *normative-evidence-accumulation model*, we
 1653 removed the oscillation from the likelihood and prior terms by setting the amplitudes a_{LLR}
 1654 and a_ψ to zero. Simulated data thus depended only on the participant-wise estimates for
 1655 hazard rate H and inverse decision temperature ζ .

1656 A. Similar to the full model (Figure 1F and Figure 4), simulated perceptual choices were
 1657 stimulus-congruent in $71.97\% \pm 0.17\%$ of trials (in red). History-congruent amounted to
 1658 $50.73\% \pm 0.07\%$ of trials (in blue). As in the full model, the no-oscillation model showed
 1659 a significant bias toward perceptual history $T(4.32 \times 10^3) = 9.94$, $p = 4.88 \times 10^{-23}$; upper
 1660 panel). Similarly, history-congruent choices were more frequent at error trials ($T(4.31 \times 10^3)$
 1661 $= 10.59$, $p = 7.02 \times 10^{-26}$; lower panel).

1662 B. In the normative-evidence-accumulation model, we did not find significant autocor-

₁₆₆₃ relations for stimulus-congruence. Likewise, we did not observe any autocorrelation of
₁₆₆₄ history-congruence beyond the first three consecutive trials.

₁₆₆₅ C. In the normative-evidence-accumulation model, the number of consecutive trials at
₁₆₆₆ which true autocorrelation coefficients exceeded the autocorrelation coefficients for randomly
₁₆₆₇ permuted data decreased with respect to both stimulus-congruence ($1.8 \pm 1.59 \times 10^{-3}$ trials;
₁₆₆₈ $T(4.31 \times 10^3) = -5.21$, $p = 2 \times 10^{-7}$) and history-congruence ($2.18 \pm 5.48 \times 10^{-4}$ trials;
₁₆₆₉ $T(4.32 \times 10^3) = -17.1$, $p = 1.75 \times 10^{-63}$) relative to the full model.

₁₆₇₀ D. In the normative-evidence-accumulation model, the smoothed probabilities of stimulus- and
₁₆₇₁ history-congruence (sliding windows of ± 5 trials) fluctuated as **a scale-invariant process**
₁₆₇₂ **with a $1/f$ power law**, i.e., at power densities that were inversely proportional to the
₁₆₇₃ frequency (power $\sim 1/f^\beta$; stimulus-congruence: $\beta = -0.78 \pm 1.1 \times 10^{-3}$, $T(1.92 \times 10^5) =$
₁₆₇₄ -706.93 , $p < 2.2 \times 10^{-308}$; history-congruence: $\beta = -0.79 \pm 1.12 \times 10^{-3}$, $T(1.92 \times 10^5) =$
₁₆₇₅ -702.46 , $p < 2.2 \times 10^{-308}$).

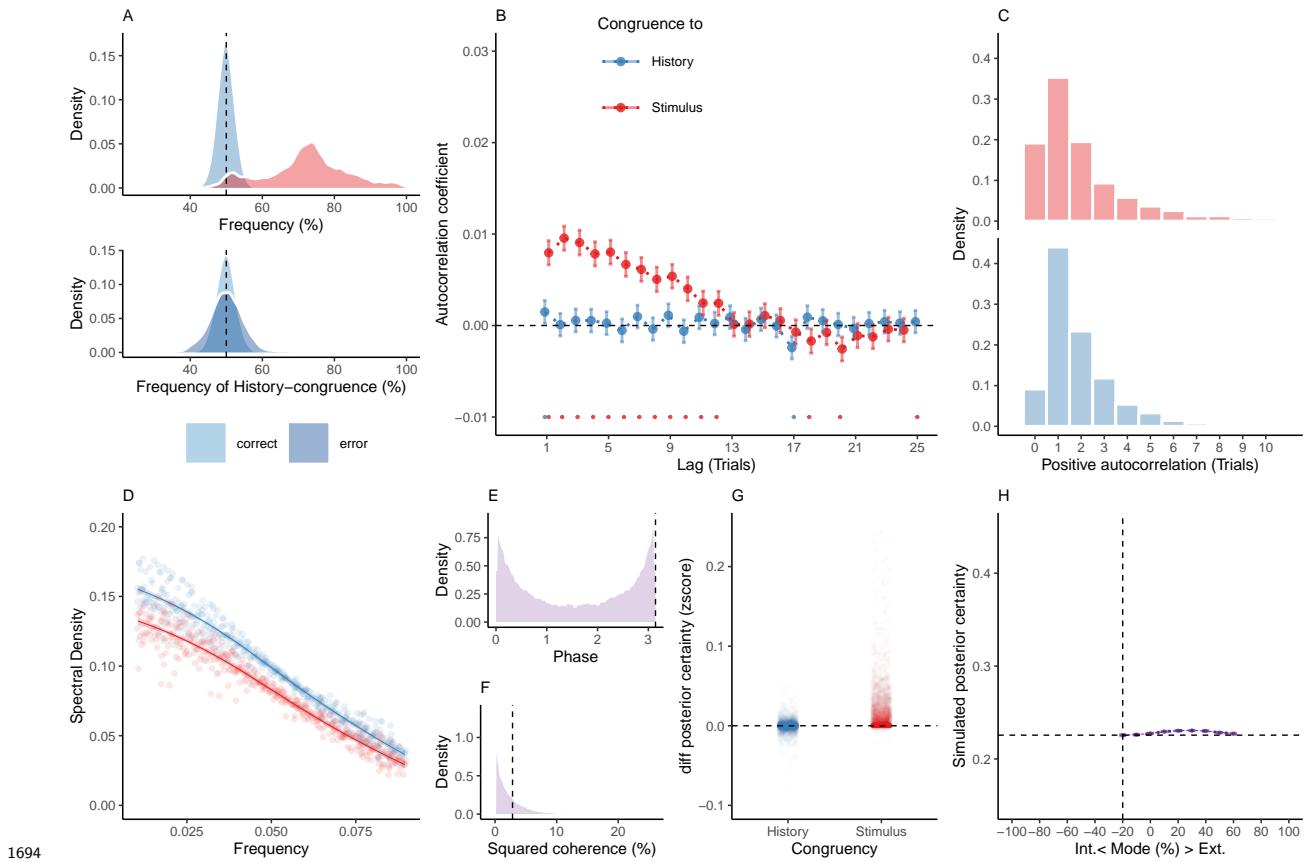
₁₆₇₆ E. In the normative-evidence-accumulation model, the distribution of phase shift between
₁₆₇₇ fluctuations in simulated stimulus- and history-congruence peaked at half a cycle (π denoted
₁₆₇₈ by dotted line). In contrast to the full model, the dynamic probabilities of simulated stimulus-
₁₆₇₉ and history-congruence were positively correlated ($\beta = 4.3 \times 10^{-3} \pm 7.97 \times 10^{-4}$, $T(1.98 \times 10^6)$
₁₆₈₀ $= 5.4$, $p = 6.59 \times 10^{-8}$).

₁₆₈₁ F. In the normative-evidence-accumulation model, the average squared coherence between
₁₆₈₂ fluctuations in simulated stimulus- and history-congruence (black dotted line) was reduced in
₁₆₈₃ comparison to the full model ($T(3.52 \times 10^3) = -6.27$, $p = 3.97 \times 10^{-10}$) and amounted to
₁₆₈₄ $3.26 \pm 8.88 \times 10^{-4}\%$.

₁₆₈₅ G. Similar to the full bimodal inference model, confidence simulated from the no-oscillation
₁₆₈₆ model was enhanced for stimulus-congruent choices ($\beta = 0.01 \pm 1.05 \times 10^{-4}$, $T(2.1 \times 10^6)$
₁₆₈₇ $= 139.17$, $p < 2.2 \times 10^{-308}$) and history-congruent choices ($\beta = 8.05 \times 10^{-3} \pm 9.2 \times 10^{-5}$,
₁₆₈₈ $T(2.1 \times 10^6) = 87.54$, $p < 2.2 \times 10^{-308}$).

₁₆₈₉ H. In the normative-evidence-accumulation model, the positive quadratic relationship between
₁₆₉₀ the mode of perceptual processing and confidence was markedly reduced in comparison to
₁₆₉₁ 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
₁₆₉₂ dotted lines indicate minimum posterior certainty and the associated mode, respectively.

1693 **9.17 Supplemental Figure S13**



1694 **1695 Supplemental Figure S13. Reduced Control Model M5: No accumulation of
1696 information across trials.** When simulating data for the *no-evidence-accumulation model*,
1697 we removed the accumulation of information across trials by setting the Hazard rate H to
1698 0.5. Simulated data thus depended only on the participant-wise estimates for the amplitudes
1699 $a_{LLR/\psi}$, frequency f , phase p and inverse decision temperature ζ .

1700 A. Similar to the full model (Figure 1F and Figure 4), simulated perceptual choices were
1701 stimulus-congruent in $72.14\% \pm 0.17\%$ of trials (in red). History-congruent amounted to
1702 $49.89\% \pm 0.03\%$ of trials (in blue). In contrast to the full model, the no-accumulation model
1703 showed a significant bias against perceptual history $T(4.32 \times 10^3) = -3.28$, $p = 1.06 \times 10^{-3}$;
1704 upper panel). In contrast to the full model, there was no difference in the frequency of
1705 history-congruent choices between correct and error trials ($T(4.31 \times 10^3) = 0.76$, $p = 0.44$;
1706 lower panel).

1707 B. In the no-evidence-accumulation model, we found no significant autocorrelation of history-
1708 congruence beyond the first trial, whereas the autocorrelation of stimulus-congruence was
1709 preserved.

