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Bimodal Inference in Humans and Mice

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2 Abstract

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

3 One sentence summary

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

4 Introduction

The capacity to respond to changes in the environment is a defining feature of life¹⁻³. Intriguingly, the ability of living things to process their surroundings fluctuates considerably over time^{4,5}. In humans and mice, perception⁶⁻¹², cognition¹³ and memory¹⁴ cycle through prolonged periods of enhanced and reduced sensitivity to external information, suggesting that the brain detaches from the world in recurring intervals that last from milliseconds to seconds and even minutes⁴. Yet breaking from external information is risky, as swift responses to the environment are often crucial to survival.

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

In this work, we sought to elucidate whether periodicities in the sensitivity to external information represent an epiphenomenon of limited processing capacity or, alternatively, result from a structured and adaptive mechanism of perceptual inference. To this end, we analyzed two large-scale datasets on perceptual decision-making in humans²⁰ and mice²¹. When less sensitive to external stimulus information, humans and mice did not behave more randomly, but showed stronger serial dependencies in their perceptual choices²²⁻³³. These

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

5 Results

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

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

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

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

These results confirm that the ability to process sensory signals is not constant over time but unfolds in multi-trial epochs of enhanced and reduced sensitivity to external information⁸. As a consequence of this autocorrelation, the dynamic probability of stimulus-congruent perception (i.e., computed in sliding windows of ± 5 trials; Figure 1C) fluctuated considerably within participants (average minimum: $35.46\% \pm 0.22\%$, maximum: $98.27\% \pm 0.07\%$). In line with previous findings⁹, such fluctuations in the sensitivity to external information had a power density that was inversely proportional to the frequency in the slow spectrum¹¹ (power $\sim 1/f^\beta$, $\beta = -1.32 \pm 3.14 \times 10^{-3}$, $T(1.84 \times 10^5) = -419.48$, $p < 2.2 \times 10^{-308}$; Figure 2D). This feature, which is also known as a *1/f power law*^{36,37}, represents a characteristic of scale-free fluctuations in complex dynamic systems such as the brain³⁸ and the cognitive processes it entertains^{9,10,13,39,40}.

5.2 Humans fluctuate between external and internal modes of sensory processing

In a second step, we sought to explain why perception cycles through periods of enhanced and reduced sensitivity to external information⁴. We reasoned that observers may intermittently rely more strongly on internal information, i.e., on predictions about the environment that

are constructed from previous experiences^{19,31}.

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

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

Second, we asked whether perception cycles through multi-trial epochs during which perception is characterized by stronger or weaker biases toward preceding experiences. In close analogy to stimulus-congruence, we found history-congruence to be significantly autocorrelated for up

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

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

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

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

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

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

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

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

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

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

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

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

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

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

between-mode fluctuations and perceptual metacognition: Metacognitive efficiency should be lower in individuals who spend more time in internal mode, since their confidence reports are less predictive of whether the corresponding perceptual decision is correct. We computed each participant’s M-ratio⁴⁵ ($\text{meta-d}'/\text{d}' = 0.85 \pm 0.02$) to probe this hypothesis independently of inter-individual differences in perceptual performance. Indeed, we found that biases toward internal information (as defined by the average probability of history-congruence) were stronger in participants with lower metacognitive efficiency ($\beta = -2.98 \times 10^{-3} \pm 9.82 \times 10^{-4}$, $T(4.14 \times 10^3) = -3.03$, $p = 2.43 \times 10^{-3}$).

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

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

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

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

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

225 When eliminating perceptual history as a predictor of individual choices at individual trials,
 226 Akaike Information Criterion (AIC⁴⁸) increased by $\delta_{AIC} = 1.64 \times 10^3$ (see Supplemental
 227 Figure S4A-B for parameter- and model-level inference at the level of individual observers).
 228 Likewise, when eliminating slow fluctuations in history-congruence as a predictor of slow
 229 fluctuations in stimulus-congruence across trials, we observed an increase in AIC by δ_{AIC}
 230 $= 7.06 \times 10^3$. These results provided model-level evidence against the null hypotheses that
 231 fluctuations in stimulus-congruence are driven exclusively by choice randomness or general
 232 response bias (see Supplemental Section 9.2 and Supplemental Figure S5 for an in-depth
 233 assessment of general response bias).

234 To confirm that changes in the sensitivity to external information are indicative of internal
 235 mode processing, we estimated full and history-dependent psychometric curves during internal,
 236 external, and across modes²¹. If, as we hypothesized, internal mode processing reflects an
 237 enhanced impact of perceptual history, one would expect a history-dependent increase in
 238 biases and lapses as well as a history-independent increase in threshold. Conversely, if internal
 239 mode processing were driven by random choices, one would expect a history-independent
 240 increase in lapses and threshold, and no change in bias. In line with our prediction, we found
 241 that internal mode processing was associated with a history-dependent increase in bias and
 242 lapse as well as a history-independent increase in threshold (Supplemental Section 9.3.1 and
 243 Supplemental Figure S6). This confirmed that internal mode processing is indeed driven by
 244 an enhanced impact of perceptual history.

245 In line with this, the quadratic relationship between mode and confidence (Figure 2J)
 246 suggested that biases toward internal information do not reflect a post-perceptual strategy

of repeating preceding choices when the subjective confidence in the perceptual decision is low. Moreover, while responses became faster with longer exposure to the experiments of the Confidence database, the frequency of history-congruent choices increased over time, speaking against the proposition that participants stereotypically repeat preceding choices when not yet familiar with the experimental task (Supplemental Section 9.4.1).

