SOCIAL SCIENCES

Technical reasoning bolsters cumulative technological culture through convergent transformations

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Understanding the evolution of human technology is key to solving the mystery of our origins. Current theories propose that technology evolved through the accumulation of modifications that were mostly transmitted between individuals by blind copying and the selective retention of advantageous variations. An alternative account is that high-fidelity transmission in the context of cumulative technological culture is supported by technical reasoning, which is a reconstruction mechanism that allows individuals to converge to optimal solutions. We tested these two competing hypotheses with a microsociety experiment, in which participants had to optimize a physical system in partial- and degraded-information transmission conditions. Our results indicated an improvement of the system over generations, which was accompanied by an increased understanding of it. The solutions produced tended to progressively converge over generations. These findings show that technical reasoning can bolster high-fidelity transmission through convergent transformations, which highlights its role in the cultural evolution of technology.

INTRODUCTION

Today, technology pervades human life, and it is often taken for granted that technology and science progressively become more advanced and more refined through time. Yet, the origin of this capacity remains a fascinating mystery. Other primates sometimes use tools [e.g., chimpanzees (1), capuchins (2), and orangutans (3)] and have sometimes been shown to be doing so for very long periods of time (4). There is also evidence that, like humans, nonhuman primates learn to use tools through social learning, by the observation of tool-using conspecifics (5). However, human technology is notably different because nonhuman primate tool use does not evolve and does not gradually become more efficient and more complex through time (6). The term cumulative technological culture (CTC) has been coined to refer to the progressive increase in the complexity and/or efficiency of tools and techniques that are too complex to be invented by a single individual (7-9). There is increasing evidence that some nontechnological aspects of animal culture can cumulatively evolve (10-12), raising the question of how and why technology became cumulative in humans and not in other primates.

CTC has been considered to be driven by two engines: high-fidelity transmission, the similarity between tools and techniques across episodes of transmission [also called episodic fidelity; see (13)] and innovation (14). The crucial role of high-fidelity transmission in CTC has been repeatedly stressed with the rationale that, when an innovation appears, it will quickly be lost if it cannot be faithfully transmitted to others (7, 15–19). High-fidelity transmission has often been assumed to result from unique social-cognitive skills that allow humans to imitate or "infocopy" [(6, 18, 20, 21); also called high-fidelity copying or propensity fidelity; see (13)].

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Following this view, the role of causal reasoning in CTC has often been minimized by assuming that complex technologies result from the accumulation of many often poorly understood improvements made over generations (7, 22, 23) combined with rare intentional improvements achieved through causal reasoning (24). Although the term causal reasoning is widely used in the literature, we have stressed (25) that the term technical reasoning may be more appropriate in the field of CTC because it refers to a specific form of causal—and analogical—reasoning directed toward the physical world. Thus, the term technical reasoning will be hereafter used to refer to this specific kind of reasoning.

The similarity observed between tools or techniques in CTC need not come from the existence of copying mechanisms (26, 27). An alternative explanation, the cultural attraction theory (26, 28, 29), is that humans are endowed with cognitive mechanisms that are not specifically designed for copying but that transform and adapt what is socially learned to the ends and characteristics of the learning individual. Under such a view, high-fidelity transmission is achieved through convergent transformations; that is, individuals with the same goal will give rise to similar cultural products through shared cognitive skills, goals, and environments (30, 31). This view has recently received support from theoretical, experimental, and field studies on cultural evolution in humans (32-37) and nonhuman primates (31, 38) and is also in line with studies on language evolution (39). For instance, arguments transmitted along transmission chains could become degraded and then fully reconstructed through deductive reasoning (40). With respect to CTC, the cultural attraction theory translates into the fact that individuals use technical reasoning skills to solve complex technological problems and that highfidelity transmission is the result of convergent transformations.

To experimentally examine the role of convergent transformations versus copying mechanisms in CTC, we used a recently developed task that was aimed at providing the sort of complexity encountered in CTC. Derex *et al.* (22) reported a microsociety study designed to investigate the role of causal understanding in CTC. The task consisted of optimizing a wheel system (Fig. 1A).

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Fig. 1. Experimental task and design. (A) The task consisted of minimizing the time it took a wheel to travel down an inclined track. The wheel had four radial spokes. On each spoke, a weight could be moved closer to or farther from the center of the wheel on 12 positions. (B) The participants performed the task as members of chains of five participants. Each of the participants had five trials to improve the wheel system by modifying the wheel configuration. The experimenter transmitted to each participant (except those of the first generation) the information about the last two trials (gray) of the previous participant. After the five trials, the participants' understanding of the wheel system was assessed with an understanding test (12 center-of-mass items and 12 inertia items). (C) In the Speed-Only condition, only the wheel speeds of the last two trials (gray) were transmitted to the next participant. In the Configurations+Speed+Noise condition, the participants were given two weight configurations and their associated speeds (gray). The configurations came from the previous participant in the chain but were modified by randomly moving the four weights six positions closer to or farther from the center of the wheel.