1710 C. In the no-evidence-accumulation model, the number of consecutive trials at which true
1711 autocorrelation coefficients exceeded the autocorrelation coefficients for randomly permuted
1712 data increased with respect to stimulus-congruence ($2.83 \pm 1.49 \times 10^{-3}$ trials; $T(4.31 \times 10^3) =$
1713 3.45 , $p = 5.73 \times 10^{-4}$) and decreased with respect to history-congruence ($1.85 \pm 3.49 \times 10^{-4}$
1714 trials; $T(4.32 \times 10^3) = -19.37$, $p = 3.49 \times 10^{-80}$) relative to the full model.

1715 D. In the no-evidence-accumulation model, the smoothed probabilities of stimulus- and
1716 history-congruence (sliding windows of ± 5 trials) fluctuated as **a scale-invariant process**
1717 **with a 1/f power law**, i.e., at power densities that were inversely proportional to the
1718 frequency (power $\sim 1/f^\beta$; stimulus-congruence: $\beta = -0.82 \pm 1.2 \times 10^{-3}$, $T(1.92 \times 10^5) =$
1719 -681.98 , $p < 2.2 \times 10^{-308}$; history-congruence: $\beta = -0.78 \pm 1.11 \times 10^{-3}$, $T(1.92 \times 10^5) =$
1720 -706.57 , $p < 2.2 \times 10^{-308}$).

1721 E. In the no-evidence-accumulation model, the distribution of phase shift between fluctuations
1722 in simulated stimulus- and history-congruence peaked at half a cycle (π denoted by dotted
1723 line). In contrast to the full model, the dynamic probabilities of simulated stimulus- and
1724 history-congruence were not significantly anti-correlated ($\beta = 6.39 \times 10^{-4} \pm 7.22 \times 10^{-4}$,
1725 $T(8.89 \times 10^5) = 0.89$, $p = 0.38$).

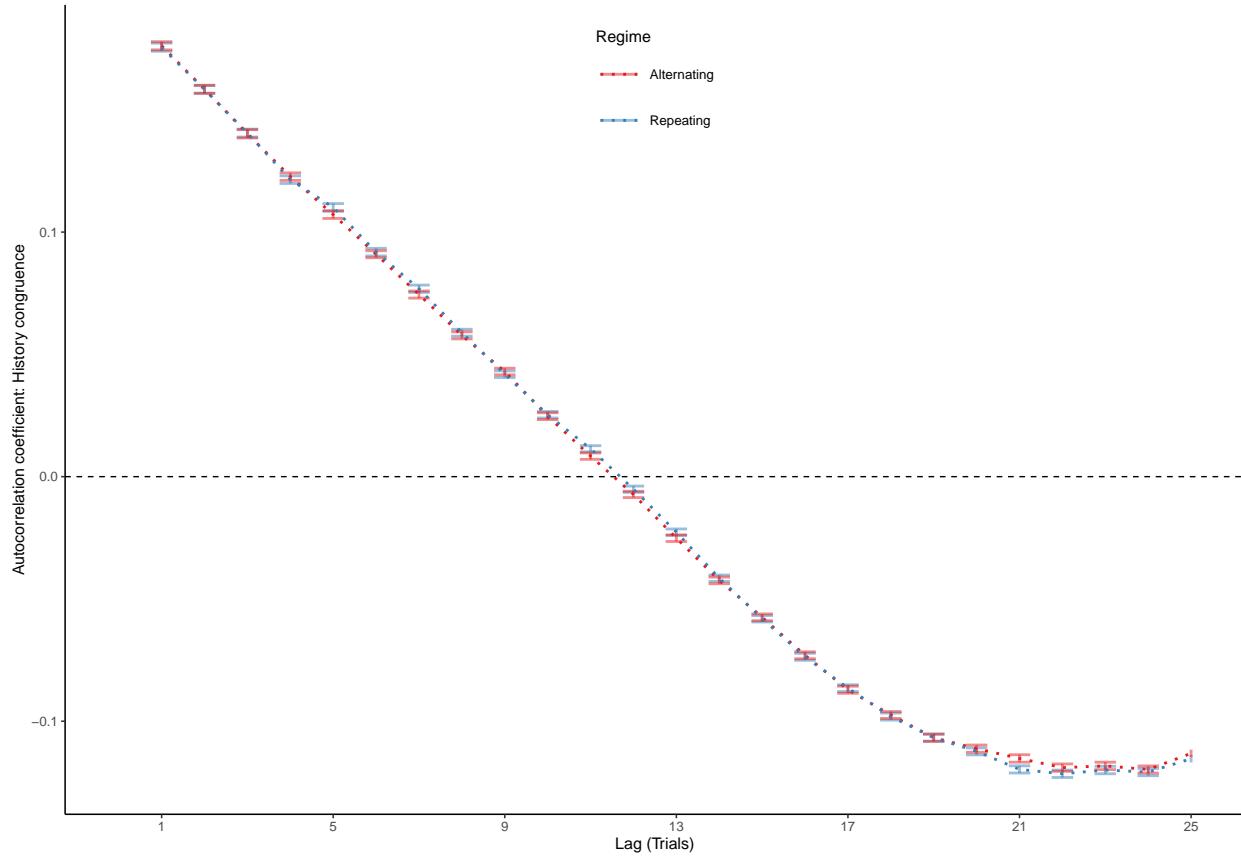
1726 F. In the no-evidence-accumulation model, the average squared coherence between fluctuations
1727 in simulated stimulus- and history-congruence (black dotted line) was reduced in comparison
1728 to the full model ($T(3.56 \times 10^3) = -9.96$, $p = 4.63 \times 10^{-23}$) and amounted to $2.8 \pm 7.29 \times 10^{-4}\%$.

1729 G. Similar to the full bimodal inference model, confidence simulated from the no-evidence-
1730 accumulation model was enhanced for stimulus-congruent choices ($\beta = 0.01 \pm 9.4 \times 10^{-5}$,
1731 $T(2.11 \times 10^6) = 158.1$, $p < 2.2 \times 10^{-308}$). In contrast to the full bimodal inference model,
1732 history-congruent choices were not characterized by enhanced confidence ($\beta = 8.78 \times 10^{-5} \pm$

₁₇₃₃ 8.21×10^{-5} , $T(2.11 \times 10^6) = 1.07$, $p = 0.29$).

₁₇₃₄ H. In the no-evidence-accumulation model, the positive quadratic relationship between the
₁₇₃₅ mode of perceptual processing and confidence was markedly reduced in comparison to the full
₁₇₃₆ 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
₁₇₃₇ dotted lines indicate minimum posterior certainty and the associated mode, respectively.

1738 **9.18 Supplemental Figure S14**



1739
1740 **Supplemental Figure S14. Autocorrelation of history-congruence of alternating**
1741 **and repeating biases.** Here, we simulate the autocorrelation of history-congruence in 10^3
1742 synthetic participants. In the repeating regime (blue), history-congruence fluctuated between
1743 50% and 80% (blue) in interleaved blocks (10 blocks per condition with a random duration
1744 between 15 and 30 trials). In the alternation regime (red), history-congruence fluctuated
1745 between 50% and 20%. The resulting autocorrelation curves for history-congruence overlap,
1746 indicating that our analysis is able to accommodate both repeating and alternating biases.

¹⁷⁴⁷ 9.19 Supplemental Table T1

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

(continued)

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

¹⁷⁴⁸ **9.20 Supplemental Table T2**

Parameters	Interpretation
α	Sensitivity to sensory information
H	Expected probability of a switch in the cause of sensory information (Hazard)
a_{LLR}	Amplitude of fluctuations in likelihood precision ω_{LLR}
a_ψ	Amplitude of fluctuations in prior precision ω_ψ
f	Frequency of ω_{LLR} and ω_ψ
p	Phase (p for ω_{LLR} ; p + π for ω_ψ)
ζ	Inverse decision temperature

1749 **10 Response to Reviewers**

1750 **10.1 Reviewer 1**

1751 This was an interesting and thought-provoking submission. I note that it is
1752 a revision: I am therefore supposing that the authors have already responded
1753 to one round of reviewer comments and that you are potentially interested in
1754 publishing this work. In brief, I think there are many elements of this report that
1755 warrant publication; however, there are some parts that are less compelling and
1756 could be deferred to a subsequent paper. The paper is far too long and would
1757 benefit greatly from being streamlined. Furthermore, some of the modeling is
1758 overengineered and is difficult to follow. I have tried to suggest how the authors
1759 might improve the presentation of their work in my comments to authors.

1760 I enjoyed reading this long but thought-provoking report of fluctuations in the
1761 sensitivity to sensory evidence in perceptual decision-making tasks. There were
1762 some parts of this report that were compelling and interesting. Other parts were
1763 less convincing and difficult to understand. Overall, this paper is far too long. An
1764 analogy that might help here is that a dinner guest is very entertaining for the
1765 first hour or so - and then overstays their welcome; until you start wishing they
1766 would leave. Another analogy, which came to mind, was that the modeling—and
1767 its interpretation—was a bit autistic (i.e., lots of fascinating if questionable detail
1768 with a lack of central coherence).

1769 I think that both issues could be resolved by shortening the paper and removing
1770 (or, at least, greatly simplifying) the final simulation studies of metacognition. I
1771 try to unpack this suggestion in the following.

1772 We would like to thank Prof. Friston for the very insightful and helpful comments on our
1773 manuscript. We fully agree that our ideas about the computational function of between-mode

1774 fluctuations and the associated simulations may be presented in a more accessible form in a
1775 standalone paper. As we outlined in more detail below, we have streamlined our findings
1776 and rewrote the paper and reduced it's length by shortening the sections on computational
1777 modeling. We have also followed Prof. Friston's suggestion to interpret the effects of mode
1778 on RT and confidence in the context of predictive processing definitions of attention, namely
1779 the allocation of precision between prior and likelihood.