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

5.5 Mice fluctuate between external and internal modes of sensory processing

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

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

We found perception to be stimulus-congruent in $81.37\% \pm 0.3\%$ of trials (Figure 3A, upper panel). In line with humans, mice were biased toward perceptual history in $54.03\% \pm 0.17\%$

272 of trials ($T(164) = 23.65$, $p = 9.98 \times 10^{-55}$; Figure 3A and Supplemental Figure S1D). Since
 273 the *basic* task of the IBL dataset presented stimuli at random in either the left or right
 274 hemifield²¹, we expected stronger biases toward perceptual history to decrease perceptual
 275 performance. Indeed, history-congruent choices were more frequent when perception was
 276 stimulus-incongruent ($61.59\% \pm 0.07\%$) as opposed to stimulus-congruent ($51.81\% \pm 0.02\%$,
 277 $T(164) = 31.37$, $p = 3.36 \times 10^{-71}$; $T(164) = 31.37$, $p = 3.36 \times 10^{-71}$; Figure 3A, lower panel),
 278 confirming that perceptual history was a source of bias^{24,28,30,31,43} as opposed to a feature of
 279 the experimental paradigm.

280 At the group level, we found significant autocorrelations in both stimulus-congruence (42
 281 consecutive trials) and history-congruence (8 consecutive trials; Figure 3B), while controlling
 282 for the respective autocorrelation of task difficulty and external stimulation (Supplemental
 283 Figure 2C-D). In contrast to humans, mice showed a negative autocorrelation coefficient
 284 of stimulus-congruence at trial 2, which was due to a feature of the experimental design:
 285 Errors at a contrast above 50% were followed by a high-contrast stimulus at the same
 286 location. Thus, stimulus-incongruent choices on easy trials were more likely to be followed by
 287 stimulus-congruent perceptual choices that were facilitated by high-contrast visual stimuli²¹.

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

296 The above results confirm that fluctuations between internally- and externally-biased modes
 297 generalize to perceptual decision-making in mice. Following our hypothesis that bimodal

inference operates at the level of perception, we predicted that between-mode fluctuations modulate a decision variable⁴⁴ that determines not only perceptual choices, but also downstream aspects of mouse behavior⁴⁴. We therefore asked how external and internal modes relate to the trial duration (TD, a coarse measure of RT in mice that spans the interval from stimulus onset to feedback²¹). Stimulus-congruent (as opposed to stimulus-incongruent) choices were associated with shorter TDs ($\delta = -262.48 \pm 17.1$, $T(164) = -15.35$, $p = 1.55 \times 10^{-33}$), while history-congruent choices were characterized by longer TDs ($\delta = 30.47 \pm 5.57$, $T(164) = 5.47$, $p = 1.66 \times 10^{-7}$; Figure 3G).

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

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

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

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

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

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

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

The empirical data presented above indicate that, for both humans and mice, perception fluctuates between external and modes, i.e., multi-trial epochs that are characterized by enhanced sensitivity toward either external sensory information or internal predictions generated by perceptual history. Since natural environments typically show high temporal redundancy³⁴, previous experiences are often good predictors of new stimuli^{30,31,35,41}. Serial dependencies may therefore induce autocorrelations in perception by serving as internal

349 predictions (or *memory* processes^{9,13}) that actively integrate noisy sensory information over
 350 time⁵⁰.

351 Previous work has shown that such internal predictions can be built by dynamically updating
 352 the estimated probability of being in a particular perceptual state from the sequence of
 353 preceding experiences^{35,46,51}. The integration of sequential inputs may lead to accumulating
 354 effects of perceptual history that progressively override incoming sensory information, enabling
 355 internal mode processing¹⁹. However, since such a process would lead to internal biases that
 356 may eventually become impossible to overcome⁵², changes in mode may require ongoing
 357 wave-like fluctuations^{9,13} in the perceptual impact of external and internal information that
 358 occur *irrespective* of the sequence of previous experiences and temporarily de-couple the
 359 decision variable from implicit internal representations of the environment¹⁹.

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

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

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

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

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

370 α that controls the sensitivity of perception to the available sensory information (see Methods
 371 for details on s_t in humans and mice):

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

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

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

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

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

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

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

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). We validated our model in three steps:

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

Model M2 ($AIC_2 = 9.76 \times 10^4$ in humans and 4.91×10^4 in mice) and Model M3 ($AIC_3 = 1.19 \times 10^5$ in humans and 5.95×10^4 in mice) incorporated only oscillations of either likelihood or prior precision. Model M4 ($AIC_4 = 1.69 \times 10^5$ in humans and 9.12×10^4 in mice) lacked any oscillations of likelihood and prior precision and corresponded to the normative model proposed by Glaze et al.⁵¹. In model M5 ($AIC_5 = 2.01 \times 10^5$ in humans and 1.13×10^5 in mice), we furthermore removed the integration of information across trials, such that perception depended only in incoming sensory information (Figure 1G).