This task was multidimensional because the speed of the wheel depended on its moment of inertia (i.e., a wheel with its four weights close to its center is faster than a wheel with its four weights farther from the center) and the position of its center of mass (i.e., the initial acceleration is better when the wheel is unbalanced with the center of the mass located ahead and above the axis of the wheel; fig. S1). The participants performed the task as members of chains of five participants (Fig. 1B). The experimenter transmitted to each participant (except those of the first generation) the weight configurations and their associated speeds from the last two trials of the previous participant (hereafter called Configurations+Speed condition). Participants' understanding of the wheel system was assessed with an understanding test consisting of selecting the fastest wheel configuration out of several presented. The results indicated that the wheel system became progressively optimized, and although Derex *et al.* (22) found no improvement in understanding, we performed a partial replication (41) motivated by some methodological issues and demonstrated that the improvement was linked to the participants' understanding of the technology (i.e., their understanding increased through time, they were able to transfer this understanding to other problems, and they were better than controls).

The findings reported in both Derex *et al.* (22) and our prior study (41) gave limited insight into the process through which participants arrived at better configurations because the participants had access to all the information they needed (wheel configurations and associated speeds) to reproduce with high fidelity the wheel

systems produced by their predecessors. Nevertheless, our findings (41) indicated that even when individuals had access to all the information needed to blindly copy, they formed a causal representation of the physical system that they used to produce improvements. The role of technical reasoning may appear redundant here but could reveal its full potential if the information transmitted between individuals is incomplete or incorrect (25). Partial information combined with technical reasoning skills might allow an individual to converge toward the same technical solution or another technical solution that maintains—or even improves—the technology (25).

The present study aimed to test this possibility through two microsociety conditions, in which participants had five trials to improve a wheel system, as described above (14 chains of five participants in each condition; Fig. 1, A and B). After their five trials, the participants' understanding of the physical system was assessed with an understanding test (12 items for center of mass and 12 for inertia). In the Speed-Only condition, the only information that was transmitted to the next participant was the last two wheel speeds of the previous participant in the chain (i.e., no information at all about the configurations associated; Fig. 1C). In the Configurations+Speed+Noise condition, the participants were given two weight configurations and their associated speeds. The configurations came from the previous participant in the chain but were modified by randomly changing the position of the four weights closer to or farther from the center of the wheel (Fig. 1C). Therefore, the participants had access to partial or degraded information in both conditions. If copying is crucial for CTC and technical reasoning is nonnecessary, no improvement of the physical system should be observed in both conditions, nor should an increase in understanding be found. By contrast, if technical reasoning is important for completing partial or biased information, then an improvement of the physical system should be observed in both conditions, and it should be accompanied by an increase in understanding.

RESULTS AND DISCUSSION

The results supported the second prediction. The wheel speed increased over generations in both the Speed-Only condition [generation estimate, 3.03 m hour⁻¹; 95% confidence interval (CI): 1.28 to 4.73] and the Configurations+Speed+Noise condition (generation estimate, 1.77 m hour^{-1} ; 95% CI: 0.53 to 2.96; Fig. 2A and fig. S2) in parallel to the participants' total understanding score (Speed-Only: generation estimate, 2.04; 95% CI: 0.35 to 3.88; Configurations+Speed+Noise: generation estimate, 1.85; 95% CI: 0.40 to 3.05; Fig. 2B). A link was also found in both conditions between the wheel speed (the best speed of the last two trials) and the total understanding score (Speed-Only: wheel speed estimate, 0.55; 95% CI: 0.39 to 0.73; Configurations+Speed+Noise: wheel speed estimate, 0.65; 95% CI: 0.46 to 0.84; Fig. 3B). To examine convergence, we computed an intrageneration similarity score, which reflected the similarity between the wheel configurations of the participants of the same generation. We found that this intrageneration similarity score increased over generations within both conditions but not between conditions (Speed-Only: generation estimate, 1.41; 95% CI: 0.72 to 2.10; Configurations+Speed+Noise: generation estimate, 1.75; 95% CI: 1.25 to 2.18; Between: generation estimate, 0.67; 95% CI: -0.14 to 1.36; Fig. 3C). Together, these results indicate that high-fidelity transmission can arise through an increased

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understanding of the task that allow individuals to converge to optimal solutions [for similar results in a Configurations+Speed condition, see (41); see also fig. S3].

