COMPARATIVE COGNITION

Chimpanzees rationally revise their beliefs

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The selective revision of beliefs in light of new evidence has been considered one of the hallmarks of human-level rationality. However, tests of this ability in other species are lacking. We examined whether and how chimpanzees (*Pan troglodytes*) update their initial belief about the location of a reward in response to conflicting evidence. Chimpanzees responded to counterevidence in ways predicted by a formal model of rational belief revision: They remained committed to their initial belief when the evidence supporting the alternative belief was weaker, but they revised their initial belief when the supporting evidence was stronger. Results suggest that this pattern of belief revision was guided by the explicit representation and weighing of evidence. Taken together, these findings indicate that chimpanzees metacognitively evaluate conflicting pieces of evidence within a reflective process.

Rationality is a hallmark of human thinking. Rational agents form beliefs about the world on the basis of evidence (*1*), but as new evidence emerges, they revise their beliefs by weighing the strength of their prior beliefs in relation to the strength of the new evidence (*2*). Selective belief revision is a particularly strong indicator of rationality (*3*).

From a Bayesian perspective, the rational response to counter-evidence is to revise a belief in hypothesis h_1 to a belief that supports an alternative hypothesis h_2 when the counterevidence causes the posterior probability of h_2 to exceed the posterior probability of h_1:

$$\frac{p(h_2 \mid e_{Old}, e_{New})}{p(h_1 \mid e_{Old}, e_{New})} = \frac{p(e_{Old}, e_{New} \mid h_2)\, p(h_2)}{p(e_{Old}, e_{New} \mid h_1)\, p(h_1)} > 1$$

When both hypotheses have equal probabilities a priori, this condition is met when the strength of the evidence (e_{Old}) supporting the initial hypothesis is exceeded by the strength of new evidence (e_{New}) supporting the alternative hypothesis [see supplementary materials (SM)]. A reasoner should maintain their initial belief when the evidence in support of their initial belief is stronger and revise their belief if the evidence in support of the alternative belief is stronger.

Humans' closest primate relatives adjust their beliefs in response to evidence. For example, great apes draw inferences based on auditory, visual, and tactile cues during problem solving (*4–12*). Chimpanzees infer food locations from left-behind traces (*13*, *14*), weight effects (*15*), or a food's absence from an alternative location (*16*, *17*). They flexibly distinguish between appearance and reality, discounting misleading cues such as apparent food size (*18*), and they actively seek additional information when faced with contradictory evidence (*19*). It is not known, however, whether chimpanzees demonstrate the metacognitive ability to rationally evaluate the strength of new evidence and compare it with the strength of their existing beliefs—and so revise their beliefs only when appropriate, as humans can.

We tested whether chimpanzees' patterns of belief change conform to the predictions of a Bayesian formulation of rational belief revision (Experiments 1 and 2). We then probed the cognitive mechanisms underlying chimpanzees' belief revision. We asked whether chimpanzees represent both possible hypotheses before choosing between them (Experiment 3), individuate evidence (differentiate new from redundant evidence; Experiment 4), and respond to second-order evidence (evidence about the validity of the first-order evidence; Experiment 5).

Chimpanzees' response to counterevidence

In Experiments 1 and 2 (preregistered), chimpanzees ($N = 15$) were presented with a piece of food, which was then hidden in one of two possible locations. Next, they were given evidence that the food was in one of the locations and made their first choice. Subjects were then given a different form of evidence that favored the other location and made a second choice (which confirmed or changed their first choice). In the "strong evidence first" condition, chimpanzees were provided with strong evidence for one of the locations before their first choice and then weak evidence for the alternative location before their second choice. In the "weak evidence first" condition, the order was reversed (Fig. 1). Our classifications for strong versus weak evidence were based on previous research (*13*, *16*). In Experiment 1, we classified visual evidence (seeing food) as strong evidence and auditory evidence (hearing food) as weak evidence (Fig. 1A). In Experiment 2, we classified auditory evidence as strong evidence and indirect visual evidence (seeing food traces) as weak evidence (Fig. 1B). Chimpanzees' first choices validated these classifications (Experiment 1: $\chi^2 = 8.37$, df = 1, $p = 0.004$; Experiment 2: $\chi^2 = 11.99$, df = 1, $p = 0.001$; Fig. 2A and SM).

We assessed whether chimpanzees' choices aligned with the predictions of rational belief revision. In Experiment 1, chimpanzees were significantly more likely to revise their beliefs in the "weak evidence first" condition than in the "strong evidence first" condition ($\chi^2 = 14.03$, df = 1, $p < 0.001$; Fig. 2B). We found no evidence that chimpanzees simply learned the appropriate behavior over time: Neither trial number ($\chi^2 = 0.85$, df = 1, $p = 0.398$) nor the interaction between trial number and condition ($\chi^2 = 3.56$, df = 1, $p = 0.151$) had a significant effect on performance. In Experiment 2, chimpanzees also revised their belief significantly more often in the "weak evidence first" condition than in the "strong evidence first" condition ($\chi^2 = 20.52$, df = 1, $p < 0.001$; Fig. 2B). Again, we found no evidence that chimpanzees simply learned the behavior across trials: Neither trial number ($\chi^2 = 0.93$, df = 1, $p = 0.336$) nor the interaction between trial number and condition ($\chi^2 = 1.60$, df = 1, $p = 0.206$) had a significant effect on the likelihood of belief revision.