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

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

model predicted within-training and out-of-training variables. The bimodal inference model characterizes each subject by a sensitivity parameter 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 $0.11 \pm 1.68 \times 10^{-5} \text{ } 1/N_{\text{trials}}$ and $0.11 \pm 1.63 \times 10^{-4} \text{ } 1/N_{\text{trials}}$ 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 correlated 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: $\hat{H}_{\text{Humans}} = 0.5 \pm 1.58 \times 10^{-5}$; IBL database²¹: $\hat{H}_{\text{Mice}} = 0.49 \pm 6.47 \times 10^{-5}$). Indeed, when fitting the bimodal inference model to the trial-wise perceptual choices, we found that the estimated (i.e., subjective) hazard rate H was lower than \hat{H} for both humans ($\beta = -6.87 \pm 0.94$, $T(61.87) = -7.33$, $p = 5.76 \times 10^{-10}$) and mice ($\beta = -2.91 \pm 0.34$, $T(112.57) = -8.51$, $p = 8.65 \times 10^{-14}$).

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

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

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

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

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

6 Discussion

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

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

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

At the level of individual traits, increased biases toward preceding choices were associated with reduced sensitivity to external information (Supplemental Figure 1C-D) and lower metacognitive efficiency. When investigating how serial dependencies evolve over time, we observed dynamic changes in the strength of perceptual history (Figures 2 and 3B) that created wavering biases toward internally- and externally-biased modes of sensory processing. Between-mode fluctuations may thus provide a new explanation for ongoing changes in perceptual performance⁶⁻¹¹.

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

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

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

518 We hypothesized that observers have certain hyperpriors that are apt for accommodating
 519 fluctuations in the predictability of their environment, i.e., people believe that their world is
 520 inherently volatile. To be Bayes optimal, it is therefore necessary to periodically re-evaluate
 521 posterior beliefs about the parameters that define an internal generative model of the external
 522 sensory environment. One way to do this is to periodically suspend the precision of prior
 523 beliefs and increase the precision afforded to sensory evidence, thus updating Bayesian beliefs
 524 about model parameters.

525 The empirical evidence above suggests that the timescale of this periodic scheduling of
 526 evidence accumulation may be scale-invariant. This means that there may exist a timescale
 527 of periodic fluctuations in precision over every window or length of perceptual decision-
 528 making. Bimodal inference predicts perceptual decisions under a generative model (based
 529 upon a hazard function to model serial dependencies between subsequent trials) with periodic
 530 fluctuations in the precision of sensory evidence relative to prior beliefs at a particular
 531 timescale. Remarkably, a systematic model comparison based on AIC indicated that a model
 532 with fluctuating precisions has much greater evidence, relative to a model in the absence of
 533 fluctuating precisions. This ad-hoc addition of oscillations to a normative Bayesian model of

evidence accumulation⁵¹ allowed us to quantify the dominant timescale of periodic fluctuations mode at approximately $0.11\ 1/N_{trials}$ in humans and mice that is appropriate for these kinds of paradigms.

6.2 Bimodal inference versus normative Bayesian evidence accumulation

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

While it is thus clear that the impact of perceptual history and sensory evidence are anti-correlated *at each individual trial*, we here introduce anti-phase oscillations as an ad-hoc modification to model slow fluctuations in prior and likelihood precision that evolve *over many consecutive trials* and are not mandated by normative Bayesian or mechanistic drift diffusion models. The bimodal inference model provides a reasonable explanation of the linked autocorrelations in stimulus- and history-congruence, as evidenced by formal model

comparison, successful prediction of RTs and confidence as out-of-training variables, and a qualitative reproduction of our empirical data from posterior model parameter as evidence against over- or under-fitting.

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

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

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

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

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

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

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

618 Residual activation of the motor system may provide another contribution to serial biases
619 in perceptual choices⁷². Such motor-driven priming may lead to errors in randomized
620 psychophysical designs, resembling the phenomenon that we identify as internally-biased
621 processing⁷³. Moreover, residual activation of the motor system may lead to faster responses,
622 and thus constitutes an alternative explanation for the quadratic relationship of mode with
623 RTs⁷². The observation of elevated confidence for stronger biases toward internal mode speaks
624 against the proposition that residual activation of the motor system is the primary driver of
625 serial choice biases, since strong motor-driven priming should lead to frequent lapses that are
626 typically associated reduced confidence⁷⁴. Likewise, perceptual history effects have repeatedly
627 been replicated in experiments with counter-balanced stimulus-response mappings^{30: Feigin2021}.

628 No-response paradigms, in which perceptual decision are inferred from eye-movements alone,
629 could help to better differentiate perceptual from motor-related effects. Likewise, video-
630 tracking of response behavior and neural recording from motor- and premotor, which has
631 recently been released for the IBL database[IBL2023], may provide further insight into the
632 relation of motor behavior to the perceptual phenomenon of between-mode fluctuations.

6.4 Limitations and open questions

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

First, this work sought to understand whether fluctuations between internal and external mode, which we initially observed in an experiment on bistable perception in humans¹⁹, represent a general phenomenon that occurs across a diverse set of perceptual decision-making tasks. Our analysis of the Confidence database²⁰ therefore collapsed across all available experiments on binary perceptual decision-making. Individual experiments differed with respect to the stimuli, the manipulation of difficulty, the timing of trials, and the way responses were collected, but were highly comparable with respect to the central variables of stimulus- and history-congruence (Supplemental Figure S1A-B).