1780 Major points:

1781 As I understand it, you have used publicly available data on perceptual decision-
1782 making to demonstrate slow fluctuations in the tendency to predicate perceptual
1783 decisions on the stimuli and on the history of recent decisions. You find scale-free
1784 fluctuations in this tendency — that are anti-correlated — and interpret this as
1785 fluctuations in the precision afforded sensory evidence, relative to prior beliefs.
1786 This interpretation is based upon a model of serial dependencies (parameterised
1787 with a hazard function).

1788 The stimulus and history (i.e., likelihood and prior) sensitivities are anti-correlated
1789 and both show scale free behavior. This is reproduced in men and mice. You
1790 then proceed to model this with periodic fluctuations in the precisions or weights
1791 applied to the likelihood and prior that are in anti-phase - and then estimate the
1792 parameters of the ensuing model. Finally, you then simulate the learning of the
1793 hazard parameter — and something called metacognition - to show that periodic
1794 fluctuations improve estimates of metacognition (based upon a Rescorla-Wagner
1795 model of learning). You motivate this by suggesting that the fluctuations in
1796 sensitivity are somehow necessary to elude circular inference and provide better
1797 estimates of precision.

1798 Note that I am reading the parameters omega_LL and omega_psi as the
1799 precision of the likelihood and prior, where the precision of the likelihood is

1800 called sensory precision. This contrasts with your use of sensory precision, which
1801 seems to be attributed to a metacognitive construct M.

1802 As noted above, all of this is fascinating but there are too many moving parts
1803 that do not fit together comfortably. I will list a few examples:

1804 **10.1.1 Comment 1**

1805 If, empirically, the fluctuations in sensitivity are scale-free with a 1/f power law,
1806 why did you elect to model fluctuations in precision as a periodic function with
1807 one unique timescale (i.e., f).?

1808 The reason for choosing a unique timescale f was to enable our model to depict the dominant
1809 timescale at which prior and likelihood precision fluctuate in their impact on perceptual
1810 decision-making, giving rise to between-mode fluctuations. We think that identifying this
1811 timescale is important for planning future experiments targeted at between-mode fluctuations
1812 and their manipulation by causal interventions (e.g., pharmacology or TMS). The posterior
1813 value for f lies at approximately $0.11 \frac{1}{N_{trials}}$ in both humans and mice. The value of f
1814 approximately matches the transition probabilities between *engaged* and *disengaged* states in
1815 work assessing fluctuations in perceptual decision-making using Hidden Markov models (stay
1816 probabilities ranged between 0.94 and 0.98, see Ashwood et al., Nature Neuroscience 2022).
1817 Simulating from our model (Figure 4) replicates the 1/f feature of the empirical data. Please
1818 note that the individual trial is the smallest unit of *measurement* for these fluctuations, such
1819 that our analysis is limited by definition to frequencies below 1 ($1/N_{trials}$).

1820 We now provide a rationale for choosing one value for f - identifying the dominant timescale
1821 for fluctuations in mode - in the results section:

- 1822 • To allow for *bimodal inference*, i.e., alternating periods of internally- and externally-
1823 biased modes of perceptual processing that occur irrespective of the sequence of preceding
1824 experiences, we assumed that likelihood and prior vary in their influence on the perceptual

1825 decision according to fluctuations governed by ω_{LLR} and ω_ψ . These anti-phase sine
1826 functions (defined by amplitudes $a_{LLR/\psi}$, frequency f and phase p) determine the
1827 precision afforded to the likelihood and prior⁵³. The implicit anti-phase fluctuations
1828 are mandated by Bayes-optimal formulations in which inference depends only on the
1829 relative values of prior and likelihood precision (i.e., the Kalman gain⁵⁴). As such, ω_{LLR}
1830 and ω_ψ implement a hyperprior⁵⁵ in which the likelihood and prior precisions are shifted
1831 against each other at a dominant timescale defined by f : (...)

- 1832 • (...) The parameter f captures the dominant time scale at which likelihood (amplitude
1833 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
1834 (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
1835 against each other and was estimated at $0.11 \pm 1.68 \times 10^{-5} 1/N_{trials}$ and $0.11 \pm 1.63 \times 10^{-4}$
1836 $1/N_{trials}$ in mice.
- 1837 • Table 2 (see response to Comment 22 by Reviewer 1) contains an additional definition
1838 for all model parameters, including f .

1839 10.1.2 Comment 2

1840 **At present, the estimates of meta-cognition (M) play the role of accumulated
1841 estimates of (sensory or prior) precision. Why are these not used in your model
1842 of perceptual decisions in Equation 2.**

1843 In our model, the parameter α controls the encoding precision by governing the transformation
1844 from sensory stimuli to the log likelihood ratio (LLR) via the equations (13-16) (the LLR
1845 ends up closer to zero when α is low). Our simulations on the adaptive benefits of bimodal
1846 inference rest on the assumption that α may change unpredictably. The construct M is a
1847 belief about α that may be useful for, e.g., communicating the precision of sensory encoding
1848 to other cognitive domains or agents. To our mind, α is a feature of low-level sensory encoding
1849 that cannot be modulated by top-down beliefs such as M . This is why we did not include

1850 M in equation (2). Please note that we have removed this section following Comment 9 of
1851 Reviewer 1.

1852 **10.1.3 Comment 3**

1853 **Why do you assume that non-specific increases in attention and arousal will**
1854 **increase reaction times? If one has very precise prior beliefs (and is not attending**
1855 **to stimuli), would you not expect a decrease in reaction time?**

1856 Thanks a lot for pointing this out (see also the Comment below and Comment 6 by Reviewer
1857 3). Both high prior and high likelihood precision lead to higher absolute values of the log
1858 posterior ratio (reflecting certainty encoded by the decision variable), and thus faster RTs.
1859 This is reflected empirically by RTs in humans (Figure 2) and to a lesser degree in mice
1860 (Figure 3): RTs tended to be shorter for stronger biases toward both external and internal
1861 mode. Our model, which incorporates (i), the accumulation of information across trials, and
1862 (ii), fluctuations in the likelihood precision relative to the prior precision, recapitulates this
1863 feature of the data, which is lost or greatly attenuated when eliminating process (i) and/or
1864 (ii) (see model comparison and simulations below). Our data thus confirm the hypothesis
1865 that both high prior and likelihood precision lead to faster RTs.

1866 In the previous version of the manuscript, we had included the relation between mode and
1867 RTs and confidence primarily as a defensive analysis against the proposition that what we
1868 call between-mode fluctuations is not a perceptual phenomenon, but occurs downstream of
1869 perception. One may imagine that fluctuations in perceptual performance are not influenced
1870 by periods of relative increases in prior precision (which decrease performance in fully
1871 randomized designs), but by periods when participants do not attend to the task at all, i.e.,
1872 neither to sensory information nor to prior precision. We propose that the analyses of RTs
1873 and confidence can give some insight into whether such alternative mechanisms may be at
1874 play, as we would assume longer RTs and lower confidence if participants failed to attend to
1875 the task at all.

1876 That being said, we realize that, due to the potential non-linearity in their relation to arousal
1877 (see also Comment 6 by Reviewer 3), RTs and confidence cannot provide a definitive map
1878 of where fluctuations in mode are situated in relation to arousal. Such a delineation may
1879 potentially be provided by tracking of pupil size, response behavior or by neural data (e.g.,
1880 noise correlations of fluctuations in LFP). These data are not available for the studies in
1881 the Confidence Database, but were very recently published for the IBL database (after this
1882 manuscript was submitted). While we believe that this is beyond the scope of this manuscript,
1883 we will assess the relation of pupil diameter, motor behavior (turning of the response wheel)
1884 and LFPs to between-mode fluctuations in a future publication using the IBL dataset.

1885 In light of the considerations above and our response to Comment 6 by Reviewer 3, we now
1886 refer to attention in the predictive processing sense. We use the term “task engagement”
1887 instead of “on-task attention” to refer to situation in which participants may not attend to
1888 the task at all, e.g. due to low arousal or fatigue, and discuss these as alternative explanations
1889 for between-mode fluctuations. We have made three sets of changes to our manuscript:

1890 First, we present our results on the relation of mode to RT and Confidence in a more
1891 descriptive way, and do not use it as a strong defensive analysis against arousal:

1892 • The above results point to systematic fluctuations in the *decision variable*⁴⁴ that deter-
1893 mines perceptual choices, causing enhanced sensitivity to external stimulus information
1894 during external mode and increased biases toward preceding choices during internal
1895 mode. As such, fluctuations in mode should influence downstream aspects of behavior
1896 and cognition that operate on the perceptual decision variable⁴⁴. To test this hypothesis
1897 with respect to motor behavior and metacognition, we asked how bimodal inference
1898 relates to response times (RTs) and confidence reports. (...)

1899 • (...) In sum, the above results indicate that reporting behavior and metacognition do
1900 not map linearly onto the mode of sensory processing. Rather, they suggest that slow
1901 fluctuations in the respective impact of external and internal information are most likely

1902 to affect perception at an early level of sensory analysis^{46,47}. Such low-level processing
1903 may thus integrate perceptual history with external inputs into a decision variable⁴⁴
1904 that influences not only perceptual choices, but also the speed and confidence at which
1905 they are made.

- 1906 • In what follows, we probe alternative explanations for between-mode fluctuations, test
1907 for the existence of modes in mice, and propose a predictive processing model that
1908 explains fluctuations in mode by ongoing shifts in the precision afforded to external
1909 sensory information relative to internal predictions driven by perceptual history.