The results also confirm that chimpanzees' choices were in line with the principle of commutativity, which holds that one's belief should depend on the sum total of all previously perceived evidence, independent of the order in which that evidence was acquired (*20*). After receiving both strong and weak evidence, chimpanzees chose the location supported by strong evidence at above chance levels in both conditions in Experiment 1 [proportion choosing strong evidence side: weak evidence first condition = 0.93, 95% confidence interval (CI) (0.88, 1.00); strong evidence first condition = 0.92, 95% CI (0.85, 1.00)] and Experiment 2 [weak evidence first condition = 0.96, 95% CI (0.93, 1.00); strong evidence first condition = 0.86, 95% CI (0.77, 1.00)]. Moreover, the likelihood of endorsing the strong evidence at the second choice did not differ depending on whether it was presented first (strong evidence first condition) or second (weak evidence first condition) in Experiment 1 ($\chi^2 = 1.64$, df = 1, $p = 0.286$) or Experiment 2 ($\chi^2 = 1.40$, df = 1, $p = 0.330$).

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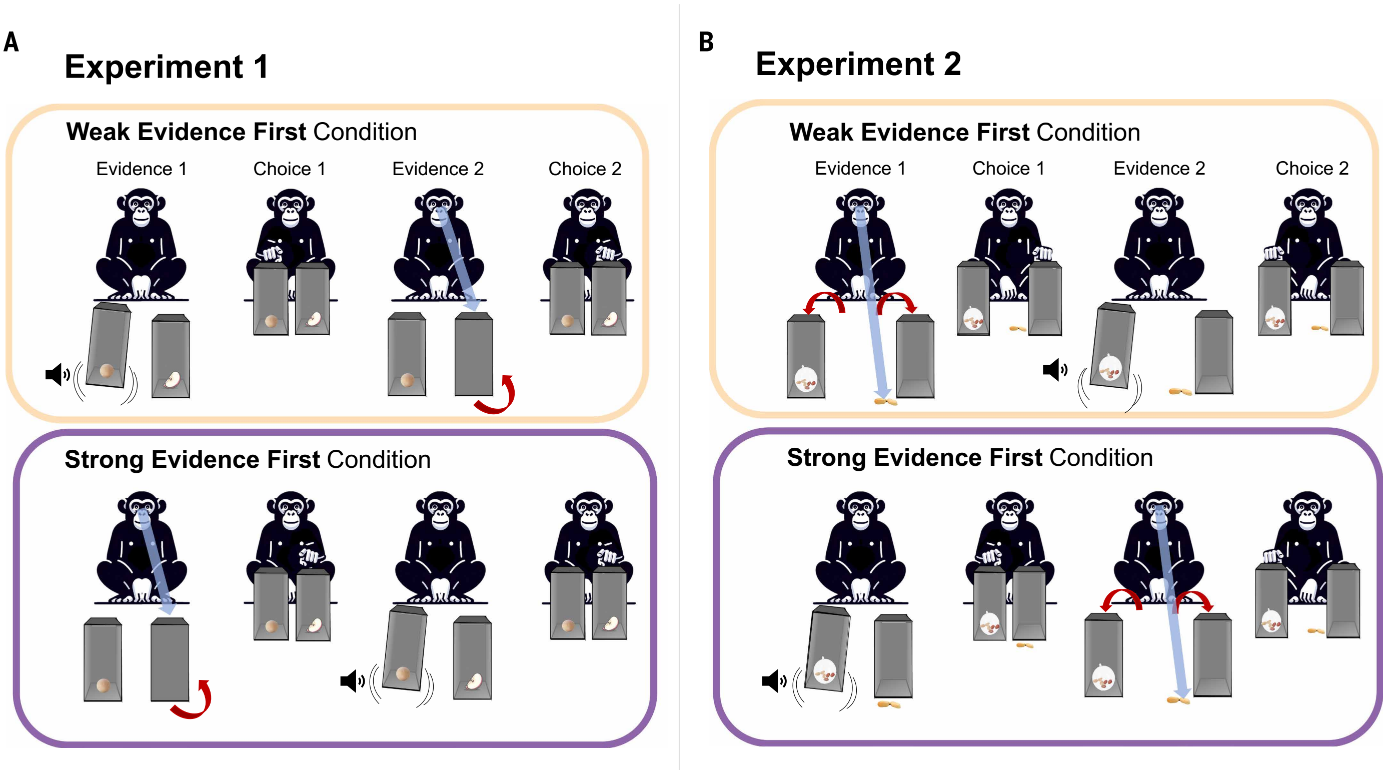