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

Second, our results point to an attraction of perception toward preceding choices. Previous work has shown that perceptual decision-making is concurrently affected by both attractive and repulsive serial biases that operate on distinct time-scales and serve complementary functions for sensory processing^{27,75,76}: Short-term attraction may serve the decoding of noisy sensory inputs and increase the stability of perception, whereas long-term repulsion may

enable efficient encoding and sensitivity to change²⁷. In the data analyzed here, history biases tended to be repetitive (Figure 2A, Figure 3A, Supplemental Figure S6 and S7), and only 2 of the 66 experiments of the Confidence database²⁰ showed significant alternating biases (Supplemental Figure S1). However, as we show in Supplemental Figure S14, fluctuations in both alternating and repeating history biases generate overlapping autocorrelation curves. Our analysis of between-mode fluctuations is therefore not tied exclusively to repeating biases, but accommodates alternating biases as well, such that both may lead to internally-biased processing and reduced sensitivity to external sensory information. Future work could apply our approach to paradigms that boost alternating as opposed to repeating biases, as this would help to better understand how repetition and alternation are linked in terms of their computational function and neural implementation²⁷.

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

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

685 ological underpinnings. Since between-mode fluctuations were found in humans and mice,
686 future studies can apply non-invasive and invasive neuro-imaging and electrophysiology to
687 better understand the neural mechanisms that generate ongoing changes in mode in terms of
688 their neuro-anatomy, -chemistry and -circuitry.

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

7 Methods

7.1 Resource availability

7.1.1 Lead contact

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

7.1.2 Materials availability

This study did not generate new unique reagents.

7.1.3 Data and code availability

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

7.2 Experimental model and subject details

7.2.1 Confidence database

We downloaded the human data from the Confidence database²⁰ on 10/21/2020, limiting our analyses to the category *perception*. Within this category, we selected studies in which participants made binary perceptual decisions between two alternatives. We excluded two experiments in which the average perceptual accuracy fell below 50%. After excluding these experiments, our sample consisted of 21.05 million trials obtained from 4317 human participants and 66 individual experiments (Supplemental Table 1). Out of the 66 included experiments, 62 investigated visual, 1 auditory, 2 proprioceptive, and 1 multimodal perception. 59 experiments were based on discrimination and 6 on detection, with one investigating both.

7.2.2 IBL database

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

7.3 Method details

7.3.1 Variables of interest

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

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

Secondary variables of interest: From the Confidence Database²⁰, we furthermore extracted trial-wise confidence reports and RTs. Out of the 58 experiments that provide information on RTs, 46 cued the response by the onset of a response screen or an additional response cue, whereas 14 allowed participants to respond at any time after stimulus onset. If RTs were available for both the perceptual decision and the confidence report, we only

extracted the RT associated with the perceptual decision. To enable comparability between studies, we normalized RTs and confidence reports within individual studies using the *scale* R function. If not available for a particular study, RTs were treated as missing variables. From the IBL database²¹, we extracted trial durations (TDs) as defined by interval between stimulus onset and feedback, which represents a coarse measure of RT²¹.

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

7.3.2 Control variables

Next to the sequence of presented stimuli, we assessed the autocorrelation of task difficulty as an alternative explanation for any autocorrelation in stimulus- and history-congruence. In the Confidence Database²⁰, 21 of the 66 included experiments used fixed difficulty levels, whereas 45 manipulated difficulty levels within participants. Difficulty was manipulated via noise masks, contrast, luminance, presentation time, or stimulus probability for gabors, dot coherence for random dot kinematograms, difference in elements and set size for comparisons of numerosity, difference in clicks for auditory discrimination, temporal distance for meta-contrast masking, and amount of self-motion for proprioception. We treated task difficulty as a missing variable for the experiments that fixed it at the participant-level, as this precluded the computation of autocorrelation curves. In analogy to RTs and confidence, difficulty levels were normalized within individual studies. For the IBL Database²¹, task difficulty was defined by the contrast of the presented grating.

7.3.3 Autocorrelations

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

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

To assess autocorrelations at the level of individual participants, we counted the number of subsequent trials (starting at the first trial after the index trial) for which less than 50% of the permuted autocorrelation coefficients exceeded the true autocorrelation coefficient. For example, a count of zero indicates that the true autocorrelation coefficients exceeded *less than 50%* of the autocorrelation coefficients computed for randomly permuted data at the first trial following the index trial. A count of five indicates that, for the first five trials following the index trial, the true autocorrelation coefficients exceeded *more than 50%* of the respective autocorrelation coefficients for the randomly permuted data; at the 6th trial following the index trial, however, *less than 50%* of the autocorrelation coefficients exceeded the respective permuted autocorrelation coefficients.

7.3.4 Spectral analysis

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

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

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

7.4 Quantification and statistical procedures

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

7.4.1 Mixed effects modeling

Unless indicated otherwise, we performed group-level inference using the R-packages *lmer* and *afex* for linear mixed effects modeling and *glmer* with a binomial link-function for logistic

regression. We compared models based on AIC. To account for variability between the studies available from the Confidence Database²⁰, mixed modeling was conducted using random intercepts defined for each study. To account for variability across experimental session within the IBL database²¹, mixed modeling was conducted using random intercepts defined for each individual session. When multiple within-participant datapoints were analyzed, we estimated random intercepts for each participant that were *nested* within the respective study of the Confidence database²⁰. By analogy, for the IBL database²¹, we estimated random intercepts for each session that were nested within the respective mouse. We report β values referring to the estimates provided by mixed effects modeling, followed by the respective T statistic (linear models) or z statistic (logistic models).