1910 Second, we have re-written our discussion of the quadratic relationship of mode to RTs
1911 and Confidence, focusing on predictive processing models of attention: - As a functional
1912 explanation for bimodal inference, we propose that perception temporarily disengages from
1913 internal predictions to form stable inferences about the statistical properties of the sensory
1914 environment. Between-mode fluctuations may thus elude circular inferences that occur when
1915 both the causes and the encoding of sensory stimuli are volatile^{19,57}. By the same token, we
1916 suggest that fluctuations in mode occur at the level of perceptual processing^{26,30,46,47}, and are
1917 not a passive phenomenon that is primarily driven by factors situated up- or downstream of
1918 sensory analysis.

- 1919 • How does attention relate to between-mode fluctuations? According to predictive
1920 processing, attention corresponds to the precision afforded to the probability distributions
1921 that underlie perceptual inference⁵³. From this perspective, fluctuations between external
1922 and internal mode can be understood as ongoing shifts in the attention afforded to either
1923 external sensory information (regulated via likelihood precision) or internal predictions
1924 (regulated via prior precision). When the precision of either likelihood or prior increases,
1925 posterior precision increases, which leads to faster RTs and higher confidence. Therefore,
1926 when defined from the perspective of predictive processing as the precision afforded to

1927 likelihood and prior⁵³, fluctuations in attention may provide a plausible explanation for
1928 the quadratic relationship of mode to RTs and confidence (Figure 2H and J; Figure 3I;
1929 Figure 3I).

1930 Third, we have added a more general discussion of our findings in the light of fluctuations in
1931 task engagement:

1932 • Outside of the predictive processing field, attention is often understood in the context of
1933 task engagement⁶³, which varies according to the availability of cognitive resources that
1934 are modulated by factors such as tonic arousal, familiarity with the task, or fatigue⁶³. Our
1935 results suggest that internal mode processing cannot be completely reduced to intervals
1936 of low task engagement: In addition to shorter RTs and elevated confidence, choices
1937 during internal mode were not random or globally biased, but driven by perceptual
1938 history (Supplemental Figures S6-7). Moreover, our computational model identified
1939 the dominant timescale of between-mode fluctuations at $0.11 \text{ } 1/N_{trials}$, which may be
1940 compatible with fluctuations in arousal⁶⁴, but is faster than to be expected for the
1941 development of task familiarity or fatigue.

1942 • However, in interpreting the impact of between-mode fluctuations on perceptual accuracy,
1943 speed of response and confidence, it is important to consider that global modulators
1944 such as tonic arousal are known to have non-linear effects on task performance⁶⁵: In
1945 perceptual tasks, performance seems to be highest during mid-level arousal, whereas low-
1946 and high-level arousal lead to reduced accuracy and slower responses⁶⁵. This contrasts
1947 with the effects of bimodal inference, where accuracy increases linearly as one moves
1948 from internal to external mode, and responses become faster at both ends of the mode
1949 spectrum.

1950 • Of note, high phasic arousal has been shown to suppress multi-domain biases in decision-
1951 making in humans and mice⁶⁶⁻⁶⁸, including the biases toward perceptual history²⁸ that

1952 we implicate in internal mode processing. The increase in response speed and history
1953 congruence over time (Supplemental Section 9.4) may argue against insufficient training
1954 as an alternative explanation for internal mode processing, but may also taken as a
1955 sign of waning arousal. The multiple mechanistic mappings to RTs and confidence
1956 therefore warrant more direct measures of arousal (such as pupil size^{28,65,66,68–70}, motor
1957 behavior^{69,70}, or neural data⁷¹) to better delineate bimodal inference from fluctuations
1958 in global modulators of task performance.

1959 **10.1.4 Comment 4**

1960 **In the predictive processing literature, attention is thought to correspond to**
1961 **fluctuations in sensory and prior precision. Why did you then consider attention**
1962 **as some additional or unrelated confound?**

1963 This point is closely related to the comment above. We realize that, in the predictive
1964 processing field, attention is equated with the precision of probability distributions that
1965 contribute to the perceptual decision, such that an observer can attend strongly to sensory
1966 information (high likelihood precision) or to internal predictions derived from the sequence of
1967 preceding percepts (high prior precision). Therefore, when following the above predictive
1968 processing definition, fluctuations in attention can be equated with fluctuations in mode.

1969 However, we feel that outside of the predictive processing field, attention is not always
1970 conceived in that way, such that low attention is often considered as low engagement with
1971 the task, i.e., relating to low likelihood and low prior precision in the predictive processing
1972 sense. It is against these caveats that our control analysis (based on psychometric functions,
1973 training effects, RTs and confidence) defend our conclusions on bimodal inference.

1974 We now provide a more nuanced interpretation of our findings of RTs and confidence in
1975 relation to attention, with a specific focus on predictive processing and precision. We hope
1976 that our responses to the comment above resolve the points raised in this comment.

1977 **10.1.5 Comment 5**

1978 **What licences the assumption that “agents depend upon internal confidence
1979 signals” in the absence of feedback?**

1980 In the absence of feedback, observers can only rely on internal estimates of performance to
1981 guide updates to their model of the reliability of their sensory apparatus (inferences about
1982 M). Previous work (e.g. Guggenmos et al., Elife 2106, <https://doi.org/10.7554/eLife.13388>)
1983 has shown that confidence signals can provide signals that drive perceptual learning in the
1984 absence of feedback. This has motivated our model simulation on the adaptive benefits of
1985 bimodal inference for metacognition, where the learning signal ϵ_M (i.e., the difference between
1986 the choice and its probability) drives inferences about M . Please note that we have removed
1987 this section following Comment 9 of Reviewer 1.

1988 **10.1.6 Comment 6**

1989 **And what licences the assumption that internal confidence feedback corresponds
1990 to “the absolute of the posterior log ratio” (did you mean the log of the posterior
1991 ratio)?**

1992 We mean the absolute of the log of the posterior ratio. Following first order models (see
1993 e.g., Fleming & Daw, Self-evaluation of decision-making: A general Bayesian framework for
1994 metacognitive computation, Psychol. Rev. 2017, <https://doi.org/10.1037/rev0000045>), the
1995 perceptual decision and the confidence report rely on the posterior. The distance of the log
1996 of the posterior ratio L_t from zero becomes a measure of decision-certainty or confidence.

1997 **10.1.7 Comment 7**

1998 **I got a bit lost here when you say that “the precision of sensory coding M a
1999 function of u_t. This is largely because I couldn’t find a definition of u_t.**

2000 We apologize for this lack of clarity. In the model simulations on the adaptive benefits of

2001 bimodal inference, we generated stimuli s_t from a Bernoulli-distribution with $p = q = 0.5$.
2002 The value of u_t was then defined via equation (13), following our modeling of the human
2003 data. Please note that we have removed this section following Comment 9 of Reviewer 1.

2004 **10.1.8 Comment 8**

2005 **What licences an application of Rescorla-Wagner to learning the parameters (as**
2006 **in Equation 11) and, learning sensory precision as described by M_T (Equation**
2007 **13). Are you moving from a Bayesian framework to a reinforcement learning**
2008 **framework?**

2009 We would like to thank the reviewer for pointing out this inconsistency. We have chosen the
2010 Rescorla-Wagner learning rule for simplicity: In our model, the speed of learning about H
2011 and M varied according to the current mode of perceptual processing and a constant learning
2012 rate. Allowing the learning rate itself to vary as a function of preceding experiences would
2013 add an additional level of complexity that we sought to omit in this analysis. However, we
2014 fully agree that choosing a Bayesian framework (e.g., a three-level HGF) would indeed be
2015 more consistent. Please note that we have removed this section following Comment 9 of
2016 Reviewer 1.

2017 **10.1.9 Comment 9**

2018 **I am sure you have answers to these questions - but with each new question**
2019 **the reader is left more and more skeptical that there is a coherent story behind**
2020 **your analyses. It would have been more convincing had you just committed to**
2021 **a Bayesian filter and made your points using one update scheme, under ideal**
2022 **Bayesian observer assumptions.**

2023 **Unlike your piecemeal scheme, things like the hierarchical Gaussian filter estimates**
2024 **the sensory and prior decisions explicitly and these estimates underwrite posterior**
2025 **inference. In your scheme, the sensory precision M appears to have no influence**

2026 on perceptual inference (which is why, presumably you call it metacognition).
2027 The problem with this is that your motivation for systematic fluctuations in
2028 precision is weakened. This is because improved metacognition does not improve
2029 perception — it only improves the perception of perception.

2030 In light of the above, can I suggest that you remove Section 5.8 and use your
2031 model in the preceding section to endorse your hypothesis along the following
2032 lines:

2033 “In summary, we hypothesized that subjects have certain hyperpriors that are
2034 apt for accommodating fluctuations in the predictability of their environment;
2035 i.e., people believe that their world is inherently volatile. This means that to be
2036 Bayes optimal it is necessary to periodically re-evaluate posterior beliefs about
2037 model parameters. One way to do this is to periodically suspend the precision
2038 of prior beliefs and increase the precision afforded to sensory evidence that
2039 updates (Bayesian) beliefs about model parameters. The empirical evidence above
2040 suggests that the timescale of this periodic scheduling of evidence accumulation
2041 may be scale-invariant. This means that there may exist a timescale of periodic
2042 fluctuations in precision over every window or length of perceptual decision-
2043 making. In what follows, we model perceptual decisions under a generative model
2044 (based upon a hazard function to model historical or serial dependencies) with, a
2045 periodic fluctuation in the precision of sensory evidence relative to prior beliefs
2046 at a particular timescale. Remarkably—using Bayesian model comparison—we
2047 find that a model with fluctuating precisions has much greater evidence, relative
2048 to a model in the absence of fluctuating precisions. Furthermore, we were able
2049 to quantify the dominant timescale of periodic fluctuations; appropriate for these
2050 kinds of paradigm.”