Fig. 1. Procedure of Experiments 1 and 2. (**A**) Experiment 1, Weak evidence first condition: Chimpanzees first received weak evidence (auditory evidence: shaking the box with a piece of wood in it) for one of the boxes and made a first choice. Then they received strong evidence (direct visual evidence: seeing into the box through a glass pane) for the other box and made a second choice. Strong evidence first condition: The same types of evidence were presented but in reverse order. (**B**) Experiment 2, Weak evidence first condition: Chimpanzees first received weak evidence (indirect visual evidence: seeing traces of the food behind the box) for one of the boxes and made a first choice. Then they received strong evidence (auditory evidence: shaking the box with a plastic capsule containing peanuts in it) for the other box and made a second choice. Strong evidence first condition: The same types of evidence were presented but in opposite order. Note: The red arrows indicate that the box was rotated (Experiment 1) or moved to the side (Experiment 2) to reveal visual evidence. In Experiments 1 and 2, in addition to the weak evidence first condition and the strong evidence first condition, chimpanzees also participated in filler trials, during which they received one piece of evidence, made a single choice, and received the contents of the box that they picked on their first choice (there was no second piece of evidence and no second choice). Filler trials were included such that subjects could not, on any given trial, predict whether their first or second choice would count (for details, see SM).

We also implemented a Bayesian modeling analysis in Stan (*21*) to assess whether chimpanzees' choice behavior is consistent with a formal model of belief revision (rational choice model; fig. S3 and SM). We found that the core conditions for rationality were met: Inferred evidence strength for strong evidence was both larger than—and in the opposite direction of—weak evidence (Fig. 2C and SM). Furthermore, this rationality did not merely emerge at the group level: Across both experiments, this pattern held for nearly every individual subject (Fig. 2, C and D, and SM).

To assess whether the rational choice model provided the best explanation for chimpanzees' choices, we compared it against four alternatives (fig. S3 and SM): belief perseveration (*22*–*24*), recency bias (*25*, *26*), cue saliency (*27*, *28*), and a null model. For both experiments, the rational choice model outperformed the recency bias, belief perseveration, and null models, while the cue saliency model performed equally well compared with the rational choice model (see SM).

The cognitive underpinnings of chimpanzees' belief revision

The findings of Experiments 1 and 2 suggest that chimpanzees compare evidence in favor of two alternative options and endorse the option supported by stronger evidence. It is possible, however, that receiving strong evidence—such as seeing the food directly in Experiment 1—simply replaced representations based on weak evidence, without any comparison across represented options (cue saliency model). In Experiment 3, we tested whether the saliency of the strongest cue overrides other representations. Subjects ($N = 23$) were presented with three hiding locations and received strong evidence (seeing food) for one of the locations, weak evidence (hearing food) for a second location, and no evidence for the third location (Fig. 3). Then, the box supported by strong evidence was removed. Lastly, chimpanzees made a choice. We tested whether chimpanzees would select the option supported by weak evidence more often than the option supported by no evidence, which would suggest that weaker representations are maintained even when the evidence supporting them is not the most salient. Alternatively, they could choose randomly between the two remaining options, suggesting that only the representation supported by the most salient evidence is maintained. Chimpanzees chose the weak evidence option at a rate significantly above chance ($\beta_0 = 1.41$, standard error = 0.19, $z = 7.61$, $p < 0.001$), and the Bayesian analysis confirmed that their weight on weak evidence was significantly greater than 0 (see SM). This suggests that chimpanzees indeed represented both options during Experiments 1 and 2 [see fig. S4 and SM for an additional experiment replicating this finding; see also (*29*–*32*)].

If chimpanzees in Experiments 1 and 2 explicitly represented the evidence in favor of both options and compared their relative strength, they should demonstrate two further capacities: differentiating between new and redundant evidence (Experiment 4) and sensitivity to second-order evidence—evidence about the validity of the previous evidence (Experiment 5).