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

7.4.2 Psychometric function

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

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

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

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

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

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

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

848 7.4.3 Computational modeling

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

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

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

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

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

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

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

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

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

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

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

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

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

follows:

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

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

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

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

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

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

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

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

- The full *bimodal inference model* (M1; Figure 1F) incorporates the influence of sensory information according to the parameter α (likelihood); the integration of evidence across trials according to the parameter H (prior); anti-phase oscillations in between likelihood and prior precision according to ω_{LLR} and ω_ψ with parameters a_{LLR} (amplitude likelihood fluctuation), a_ψ (amplitude prior fluctuation), f (frequency) and p (phase).
- The *likelihood-oscillation-only model* (M2; Figure 1G) incorporates the influence of sensory information according to parameter α (likelihood); the integration of evidence across trials according to parameter H (prior); oscillations in likelihood precision according to ω_{LLR} with parameters a_{LLR} (amplitude likelihood fluctuation), f (frequency) and p (phase).
- The *prior-oscillation-only model* (M3; Figure 1G) incorporates the influence of sensory information according to parameter α (likelihood); the integration of evidence across trials according to parameter H (prior); oscillations in the prior precision according to ω_ψ with parameters a_ψ (amplitude prior fluctuation), f (frequency) and p (phase). Please note that all models M1-3 lead to shifts in the relative precision of likelihood and prior.

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

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

Simulations. Finally, we used simulations (Figure 4, Supplemental Figures S10-13) to show that all model components, including the anti-phase oscillations governed by a_ψ , a_{LLR} , f and p , were necessary for our model to reproduce the characteristics of the empirical data. This enabled us to assess over- or under-fitting in the bimodal inference model and

945 all reduced models M2-M5. We used the posterior model parameters observed for humans
 946 (H , α , a_ψ , a_{LLR} , f , p and ζ) to define individual parameters for simulation in 4317 simulated
 947 participants (i.e., equivalent to the number of human participants). For each participant, the
 948 number of simulated trials was drawn at random between 300 to 700. Inputs s were drawn
 949 at random for each trial, such that the sequence of inputs to the simulation did not contain
 950 any systematic seriality. Noisy observations u were generated by applying the posterior
 951 parameter α to inputs s , thus generating stimulus-congruent choices in $71.36 \pm 2.6 \times 10^{-3}\%$
 952 of trials. Choices were simulated based on the trial-wise choice probabilities y_p obtained from
 953 our model. Simulated data were analyzed in analogy to the human and mouse data. As a
 954 substitute of subjective confidence, we computed the absolute of the trial-wise log posterior
 955 ratio $|L|$ (i.e., the posterior decision certainty).