2051 Note, again, I am reading your omega_LL and omega_psi as precisions and

2052 that the periodic modulation is the hyperprior that you are characterizing—and
2053 have discovered.

2054 We would like to thank Prof. Friston for these very helpful and precise suggestions. In brief,
2055 we now provide a quantitative assessment of model space based on AIC (i) and have followed
2056 the suggestion of omitting section 5.8 (ii).

2057 In addition to the qualitative assessment of our models in the initial version of our manuscript,
2058 we have conducted a formal model comparison (i). Following the model comparisons in
2059 other sections of the manuscript, we based the model comparison on AIC. We furthermore
2060 show that the winning *bimodal inference model* predicts out-of-training variables (RT and
2061 confidence) and use simulations from posterior model parameters to show that, in contrast to
2062 reduced models, the bimodal inference model neither over- nor underfits the empirical data.

2063 We have added a description of our model comparison to the Method section:

2064 • We validated the bimodal inference model in three steps: a formal model comparison to
2065 reduced models based on AIC (Figure 1F-G; Supplemental Figure S9), the prediction of
2066 within-training (stimulus- and history-congruence) as well as out-of-training variables
2067 (RT and confidence), and a qualitative reproduction of the empirical data from model
2068 simulations based on estimated parameters (Figure 4).

2069 • **Model comparison.** We assessed the following model space based on AIC:

2070 • The full *bimodal inference model* (M1; Figure 1F) incorporates the influence of sensory
2071 information according to the parameter α (likelihood); the integration of evidence across
2072 trials according to the parameter H (prior); anti-phase oscillations in between likelihood
2073 and prior precision according to ω_{LLR} and ω_ψ with parameters a_{LLR} (amplitude likelihood
2074 fluctuation), a_ψ (amplitude prior fluctuation), f (frequency) and p (phase).

2075 • The *likelihood-oscillation-only model* (M2; Figure 1G) incorporates the influence of sen-
2076 sory information according to parameter α (likelihood); the integration of evidence across

2077 trials according to parameter H (prior); oscillations in likelihood precision according
2078 to ω_{LLR} with parameters a_{LLR} (amplitude likelihood fluctuation), f (frequency) and p
2079 (phase).

- 2080 • The *prior-oscillation-only model* (M3; Figure 1G) incorporates the influence of sensory
2081 information according to parameter α (likelihood); the integration of evidence across
2082 trials according to parameter H (prior); oscillations in the prior precision according
2083 to ω_ψ with parameters a_ψ (amplitude prior fluctuation), f (frequency) and p (phase).
2084 Please note that all models M1-3 lead to shifts in the relative precision of likelihood and
2085 prior.
- 2086 • The *normative-evidence-accumulation* (M4; Figure 1G) incorporates the influence of
2087 sensory information according to parameter α (likelihood); the integration of evidence
2088 across trials according to parameter H (prior), There are no additional oscillations.
2089 Model M4 thus corresponds to the model proposed by Glaze et al. and captures normative
2090 evidence accumulation in unpredictable environments using a Bayesian update scheme⁵¹.
2091 The comparison against M4 tests the null hypothesis that fluctuations in mode emerge
2092 from a normative Bayesian model without the ad-hoc addition of oscillations as in models
2093 M1-3.
- 2094 • The *no-evidence-accumulation* (M5; Figure 1G) incorporates the influence of sensory
2095 information according to parameter α (likelihood). The model lacks integration of
2096 evidence across trials (flat prior) and oscillations. The comparison against M5 tests
2097 the null hypothesis that observers do not use prior information derived from serial
2098 dependency in perception.

- 2099 • **Prediction of within-training and out-of-training variables.** To validate our
2100 model, we correlated individual posterior parameter estimates with the respective
2101 conventional variables. As a sanity check, we tested (i), whether the estimated hazard
2102 rate H correlated negatively with the frequency of history-congruent choices and, (ii),

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

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

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

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

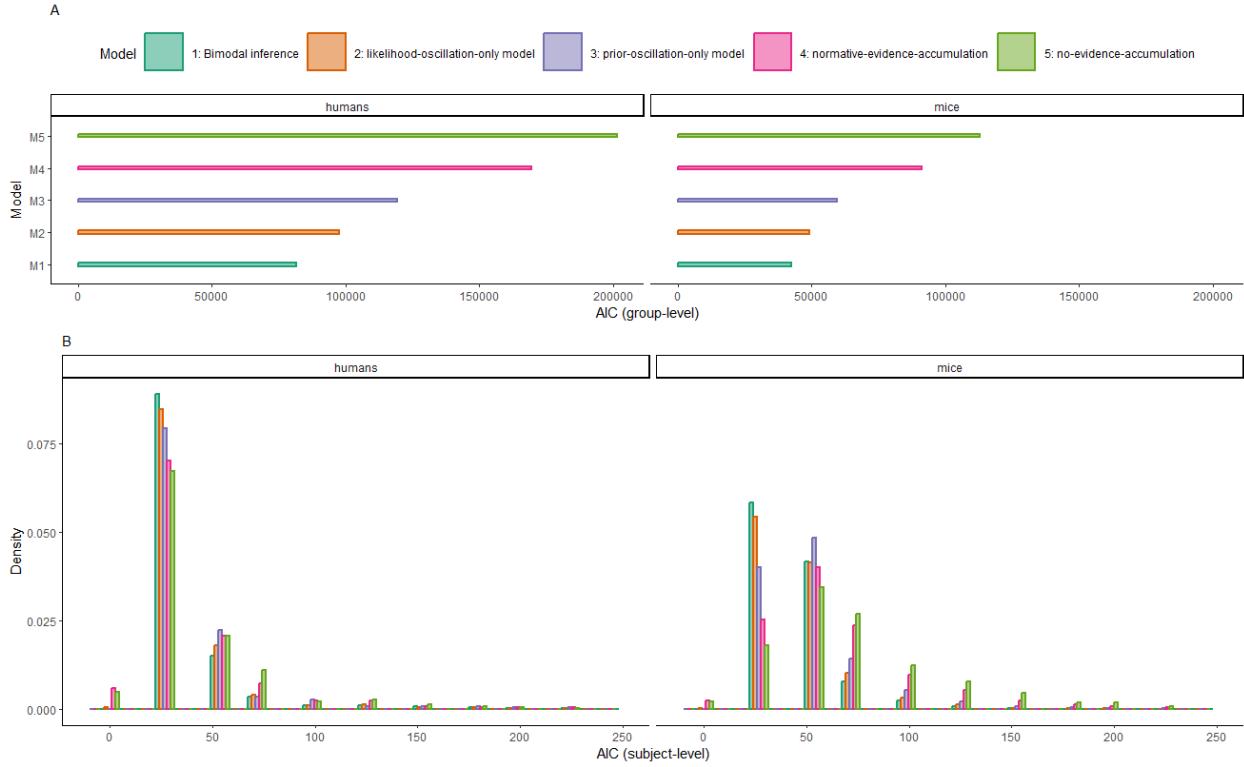


Figure 1 F-G

of evidence according to parameters H (middle panel), and anti-phase oscillations in the precision terms ω_{LLR} and ω_ψ (right panel).

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

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

2140 summarize these findings in the Results section and have added a Supplemental Figure S9 to
2141 show the distribution of observer-level AIC at the session-level (see below):

- 2142 • We used a maximum likelihood procedure to fit the bimodal inference model (M1, Figure
2143 1F) to the behavioral data from the Confidence database²⁰ and the IBL database²¹,
2144 optimizing the parameters α , H , amp_{LLR} , amp_ψ , f , p , and ζ (see Methods for details and
2145 Supplemental Table T2 for a summary of the parameters of the bimodal inference model).
2146 We validated our model in three steps: First, to show that bimodal inference does not
2147 emerge spontaneously in normative Bayesian models of evidence accumulation, but
2148 requires the ad-hoc addition of anti-phase oscillations in prior and likelihood precision,
2149 we compared the bimodal inference model to four control models (M2-5, Figure 1G).
2150 In these models, we successively removed the anti-phase oscillations (M2-M4) and the
2151 integration of information across trials (M5) from the bimodal inference model and
2152 performed a model comparison based on AIC.
- 2153 • Model M2 ($AIC_2 = 9.76 \times 10^4$ in humans and 4.91×10^4 in mice) and Model M3 (AIC_3
2154 $= 1.19 \times 10^5$ in humans and 5.95×10^4 in mice) incorporated only oscillations of either
2155 likelihood or prior precision. Model M4 ($AIC_4 = 1.69 \times 10^5$ in humans and 9.12×10^4 in
2156 mice) lacked any oscillations of likelihood and prior precision and corresponded to the
2157 normative model proposed by Glaze et al.⁵¹. In model M5 ($AIC_4 = 2.01 \times 10^5$ in humans
2158 and 1.13×10^5 in mice), we furthermore removed the integration of information across
2159 trials, such that perception depended only in incoming sensory information (Figure 1G).
- 2160 • The bimodal inference model achieved the lowest AIC across the full model space (AIC_1
2161 $= 8.16 \times 10^4$ in humans and 4.24×10^4 in mice) and was clearly superior to the normative
2162 Bayesian model of evidence accumulation ($\delta_{AIC} = -8.79 \times 10^4$ in humans and -4.87×10^4
2163 in mice; Supplemental Figure S9).
- 2164 • As a second validation of the bimodal inference model, we tested whether the posterior
2165 model predicted within-training and out-of-training variables. The bimodal inference