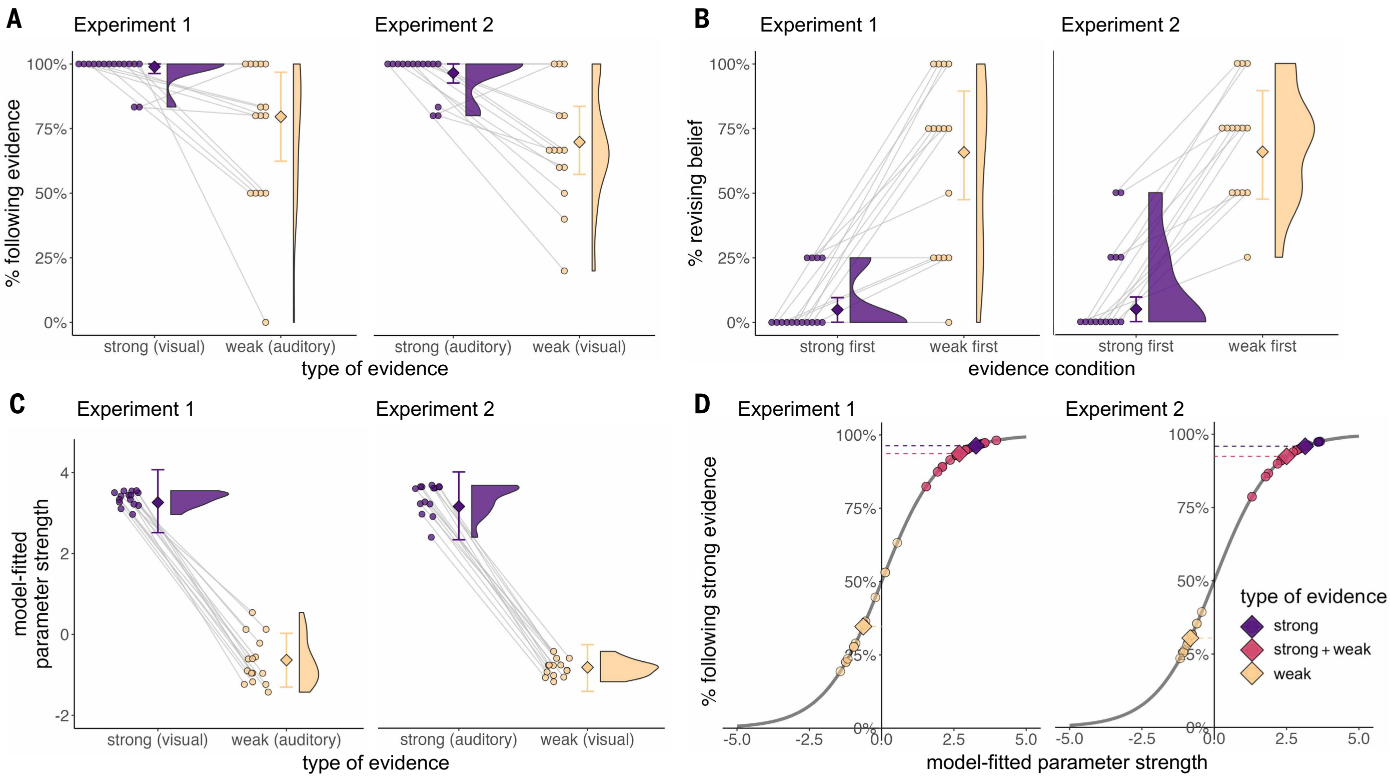

Fig. 2. Results of Experiments 1 and 2. (**A**) First choices by evidence type. Each point represents one chimpanzee's average response for that trial type. Error bars represent the bootstrapped 95% CIs of the generalized linear mixed model (GLMM) including all main effects. Diamonds represent the model predictions. Gray lines connect the behavior of one chimpanzee across both conditions within each experiment. (**B**) Belief revision by condition. Error bars represent the bootstrapped 95% CIs of the GLMM including all main effects. Diamonds represent the model predictions. Gray lines connect the behavior of one chimpanzee across both conditions within each experiment. (**C**) Rational choice model parameter estimates for individual subjects' e_{Strong} and e_{Weak} in Experiments 1 and 2. Error bars represent the model's 95% CIs on the group mean estimates (diamonds). (**D**) Predicted choice rates based on model-fitted evidence strengths across different evidence types (strong, weak, and strong + weak). Dots reflect individual subject parameters, and diamonds reflect group means. The dashed lines reflect the model's assumed relationship between evidence strength and choice rate.