8 Figures

8.1 Figure 1

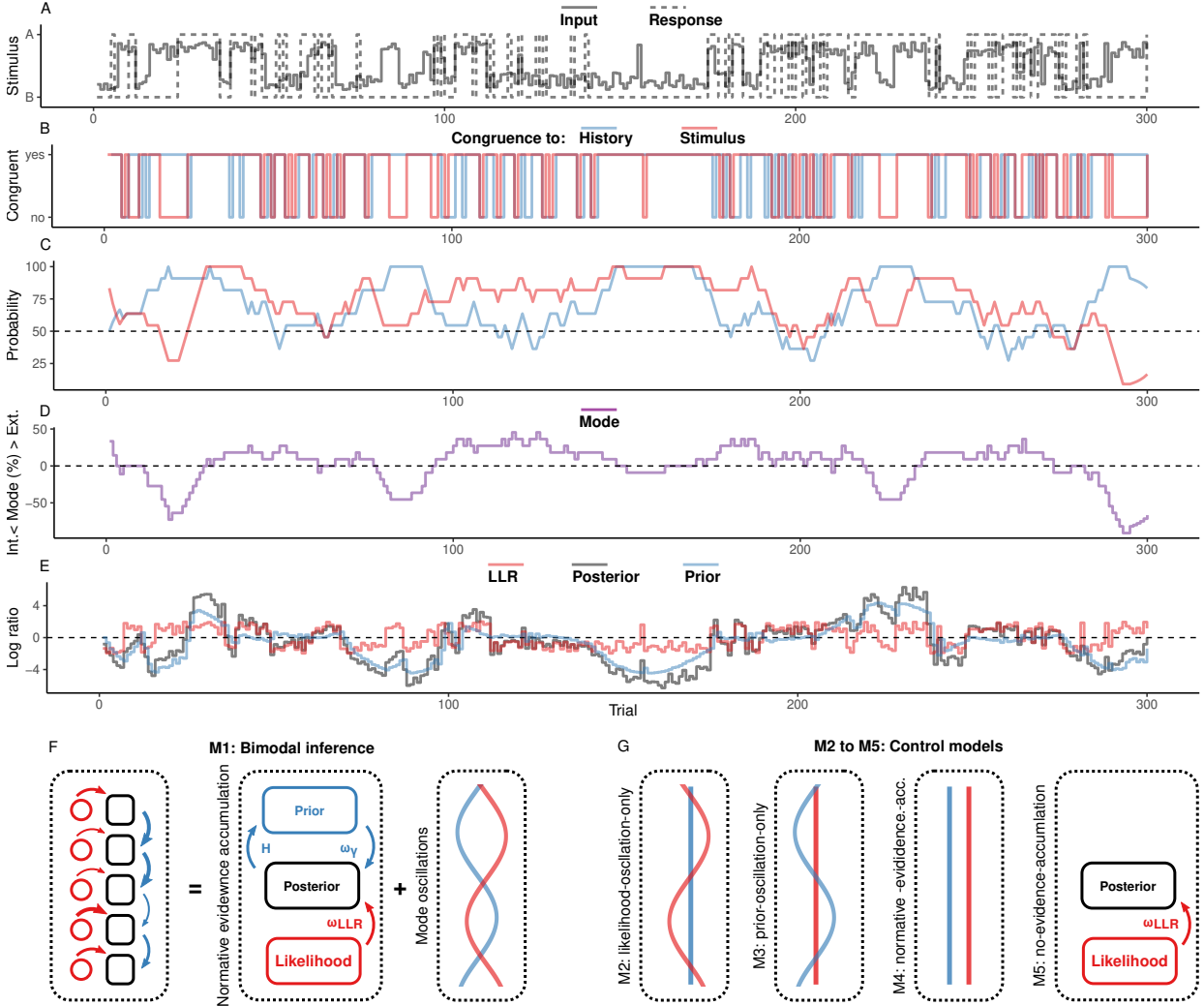


Figure 1. Concept.

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.

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

(blue line).

C. The dynamic probabilities of stimulus- and history-congruence (i.e., computed in sliding windows of ± 5 trials) fluctuate over time.

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

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

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

8.2 Figure 2

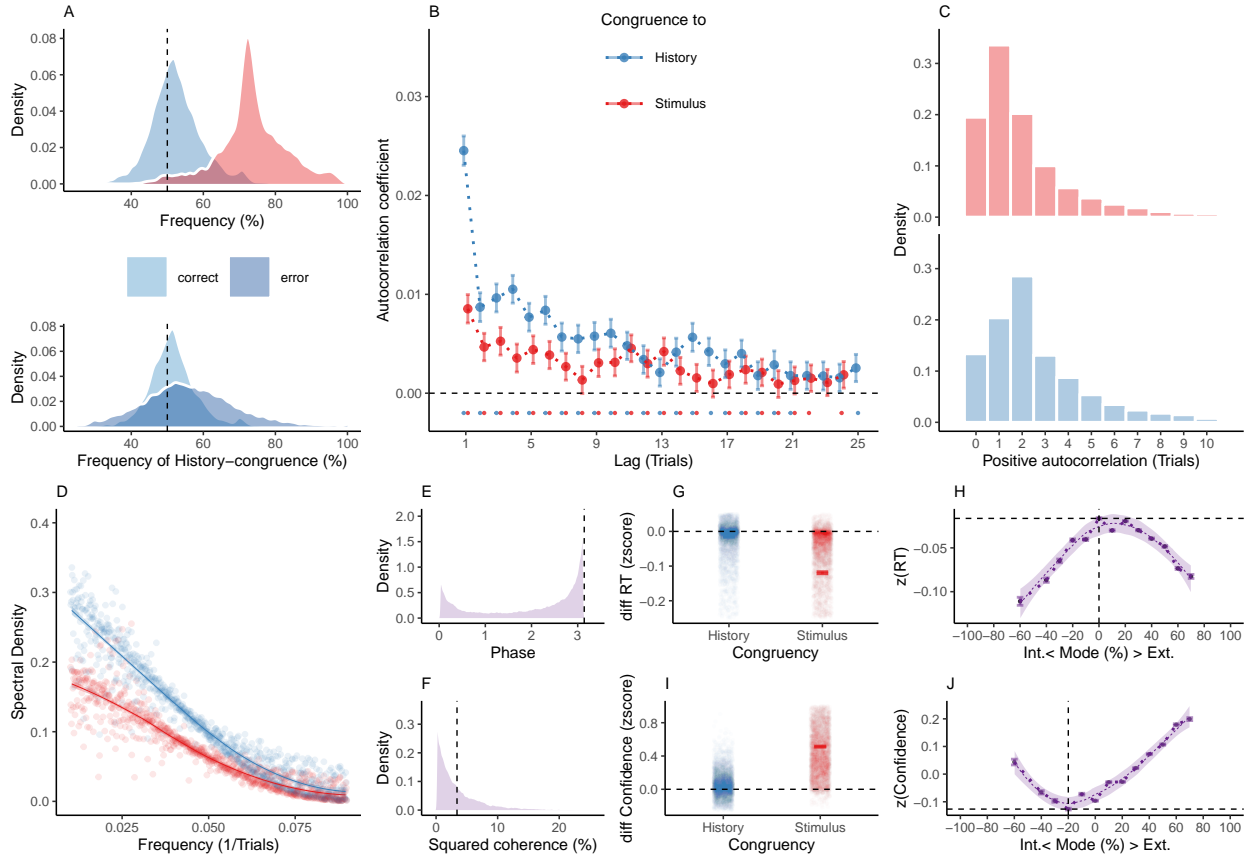


Figure 2. Internal and external modes in human perceptual decision-making.

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.

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

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

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

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

1011 E. The distribution of phase shift between fluctuations in stimulus- and history-congruence
1012 peaked at half a cycle (π denoted by dotted line).

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

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

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

1024 I. Confidence was enhanced for both stimulus-congruence (as opposed to stimulus-

1025 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
1026 history-congruence ($\beta = 0.04 \pm 1.18 \times 10^{-3}$, $T(2.06 \times 10^6) = 36.85$, $p = 3.25 \times 10^{-297}$).