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

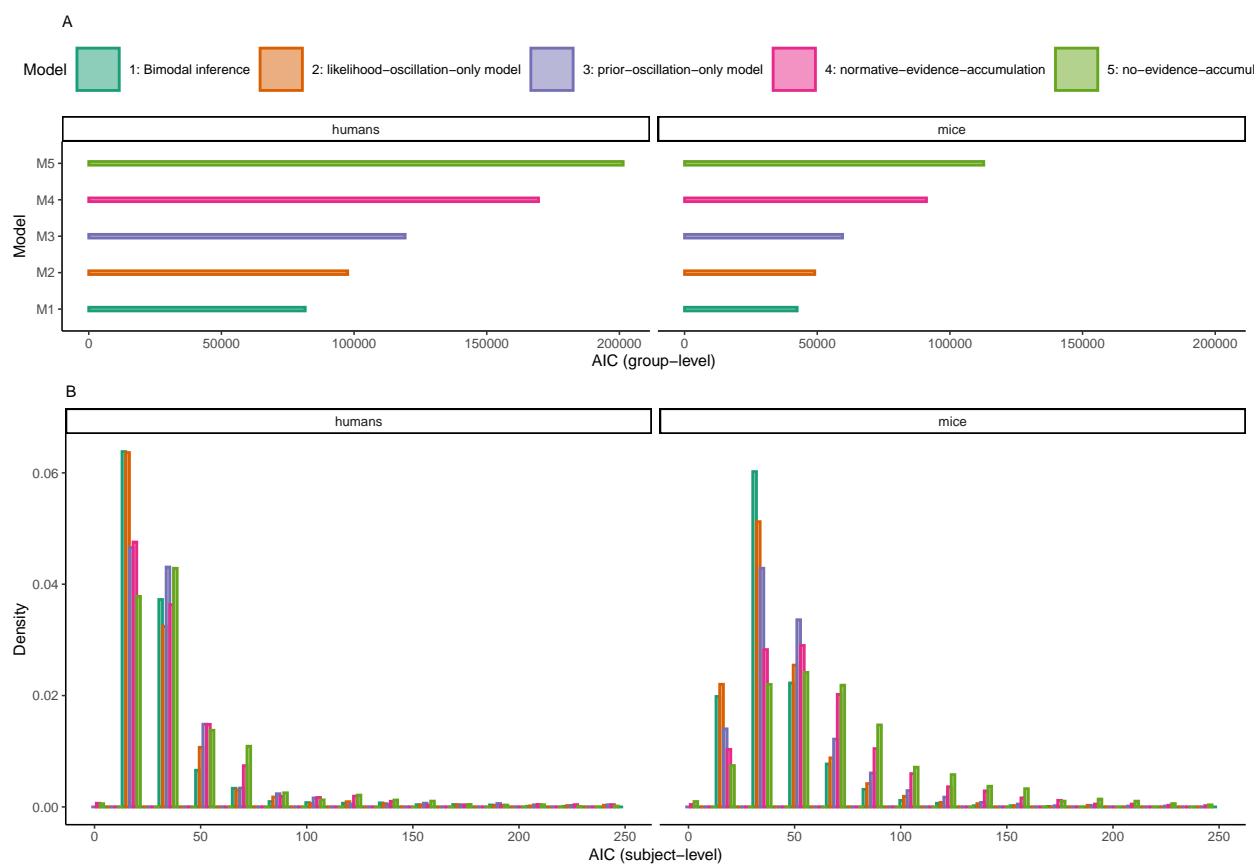
- As a sanity check for model fit, we tested whether the frequency of stimulus- and history-congruent trials in the Confidence database²⁰ and IBL database²¹ correlate with the estimated parameters α and H , respectively. As expected, the estimated sensitivity toward stimulus information α was positively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

2192 $T(112.57) = -8.51$, $p = 8.65 \times 10^{-14}$.

- 2193 • To further probe the validity of the bimodal inference model, we tested whether posterior
2194 model quantities could explain aspects of the behavioral data that the model was not
2195 fitted to. We predicted that the posterior decision variable L_t not only encodes perceptual
2196 choices (i.e., the variable used for model estimation), but should also predict the speed
2197 of response and subjective confidence^{30,44}. Indeed, the estimated trial-wise posterior
2198 decision certainty $|L_t|$ correlated negatively with RTs in humans ($\beta = -4.36 \times 10^{-3} \pm$
2199 4.64×10^{-4} , $T(1.98 \times 10^6) = -9.41$, $p = 5.19 \times 10^{-21}$) and TDs mice ($\beta = -35.45 \pm$
2200 0.86 , $T(1.28 \times 10^6) = -41.13$, $p < 2.2 \times 10^{-308}$). Likewise, subjective confidence reports
2201 were positively correlated with the estimated posterior decision certainty in humans (β
2202 $= 7.63 \times 10^{-3} \pm 8.32 \times 10^{-4}$, $T(2.06 \times 10^6) = 9.18$, $p = 4.48 \times 10^{-20}$).
- 2203 • The dynamic accumulation of information inherent to our model entails that biases
2204 toward perceptual history are stronger when the posterior decision certainty at the
2205 preceding trial is high^{30,31,51}. Due to the link between posterior decision certainty and
2206 confidence, we reasoned that confident perceptual choices should be more likely to induce
2207 history-congruent perception at the subsequent trial^{30,31}. Indeed, logistic regression
2208 indicated that history-congruence was predicted by the posterior decision certainty
2209 $|L_{t-1}|$ (humans: $\beta = 8.22 \times 10^{-3} \pm 1.94 \times 10^{-3}$, $z = 4.25$, $p = 2.17 \times 10^{-5}$; mice: $\beta =$
2210 $-3.72 \times 10^{-3} \pm 1.83 \times 10^{-3}$, $z = -2.03$, $p = 0.04$) and subjective confidence (humans:
2211 $\beta = 0.04 \pm 1.62 \times 10^{-3}$, $z = 27.21$, $p = 4.56 \times 10^{-163}$) at the preceding trial.
- 2212 • As a third validation of the bimodal inference model, we used the posterior model
2213 parameters to simulate synthetic perceptual choices and repeated the behavioral analyses
2214 conducted for the empirical data. Simulations from the bimodal inference model
2215 closely replicated our empirical results: Simulated perceptual decisions resulted from a
2216 competition of perceptual history with incoming sensory signals (Figure 4A). Stimulus-
2217 and history-congruence were significantly autocorrelated (Figure 4B-C), fluctuating in

2218 anti-phase as a scale-invariant process with a 1/f power law (Figure 4D-F). Simulated
 2219 posterior certainty^{28,30,44} (i.e., the absolute of the log posterior ratio $|L_t|$) showed a
 2220 quadratic relationship to the mode of sensory processing (Figure 4H), mirroring the
 2221 relation of RTs and confidence reports to external and internal biases in perception
 2222 (Figure 2G-H and Figure 3G-H). Crucially, the overlap between empirical and simulated
 2223 data broke down when we removed the anti-phase oscillations or the accumulation of
 2224 evidence over time from the bimodal inference model (Supplemental Figure S10-13).

- 2225 • In sum, computational modeling suggested that between-mode fluctuations are best
 2226 explained by two interlinked processes (Figure 1E): (i), the dynamic accumulation of
 2227 information across successive trials mandated by normative Bayesians model of evidence
 2228 accumulation and, (ii), ongoing anti-phase oscillations in the impact of external and
 2229 internal information.



2231 • **Supplemental Figure S9.** Comparison of the bimodal inference model against reduced
2232 control models.

- 2233 • A. Group-level AIC. The bimodal inference model (M1) achieved the lowest AIC across
2234 the full model space ($AIC_1 = 8.16 \times 10^4$ in humans and 4.24×10^4 in mice). Model
2235 M2 ($AIC_2 = 9.76 \times 10^4$ in humans and 4.91×10^4 in mice) and Model M3 ($AIC_3 =$
2236 1.19×10^5 in humans and 5.95×10^4 in mice) incorporated only oscillations of either
2237 likelihood or prior precision. Model M4 ($AIC_4 = 1.69 \times 10^5$ in humans and 9.12×10^4
2238 in mice) lacked any oscillations of likelihood and prior precision and corresponded to
2239 the normative model proposed by Glaze et al.⁵¹. In model M5 ($AIC_5 = 2.01 \times 10^5$ in
2240 humans and 1.13×10^5 in mice), we furthermore removed the integration of information
2241 across trials, such that perception depended only in incoming sensory information.
- 2242 • B. Subject-level AIC. Here, we show the distribution of AIC values at the subject-level.
2243 AIC for the bimodal inference model tended to be smaller than AIC for the comparator
2244 models (statistical comparison to the second-best model M2 in humans: $\beta = -1.71$
2245 ± 0.19 , $T(8.57 \times 10^3) = -8.85$, $p = 1.06 \times 10^{-18}$; mice: $T(1.57 \times 10^3) = -3.08$, $p =$
2246 2.12×10^{-3}).

2247 In light of our response to Comments 1 - 9 of Reviewer 1, we agree that a complete and
2248 extensive investigation of the relation between bimodal inference, learning about changes in
2249 the environment and the relation to metacognition may be beyond the scope of the current
2250 manuscript: Both Reviewer 1 and 3 (see below) have shared that the manuscript is too long
2251 and should be streamlined. Yet evaluating the full model space (e.g., comparing update rules
2252 for inferences about H and M , testing for an influence of beliefs about M on learning about H
2253 etc.) would make the manuscript even longer. We are therefore happy to follow Prof. Fristons
2254 suggestions to omit section 5.8. We have changed the manuscript in the following ways:

2255 When introducing ω_{LLR} , we identify it as the precision afforded to the likelihood, referring to
2256 the Bayesian framework, and refer to fluctuations in mode as a hyperprior.