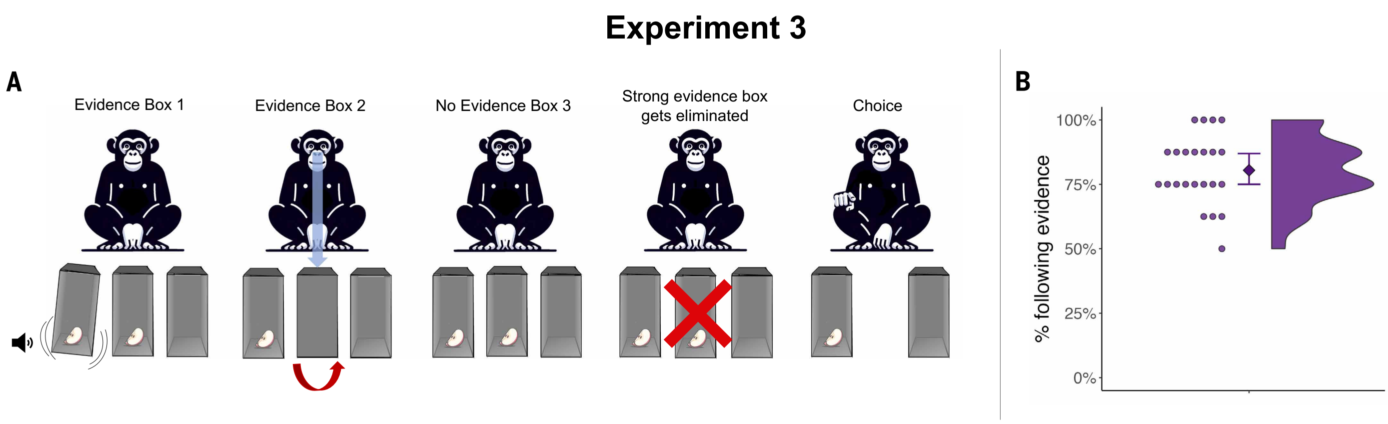

Fig. 3. Procedure and results of Experiment 3. (**A**) Chimpanzees received, in counterbalanced order, weak evidence for one box (auditory evidence: shaking the box with a piece of wood in it), strong evidence for a second box (direct visual evidence: seeing into the box through a glass pane), and no evidence for the third box (the box was touched for the same amount of time that each of the other two boxes was manipulated, but no evidence was provided). Then the experimenter removed the box supported by strong evidence before the chimpanzee was allowed to make a choice. (**B**) Chimpanzees were significantly more likely to select the box supported by weak evidence (rather than the box supported by no evidence) than would be expected by chance.

In Experiment 4, we asked whether chimpanzees ($N = 23$) would be swayed more by new evidence (evidence that comes from an independent, distinct source that provides additional information) compared with redundant evidence (evidence that comes from the same source as previous evidence and therefore provides no new information). In the "redundant evidence" condition, the weak evidence was auditory shaking evidence (which, when repeated, provides no new information), whereas in the "new evidence" condition, the weak evidence was auditory dropping evidence (which, when repeated, indicates that a second piece of food has been dropped into the box; Fig. 4 and SM).