1027 J. In analogy to RTs, we found a quadratic relationship between the mode of perceptual
1028 processing and confidence, which increased when both externally- and internally-biased modes
1029 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
1030 and vertical dotted lines indicate minimum confidence and the associated mode, respectively.

8.3 Figure 3

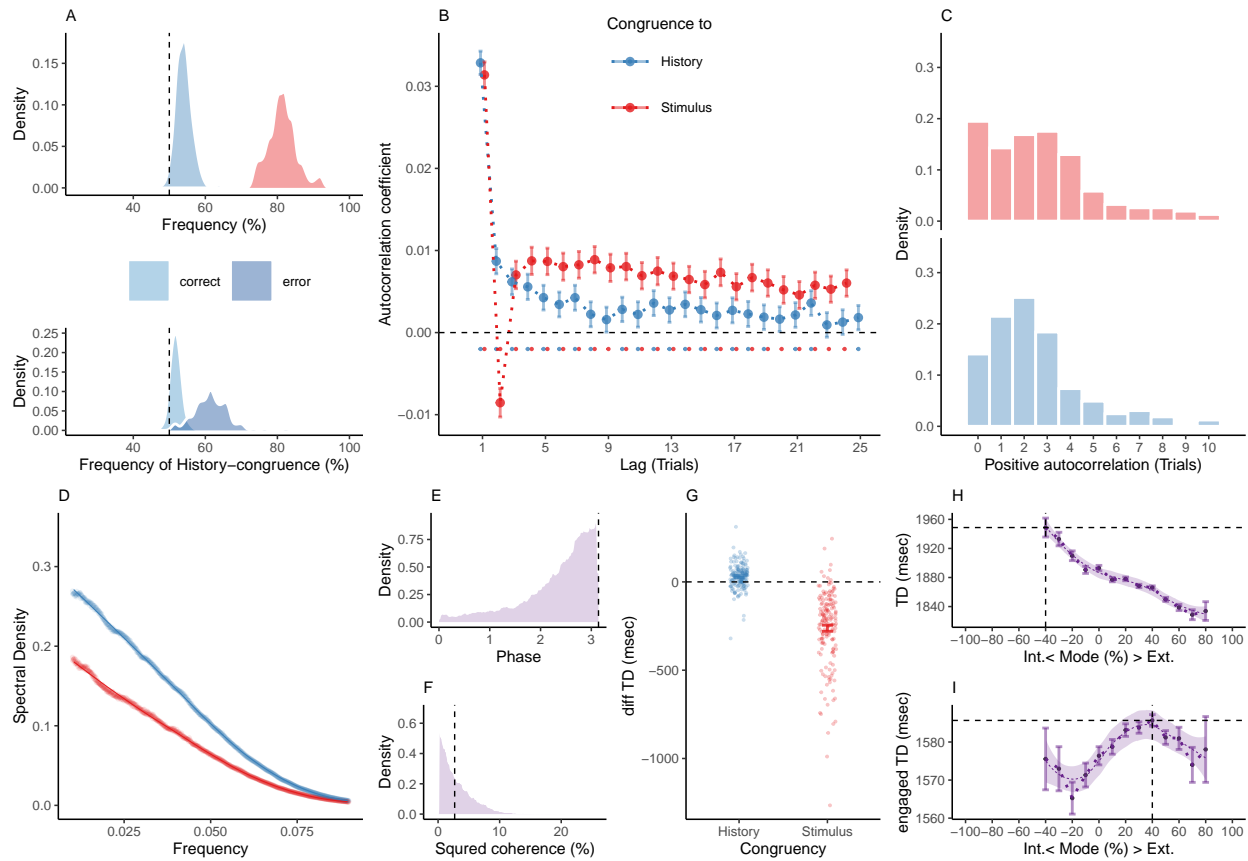


Figure 3. Internal and external modes in mouse perceptual decision-making.

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).

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:

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

1048 C. For stimulus-congruence (upper panel), the lag of positive autocorrelation was longer in
1049 comparison to humans (4.59 ± 0.06 on average). For history-congruence (lower panel), the
1050 lag of positive autocorrelation was slightly shorter relative to humans (2.58 ± 0.01 on average,
1051 peaking at trial $t+2$ after the index trial).

1052 D. In mice, the dynamic probabilities of stimulus- and history-congruence (sliding windows
1053 of ± 5 trials) fluctuated as a scale-invariant process with a $1/f$ power law.

1054 E. The distribution of phase shift between fluctuations in stimulus- and history-congruence
1055 peaked at half a cycle (π denoted by dotted line).

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

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

1062 H. TDs decreased monotonically for stronger biases toward external mode ($\beta_1 = -4.16 \times 10^4$
1063 $\pm 1.29 \times 10^3$, $T(1.35 \times 10^6) = -32.31$, $p = 6.03 \times 10^{-229}$). The horizontal and vertical dotted
1064 lines indicate maximum TD and the associated mode, respectively.

1065 I. For TDs that differed from the median TD by no more than $1.5 \times \text{MAD}$ (median absolute
1066 distance⁴⁹), mice exhibited a quadratic component in the relationship between the mode of
1067 sensory processing and TDs ($\beta_2 = -1.97 \times 10^3 \pm 843.74$, $T(1.19 \times 10^6) = -2.34$, $p = 0.02$).
1068 This explorative post-hoc analysis focuses on trials at which mice engage more swiftly with
1069 the experimental task. The horizontal and vertical dotted lines indicate maximum TD and

¹⁰⁷⁰ the associated mode, respectively.