2257 • To allow for *bimodal inference*, i.e., alternating periods of internally- and externally-
2258 biased modes of perceptual processing that occur irrespective of the sequence of preceding
2259 experiences, we assumed that likelihood and prior vary in their influence on the perceptual
2260 decision according to fluctuations governed by ω_{LLR} and ω_ψ . These anti-phase sine
2261 functions (defined by amplitudes $a_{LLR/\psi}$, frequency f and phase p) determine the
2262 precision afforded to the likelihood and prior⁵³. The implicit anti-phase fluctuations
2263 are mandated by Bayes-optimal formulations in which inference depends only on the
2264 relative values of prior and likelihood precision (i.e., the Kalman gain⁵⁴). As such, ω_{LLR}
2265 and ω_ψ implement a hyperprior⁵⁵ in which the likelihood and prior precisions are shifted
2266 against each other at a dominant timescale defined by f .

2267 We have deleted the section 5.8 and added a summary of our modeling approach to the
2268 discussion, closely following the text recommended by Prof. Friston:

- 2269 • (...) Yet relying too strongly on serial dependencies may come at a cost: When
2270 accumulating over time, internal predictions may eventually override external information,
2271 leading to circular and false inferences about the state of the environment⁵⁷. Akin to the
2272 wake-sleep-algorithm in machine learning⁵⁸, bimodal inference may help to determine
2273 whether errors result from external input or from internally-stored predictions: During
2274 internal mode, sensory processing is more strongly constrained by predictive processes
2275 that auto-encode the agent's environment. Conversely, during external mode, the
2276 network is driven predominantly by sensory inputs¹⁸. Between-mode fluctuations may
2277 thus generate an unambiguous error signal that aligns internal predictions with the
2278 current state of the environment in iterative test-update-cycles⁵⁸. On a broader scale,
2279 between-mode fluctuations may thus regulate the balance between feedforward versus
2280 feedback contributions to perception and thereby play a adaptive role in metacognition
2281 and reality monitoring⁵⁹.
- 2282 • We hypothesized that observers have certain hyperpriors that are apt for accommodating

2283 fluctuations in the predictability of their environment, i.e., people believe that their
2284 world is inherently volatile. To be Bayes optimal, it is therefore necessary to periodically
2285 re-evaluate posterior beliefs about the parameters that define an internal generative
2286 model of the external sensory environment. One way to do this is to periodically suspend
2287 the precision of prior beliefs and increase the precision afforded to sensory evidence, thus
2288 updating Bayesian beliefs about model parameters.

- 2289 • The empirical evidence above suggests that the timescale of this periodic scheduling
2290 of evidence accumulation may be scale-invariant. This means that there may exist a
2291 timescale of periodic fluctuations in precision over every window or length of perceptual
2292 decision-making. Bimodal inference predicts perceptual decisions under a generative
2293 model (based upon a hazard function to model serial dependencies between subsequent
2294 trials) with periodic fluctuations in the precision of sensory evidence relative to prior
2295 beliefs at a particular timescale. Remarkably, a systematic model comparison based
2296 on AIC indicated that a model with fluctuating precisions has much greater evidence,
2297 relative to a model in the absence of fluctuating precisions. This ad-hoc addition of
2298 oscillations to a normative Bayesian model of evidence accumulation⁵¹ allowed us to
2299 quantify the dominant timescale of periodic fluctuations mode at approximately 0.11
2300 $1/N_{trials}$ in humans and mice that is appropriate for these kinds of paradigms.

2301 Following the deletion of section 5.8, we have adapted the last sentence of the abstract and
2302 the last paragraph of the introduction:

- 2303 • (...) We propose that between-mode fluctuations generate unambiguous error signals
2304 that enable optimal inference in volatile environments.
- 2305 • When less sensitive to external stimulus information, humans and mice did not behave
2306 more randomly, but showed stronger serial dependencies in their perceptual choices^{22–33}.
2307 These serial dependencies may be understood as driven by internal predictions that reflect

2308 the autocorrelation of natural environments³⁴ and bias perception toward preceding
2309 experiences^{30,31,35}. Computational modeling indicated that ongoing changes in perceptual
2310 performance may be driven by systematic fluctuations between externally- and internally-
2311 oriented modes of sensory analysis. We suggest that such *bimodal inference* may help
2312 to build stable internal representations of the sensory environment despite an ongoing
2313 stream of sensory information.

2314 **10.1.10 Comment 11**

2315 This begs the question as to whether you want to pursue the 1/f story. You
2316 refer to this as “noise”. However, there is no noise in this setup. I think what
2317 you meant was that the fluctuations are scale free, because they evinced a power
2318 law. I am sure that there are scale free aspects of these kinds of hyperpriors;
2319 however, in the context of your paradigm I wonder whether you should just
2320 ignore the scale free aspect and focus on your estimated temporal scale implicit
2321 in f . This means you don’t have to hand wave about self-organized criticality in
2322 the discussion and focus upon your hypothesis.

2323 We would like to thank the reviewer for this suggestion. We agree that the discussion
2324 of self-organized criticality is far from the data. We have omitted this section from the
2325 discussion. With respect to f , we have adapted the manuscript to make clear that it captures
2326 the dominant timescale of fluctuations in mode:

- 2327 • (...) This implements a hyperprior⁵⁵ in which the likelihood and prior precisions are
2328 shifted against each other at a dominant timescale defined by f : (...)
- 2329 • (...) The parameter f captured the dominant time scale at which likelihood and prior
2330 precision were shifted against each other and was estimated at 0.11 $1/N_{trials}$ in both
2331 humans and mice.

2332 • Remarkably, a systematic model comparison based on AIC indicated that a model with
2333 fluctuating precisions has much greater evidence, relative to a model in the absence
2334 of fluctuating precisions. The ad-hoc addition of oscillations to a normative Bayesian
2335 model of evidence accumulation⁵¹ allowed us to quantify the dominant timescale of
2336 periodic fluctuations mode at approximately $0.11\sqrt{1/N_{trials}}$ in humans and mice that is
2337 appropriate for these kinds of paradigms.

2338 **10.1.11 Comment 12**

2339 **A final move—to make the paper more focused and digestible—would be to**
2340 **put a lot of your defensive analyses (e.g. about general arousal et cetera) in**
2341 **supplementary material. You have to be careful not to exhaust the reader by**
2342 **putting up a lot of auxiliary material before the important messages in your**
2343 **report.**

2344 We have followed this suggestion and move the following sections to the Supplement: section
2345 5.3 (Internal and external modes of processing facilitate response behavior and enhance
2346 confidence in human perceptual decision-making), section 5.4 (Fluctuations between internal
2347 and external mode modulate perceptual performance beyond the effect of general response
2348 biases), section 5.5 (Internal mode is characterized by lower thresholds as well as by history-
2349 dependent changes in biases and lapses). We have also moved secondary statistics to the
2350 figure legends and to the Supplement.

2351 **Minor points**

2352 **10.1.12 Comment 13**

2353 **I cannot resist suggesting that you change your title to “Bimodal Inference in**
2354 **Mice and Men”**

2355 We would like to thank the Reviewer for this suggestion and agree that this would indeed
2356 sound great. However, we are worried that changing the title to *mice and men* would not

2357 be as gender-neutral as *humans and mice*. We would therefore propose to stay with the
2358 current title. If we are mistaken and *mice and men* can be considered gender-neutral (we are
2359 non-native speakers), we would be happy to change the title.

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 to between-mode fluctuations? According to predictive
2403 processing, attention corresponds to the precision afforded to the probability distributions
2404 that underlie perceptual inference⁵³. As outlined above, between-mode fluctuations
2405 can be understood as ongoing shifts in the precision afforded to likelihood (*external*
2406 *mode*) and prior (*internal mode*), respectively. When the precision afforded to prior or
2407 likelihood increases, posterior precision increases, which leads to faster RTs and higher
2408 confidence. When defined from the perspective of predictive processing as the precision
2409 afforded to likelihood and prior⁵³, fluctuations in attention may thus provide a plausible
2410 explanation for the quadratic relationship between mode and RTs and confidence (Figure
2411 2H and J; Figure 3I; Figure 3I).
- 2412 • Outside of the predictive processing field, attention is often understood in the context of
2413 task engagement⁶³, which varies according to the availability of cognitive resources that
2414 are modulated by factors such as tonic arousal, familiarity with the task, or fatigue⁶³. Our
2415 results suggest that internal mode processing cannot be completely reduced to intervals
2416 of low task engagement: In addition to shorter RTs and elevated confidence, choices
2417 during internal mode were not random or globally biased, but driven by perceptual
2418 history (Supplemental Figures S6-7). Moreover, our computational model identified
2419 the dominant timescale of between-mode fluctuations at $0.11 \sqrt{N_{trials}}$, which may be
2420 compatible with fluctuations in arousal⁶⁴, but is faster than to be expected for the
2421 development of task familiarity or fatigue.
- 2422 • However, in interpreting the impact of between-mode fluctuations on perceptual accuracy,
2423 speed of response and confidence, it is important to consider that global modulators
2424 such as tonic arousal are known to have non-linear effects on task performance⁶⁵: In
2425 perceptual tasks, performance seems to be highest during mid-level arousal, whereas low-
2426 and high-level arousal lead to reduced accuracy and slower responses⁶⁵. This contrasts
2427 with the effects of bimodal inference, where accuracy increases linearly as one moves

2428 from internal to external mode, and responses become faster at both ends of the mode
2429 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_LLlR) 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_{LLR} 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 , p , and ζ (see Methods
2480 for 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
2552 psychophysical designs, resembling the phenomenon that we identify as internally-biased
2553 processing⁷³. Moreover, residual activation of the motor system may lead to faster
2554 responses, and thus constitutes an alternative explanation for the quadratic relationship
2555 of mode with RTs⁷². The observation of elevated confidence for stronger biases toward
2556 internal mode speaks against the proposition that residual activation of the motor system
2557 is the primary driver of serial choice biases, since strong motor-driven priming should lead
2558 to frequent lapses that are typically associated reduced confidence⁷⁴. Likewise, perceptual
2559 history effects have repeatedly been replicated in experiments with counter-balanced
2560 stimulus-response mappings⁸².
- 2561 • No-response paradigms, in which perceptual decision are inferred from eye-
2562 movements alone, could help to better differentiate perceptual from motor-
2563 related effects. Likewise, video-tracking of response behavior and neural
2564 recording from motor- and premotor, which has recently been released for
2565 the IBL database⁷¹, may provide further insight into the relation of motor
2566 behavior to the perceptual phenomenon of between-mode fluctuations.