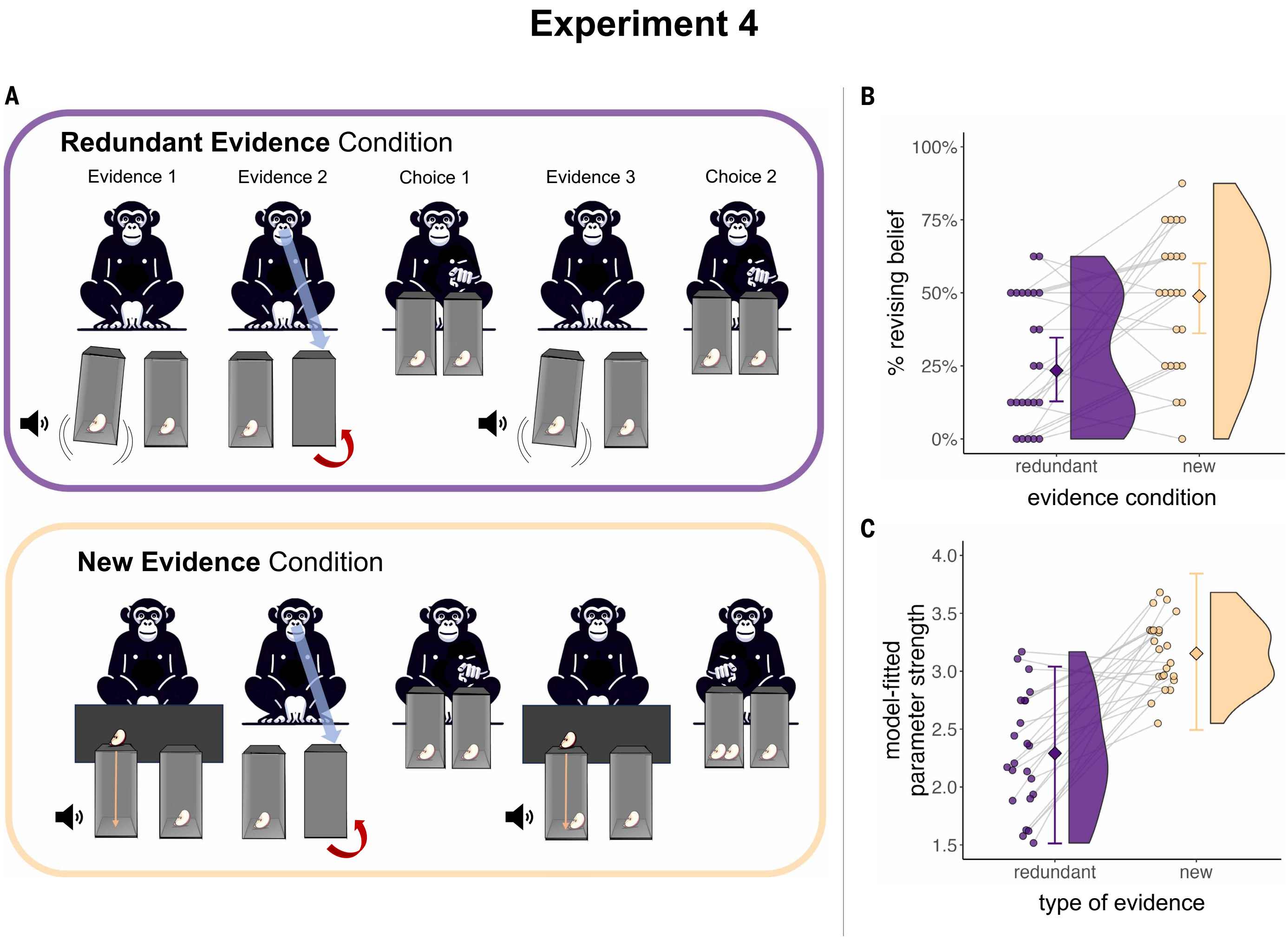

Fig. 4. Procedure and results of Experiment 4. Chimpanzees received weak evidence for one of the boxes, followed by strong evidence for the other box. They then made a first choice, after which they were presented with the same weak evidence again. The nature of the weak evidence varied according to condition. (**A**) In the redundant evidence condition, the weak evidence did not accumulate: The box was shaken a second time, providing no new information about its contents. In the new evidence condition, the weak evidence accumulated: The chimpanzees could infer on the basis of the second dropping noise that a second piece of apple had been dropped into the box. Notably, before presenting the second piece of evidence, the experimenter showed the chimpanzees a second piece of apple in both conditions. In the redundant evidence condition, the experimenter presented the apple and then placed it in their pocket. In the new evidence condition, the experimenter concealed the apple in their hands before dropping it into one of the boxes. (**B**) Chimpanzees were more likely to revise their beliefs when they heard a second piece of food drop into the box (new evidence condition) than when they heard the box shake for a second time (redundant evidence condition). (**C**) The rational choice model confirmed that for nearly every subject, the second piece of new evidence had a greater impact on their belief than the second piece of redundant evidence.

Across both conditions, chimpanzees were first presented with weak and strong (visual) evidence. Then, after they chose the option supported by the strong evidence, they were provided with a second instance of the weak evidence. Chimpanzees demonstrated a significantly higher tendency to revise their initial choice in the "new evidence" condition compared with the "redundant evidence" condition (χ^2 = 9.25, df = 1, p = 0.002; Fig. 4). Their tendency to revise beliefs decreased over trials ($\chi^2 = 5.06$, df = 1, $p = 0.024$), with a steeper decline in the "redundant evidence" condition ($\chi^2 = 5.59$, df = 1, $p = 0.018$; fig. S5 and SM). When presented on its own, the auditory dropping evidence presented in the "new evidence" condition was weaker than the auditory shaking evidence presented in the "redundant evidence" condition, showing that the strengths of these evidence types did not account for the difference in revision rate between conditions (see SM).

Furthermore, the rational choice model outperformed both the cue saliency and null models. A rational agent in this task would attribute a higher weight to the second instance of new evidence than the second instance of redundant evidence; the parameters for the rational choice model confirmed that this was the case (Fig. 5C and SM). These results confirm that chimpanzees can both remember the specific evidence used to form their beliefs and distinguish between new and redundant evidence when revising their beliefs.

In Experiment 5, we presented chimpanzees (N = 22) with second-order evidence (*33*, *34*): evidence that reduces the strength of the first-order evidence (so-called "undercutting defeaters"). This experiment consisted of two conditions: a "defeater" condition (in which first-order evidence was weakened) and a "non-defeater" condition (in which first-order evidence was not weakened). We ran both visual (Fig. 5) and auditory versions (fig. S6) of this task, using the strong evidence from Experiments 1 and 2, respectively. In the "visual defeater" condition, after chimpanzees had chosen the location supported by visual evidence (where they had seen the food), the experimenter pulled a glass