8.4 Figure 4

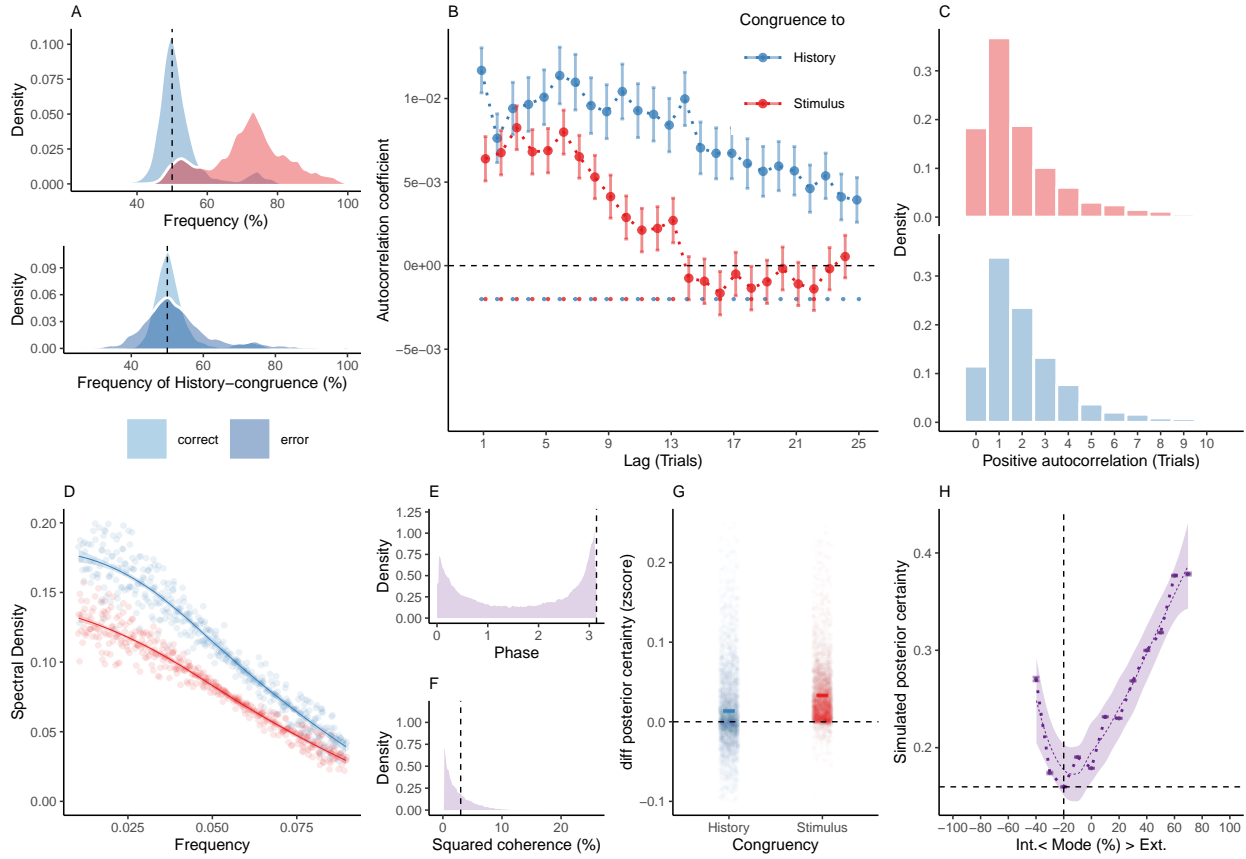


Figure 4. Internal and external modes in simulated perceptual decision-making.

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

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

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

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

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

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

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

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

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

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Supplemental Information

- Supplement_clean.pdf: Supplemental Items and Figures
- Supplement_track_changes.pdf : Supplemental Items and Figures

The above files contain the following supplemental items and figures:

Supplemental Text Items

1. Internal mode processing is driven by choice history as opposed to stimulus history
2. Internal mode is characterized by lower thresholds as well as by history-dependent changes in biases and lapses
3. Internal mode processing can not be reduced to insufficient task familiarity

Supplemental Figures

1. Supplemental Figure S1. Stimulus- and history-congruence.
2. Supplemental Figure S2. Controlling for task difficulty and external stimulation
3. Supplemental Figure S3. Reproducing group-level autocorrelations using logistic regression
4. Supplemental Figure S4. History-congruence in logistic regression.
5. Supplemental Figure S5. Correcting for general response biases
6. Supplemental Figure S6. Full and history-conditioned psychometric functions across modes in humans
7. Supplemental Figure S7. Full and history-conditioned psychometric functions across modes in mice

- 1289 8. Supplemental Figure S8. History-/stimulus-congruence and TDs during training of the
1290 basic task
- 1291 9. Supplemental Figure S9. Comparison of the bimodal inference model against reduced
1292 control models
- 1293 10. Supplemental Figure S10. Reduced Control Model M2: Only oscillation of the likelihood
- 1294 11. Supplemental Figure S11. Reduced Control Model M3: Only oscillation of the prior
- 1295 12. Supplemental Figure S12. Reduced Control Model M4: Normative evidence accumulation
- 1296 13. Supplemental Figure S13. Reduced Control Model M5: No accumulation of information
1297 across trials.
- 1298 14. Supplemental Figure S14. Autocorrelation of history-congruence of alternating and
1299 repeating biases