2567 10.3 Reviewer 3

2568 In this paper the authors propose that during perceptual decisions, humans and
2569 mice exhibit regular oscillatory fluctuations between an “external” (that places
2570 more weight on the perceptual evidence) and an “internal” (that places more
2571 weight on historical experiences) mode. In particular, the authors propose a
2572 computational scheme in which the influences of history and current stimulus on
2573 choice oscillate in anti phase, effectively implementing “bimodal inference”. The
2574 computational advantages of these scheme as well as its relation to the underlying
2575 neurophysiology are discussed.

2576 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 of perceptual decision-making
2623 in humans and mice. However, a number of limitations and open questions have to
2624 be considered: First, this work sought to understand whether fluctuations between
2625 internal and external mode, which we initially observed in an experiment on bistable
2626 perception in humans¹⁹, represent a 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
2654 which participants made binary perceptual decisions between two alternatives. We
2655 excluded two experiments in which the average perceptual accuracy fell below 50%.
2656 After excluding these experiments, our sample consisted of 21.05 million trials obtained
2657 from 4317 human participants and 66 individual experiments (Supplemental Table 1).
2658 Out of the 66 included experiments, 62 investigated visual, 1 auditory, 2 proprioceptive,
2659 and 1 multimodal perception. 59 experiments were based on discrimination and 6 on
2660 detection, with one investigating both.

- 2661 • Out of the 58 experiments that provide information on RTs, 46 cued the response by the
2662 onset of a response screen or an additional response cue, whereas 14 allowed participants
2663 to respond at any time after stimulus onset.
- 2664 • 21 of the 66 included experiments used fixed difficulty levels, whereas 45 manipulated
2665 difficulty levels within participants. Difficulty was manipulated via noise masks, contrast,
2666 luminance, presentation time, or stimulus probability for gabor, dot coherence for
2667 random dot kinematograms, difference in elements and set size for comparisons of
2668 numerosity, difference in clicks for auditory discrimination, temporal distance for meta-
2669 contrast masking, and amount of self-motion for proprioception. We treated task
2670 difficulty as a missing variable for the experiments that fixed it at the participant-level,
2671 as this precluded the computation of autocorrelation curves.

2672 10.3.2 Comment 2

2673 **The key premise that when participants do not rely on the external stimulus**
2674 **they rely more on the previous trial needs to be more clearly (and statistically)**
2675 **contrasted against a null hypothesis. For instance, an null hypothesis could be**
2676 **that when participants place a lower weight on the stimulus they simply choose**
2677 **randomly. It is important to specify a null hypothesis such that the key premise**
2678 **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 lapses (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 lapses 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 , p , and ζ (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 ($AIC_2 = 9.76 \times 10^4$ in humans and 4.91×10^4 in mice) and Model M3 (AIC_3
2837 $= 1.19 \times 10^5$ in humans and 5.95×10^4 in mice) incorporated only oscillations of either
2838 likelihood or prior precision. Model M4 ($AIC_4 = 1.69 \times 10^5$ in humans and 9.12×10^4 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 ($AIC_4 = 2.01 \times 10^5$ in humans
2841 and 1.13×10^5 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 $= 8.16 \times 10^4$ in humans and 4.24×10^4 in mice) and was clearly superior to the normative
2845 Bayesian model of evidence accumulation ($\delta_{AIC} = -8.79 \times 10^4$ in humans and -4.87×10^4
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 (i), whether between-mode fluctuations can emerge spontaneously
2897 in hierarchical models of Bayesian inference, (ii), whether modes are continuous¹⁹ or
2898 discrete⁶², and (iii), whether bimodal inference can be causally manipulated by ex-
2899 perimental variables. We speculate that between-mode fluctuations may separate the
2900 perceptual contribution of internal predictions and external sensory data in time, creating
2901 unambiguous learning signals that benefit inference about the precision of prior and
2902 likelihood, respectively. This proposition should be tested empirically by relating the
2903 phenomenon of bimodal inference to performance in, e.g., reversal learning, probabilistic
2904 reasoning, or 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.

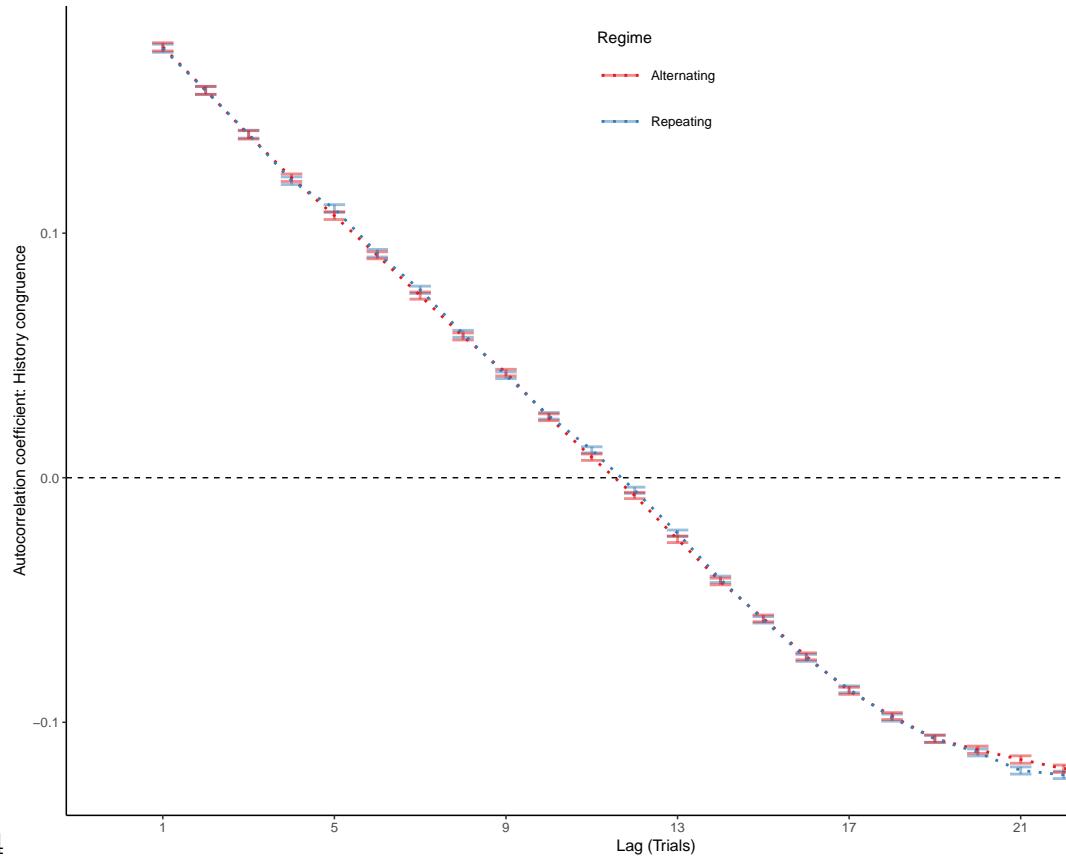
2979 Importantly, our central finding of autocorrelation in history-congruence does not distinguish

2980 between alternating and repetitive history biases. In the plot below, we show autocorrelation
2981 curves for fluctuations in 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 3A,
2999 Supplemental Figure S6 and S7), and 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 lapses 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 2J)
3106 suggested that biases toward internal information do not reflect a post-perceptual strategy
3107 or repeating preceding choices when the subjective confidence in the perceptual decision
3108 is low. Moreover, while responses became faster with longer exposure to the experiments
3109 of the Confidence database, the frequency of history-congruent choices increased over
3110 time, speaking against the proposition that participants may stereotypically repeat
3111 preceding choices when not yet familiar with the experimental task (see Supplemental
3112 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 processing models attention, which we relate to mechanistic drift diffusion models:

- 3125 • How does attention relate to between-mode fluctuations? According to predictive
3126 processing, attention corresponds to the precision afforded to the probability distributions
3127 that underlie perceptual inference⁵³. As outlined above, between-mode fluctuations
3128 can be understood as ongoing shifts in the precision afforded to likelihood (*external*
3129 *mode*) and prior (*internal mode*), respectively. When the precision afforded to prior or
3130 likelihood increases, posterior precision increases, which leads to faster RTs and higher
3131 confidence. When defined from the perspective of predictive processing as the precision
3132 afforded to likelihood and prior⁵³, fluctuations in attention may thus provide a plausible
3133 explanation for the quadratic relationship of mode to RTs and confidence (Figure 2H
3134 and J; Figure 3I; Figure 4I). Such effects of attention in the predictive processing sense
3135 can be directly related to mechanistic drift diffusion models⁶⁰, where both larger shifts
3136 in starting point (related to increased prior precision in internal mode) and lower noise
3137 in the accumulation of evidence (related to increased likelihood precision in external
3138 mode) may explain 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
 3212 by more speculative sections/ discussions. For instance, the section on the
 3213 adaptive merits of the computational model is relatively weaker compared to the
 3214 empirical results. In particular, the model is simulated without feedback (whereas
 3215 most experiments employ trial by trial feedback) and does not outperform the
 3216 baseline model in accuracy but in other secondary metrics.

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