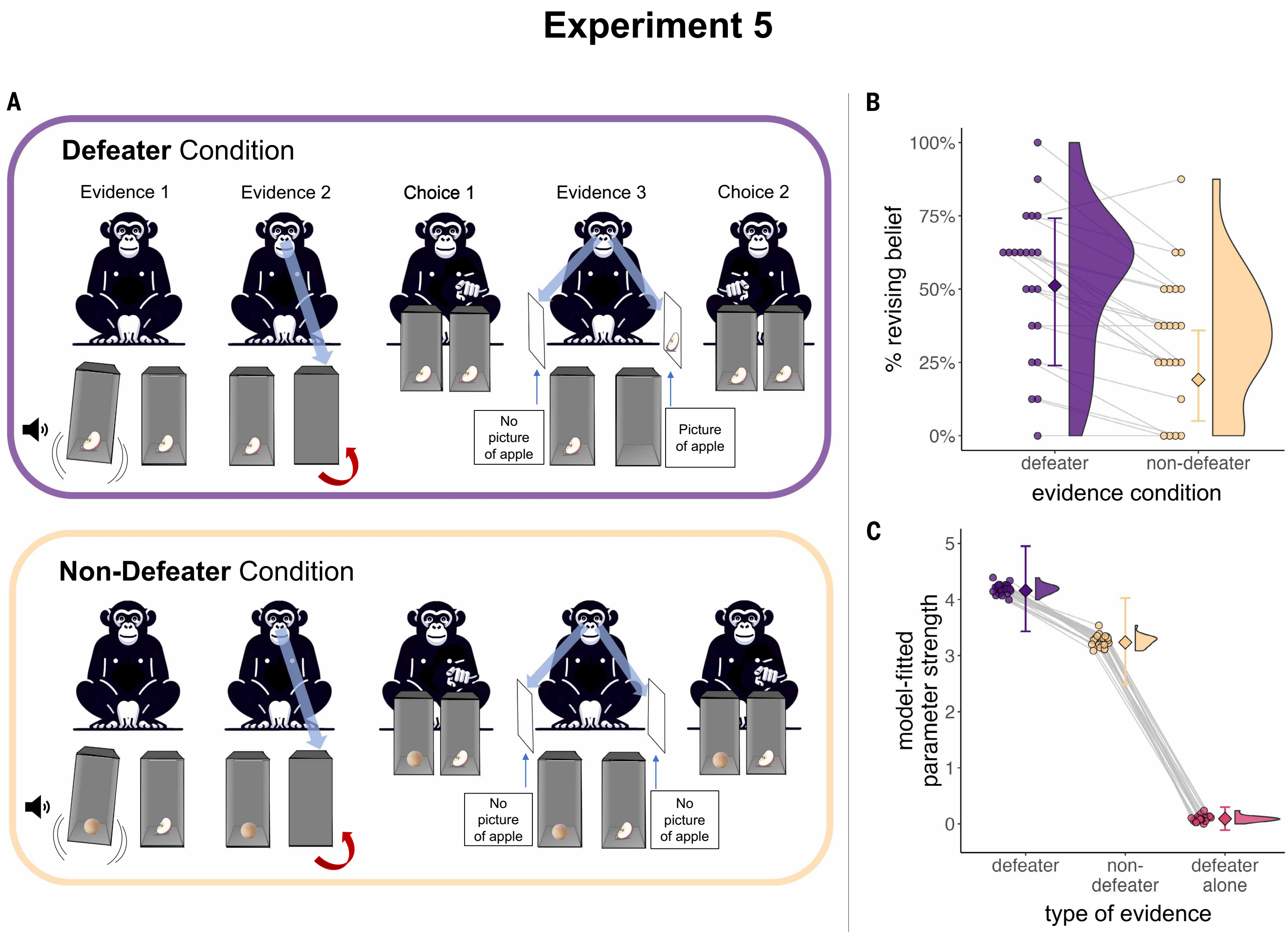

Fig. 5. Procedure and results of Experiment 5. (**A**) In the defeater condition, chimpanzees received weak evidence for one of the boxes, followed by strong evidence for the other box. They then made a first choice, after which they were presented with a defeater: second-order evidence that weakens the strength of the first-order evidence. The strong visual evidence was defeated when the experimenter revealed that the food they had previously seen inside the box was actually a picture on the box's window. In the non-defeater condition, the experimenter's actions were identical, but this time there was no picture on the window. (**B**) Chimpanzees were more likely to revise their belief in the defeater condition than in the non-defeater condition. The figure depicts the combined results of both the visual and auditory versions of the task (see SM for separate figures). (**C**) The rational choice model confirmed that the defeater affected the chimpanzees' beliefs more than the non-defeater, and that the defeater did not affect the chimpanzees' beliefs at all when it was presented alone (without first-order evidence). Note: For clarity, Fig. 5A only depicts the visual version of the task; for the auditory version, please refer to the SM and fig. S6.

window out of the box to reveal that it had a picture of an apple on it (figs. S6, S7, and SM). In the "visual non-defeater" condition, the experimenter also revealed the box's window, which was an empty pane of glass. In the "auditory defeater" condition, after chimpanzees had chosen the location supported by auditory evidence (where they had heard a sound inside the shaking box), the experimenter removed a stone from the box and showed it to the subject (fig. S7 and SM). In the "auditory non-defeater" condition, the experimenter removed a leaf from the box (which could not have caused the rattling sound). We asked whether chimpanzees would be more likely to switch to the box supported by weak evidence in the "defeater" condition, where the strong evidence had been weakened, compared with the "non-defeater" condition, where the strong evidence had not been weakened. The results confirmed this prediction: Chimpanzees were significantly more likely to switch in the "defeater" condition compared with the "non-defeater" condition ($\chi^2 = 16.27$, df = 1, $p < 0.001$). This effect held true in both the auditory (fig. S6d) and visual (fig. S6c) modalities; the interaction of task version and condition was not significant ($\chi^2 = 0.11$, df = 1, $p = 0.743$).

The rational choice model once again strongly outperformed both the cue saliency and null models on this task. Moreover, the best-fitting parameters for the rational choice model confirmed that subjects' beliefs were more affected by the defeater than the non-defeater. Notably, chimpanzees revised beliefs only when defeaters interacted with prior evidence, not when they were presented alone (Fig. 5C and SM).

Taken together, these findings suggest that chimpanzees appropriately respond to second-order evidence—evidence about evidence—which requires representing the evidential relation between evidence and belief.

Discussion

Chimpanzees' responses to counterevidence aligned with a Bayesian model of rational belief revision. They selectively maintained or revised their initial beliefs by evaluating the strength of the initial evidence relative to the strength of the counterevidence. In doing so, they demonstrated remarkable cognitive control and flexibility. Chimpanzees did not attribute a fixed value to each type of evidence; instead, they weighed the relative strength of evidence. For instance, auditory evidence was judged to be weaker than direct visual evidence in Experiment 1 and stronger than indirect visual evidence in Experiment 2. These responses were enabled by chimpanzees' capacity to represent (i) both possible hypotheses (Experiment 3) and (ii) the respective evidence in favor of them (Experiment 4). Chimpanzees also revised their beliefs in light of undercutting defeaters: second-order evidence that weakens the evidential connection between a piece of first-order evidence and a hypothesis (Experiment 5). Model comparisons demonstrate that these results are not explained in terms of nonrational processes such as belief perseveration, recency bias, or cue saliency. Instead, they suggest that chimpanzees engage in rational belief revision.

Selective belief revision is a metacognitively demanding and reflective cognitive process (*35*). Previous research has shown that chimpanzees appropriately respond to different types of direct and indirect evidence (*6*, *8*), but such evidence-based belief formation can occur in the absence of explicit reasoning about evidence and its bearing on different hypotheses. Indeed, it is often explained in terms of "unreflective evidence-responsiveness" (*33*). By contrast, the capacity to appropriately respond to counterevidence and, especially, to second-order evidence—evidence about the relevance of first-order evidence to one's belief—is thought to constitute a key standard of reflective engagement with evidence (*33*, *35*). It requires representing the three components of the so-called evidential relation: the evidence, the hypothesis, and their causal connection.

These results inform ongoing discussions about the metacognitive capacities of nonhuman animals. It has long been argued that linguistic representation is necessary for successful reflection on evidential relations (*36–39*). Yet recent empirical research on information search (*40*, *41*) and opt-out behaviors (*42–44*) has led theorists to attribute some metacognitive skills to primates (*45*). Despite this evidence, critics have maintained that behaviors such as searching for information and opting out are explainable in terms of cognition about the world and do not require metacognition—cognition about cognition (*46*).

Our findings present strong support for the view that chimpanzees have genuine metacognitive capacities. The particular form of metacognition demonstrated in the current experiments is "source monitoring": representing not only what one knows but also how one knows it (*47–50*). Evidence for this capacity comes from chimpanzees' responses to counterevidence, to new versus redundant evidence, and to second-order evidence. Reasoning about second-order evidence is, by definition, a form of metacognition. That chimpanzees represented second-order evidence as such is most strongly supported by the finding that the undercutting defeater in Experiment 5 affected chimpanzees' decisions only when it followed a piece of first-order evidence but not when presented on its own.

Accounts of major transitions in cognitive evolution identify key changes in the computational architecture of nervous systems that give rise to new cognitive capacities (*45*, *51*, *52*). The emergence of reflective processes—a system able to form representations of the cognitive processes themselves (*51*, *53*)—marks a key transition. The experiments presented here suggest that chimpanzees possess this capacity. Chimpanzees revise their beliefs selectively based on metacognitive awareness of the relation between evidence and hypothesis.

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ACKNOWLEDGMENTS

We thank T. Mukungu, I. Ampeire, P. Sekulya, A. Okello, B. Apamaku, D.y Basemera, H. Aligumisiriza, I. Ayebazibwe, and all the staff at Ngamba Island Chimpanzee Sanctuary. Thanks also go to M. Goddu, A.-C. Schneider, S. Thomaes, and M. Tomasello, who provided helpful feedback on the manuscript. **Funding:** J.M.E. and E.M.S. were supported by a grant from the Leakey Foundation, and H.S. was supported by an Audacity Grant from the Leibniz ScienceCampus Primate Cognition. **Author contributions:** Conceptualization: H.S., J.C., E.H., J.M.E., S.Z., E.M.S.; Investigation: H.S., J.M.E., E.H.; Methodology: H.S., E.M.S., B.D.T., J.C., E.H., J.M.E., S.Z.; Project administration: J.R., E.H., J.M.E.; Resources: J.R., H.S., J.M.E.; Visualization: H.S., E.M.S.; Writing – original draft: J.M.E., H.S., E.M.S.; Writing – review & editing: H.S., E.M.S., B.D.T., J.C., E.H., S.Z., J.M.E. **Competing interests:** The authors declare that they have no competing interests. **Data and materials availability:** All data and code used in the analyses are available on Dryad (*54*).

SUPPLEMENTARY MATERIALS

science.org/doi/10.1126/science.adq5229
Participant Information; Materials and Methods; Supplementary Text; Figs. S1 to S10; References (*55–67*); Tables S1 to S20; Movies S1 to S5; MDAR Reproducibility Checklist

Submitted 17 May 2024; resubmitted 22 November 2024; accepted 13 August 2025

10.1126/science.adq5229