A careful examination of the evolution of wheel speed over the 25 trials (Fig. 2A) provides additional information about the dynamics of the cognitive processes involved in each condition. In the Configurations+Speed+Noise condition, the participants in the second-to-fifth generations maintained the wheel speed from their first trials at the same level as that of the last trials of their predecessors. This pattern, which is similar to that of the Configurations+Speed condition of Osiurak et al. [(41); fig. S4; see also (22)], suggests that the participants tended to use—but also to be canalized by [(22, 41) see also (42-44)]—social information to begin to form a causal representation of what could be an effective physical system. The early impact of social information on the formation of this causal representation is confirmed by the presence of a link between the total understanding score and the wheel speed (the best speed of the first two trials; wheel speed estimate, 0.25; 95% CI: 0.01 to 0.45; Fig. 3A).

By contrast, as shown in Fig. 2A, the participants in the Speed-Only condition seemed to reinvent the wheel at each generation, with the participants in the second-to-fifth generations obtaining a very low performance in their first trial, close to that of the first trial of participants in the first generation. Nevertheless, over their five trials, the participants in the second-to-fifth generations tended to improve the physical system systematically and progressively, leading them to outperform their predecessors. This outcome suggests that the participants in this condition benefited from the social information provided by the speed of previous wheels by comparing it with the performance based on their initial causal representation of the wheel system. Thus, the greater the gap between the performance of their predecessor and their initial performance, the more the participants attempted to modify-and thus enhance-their causal representation of the physical system, thereby allowing them to improve markedly their wheel system over their own trials. Support for this interpretation comes from the absence of a link in this condition between the total understanding score and the wheel speed, when the best speed of the first two trials is considered (wheel speed estimate, 0.16; 95% CI: -0.05 to 0.36; Fig. 3A).

The inertia dimension had a greater impact on the wheel speed than the center-of-mass dimension. Therefore, the considerable increase in wheel speed over the five trials implied that the participants in the Speed-Only condition explored further the inertia dimension and preferentially enhanced their understanding of this dimension. To investigate this aspect, we computed two exploration scores, one for the inertia dimension and the other for the center-of-mass dimension, which reflected the exploration of each dimension over the five trials. We found that the inertia exploration score increased over generations in the Speed-Only condition (generation estimate, 3.63; 95% CI: 1.69 to 5.49; Fig. 3E) in parallel with the participants' inertia understanding score (generation estimate, 2.28; 95% CI: 0.42 to 4.13; Fig. 2D). In broad terms, the mere availability of information about the predecessor's performance was enough to orient the participants toward a technical reasoningbased exploration [reasoned trial and error (25, 45)].

The pattern in the Configurations+Speed+Noise condition was different, with no significant effect of generations on the inertia exploration (generation estimate, -0.81; 95% CI: -2.49 to 0.81; Fig. 3E)

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Fig. 2. Parallel improvement of the wheel system and of its understanding. (A) Wheel speed over generations for nonfailure wheels and number of failures in the Speed-Only condition (gray) and in the Configurations+Speed+Noise condition (orange). (B to D) Understanding scores over generations [(B) total; (C) center-of-mass items only; (D) inertia items only]. The performance obtained by a control group is also shown [see (41); mean: yellow; standard error: blue]. Error bars indicate standard errors.

and understanding scores [generation estimate, 0.26; 95% CI: -0.98 to 1.56; Fig. 2D; for similar results in a Configurations+Speed condition, see (41)]. By contrast, there was an increase in the participants' center-of-mass understanding score (generation estimate, 1.59; 95% CI: 0.79 to 2.50; Fig. 2C). This increase was not found in the Speed-Only condition (generation estimate, -0.24; 95% CI: -1.18 to 0.75; Fig. 2C). The increase in the center-of-mass score reported in the Configurations+Speed+Noise condition was accompanied by a decrease in the center-of-mass exploration score over generations (generation estimate, -4.88; 95% CI: -8.05 to -1.53;

Fig. 3D). The random noise added before transmission fortuitously and almost systematically led to the generation of unbalanced wheel configurations (table S1), which was critical to observe the effect of the position of the wheel's center of mass on its speed. Random noise, along with the canalizing effect associated with the transmission of wheel configurations, seems to have directed the participants' attention to the center-of-mass dimension, leading them to improve their understanding of this dimension. These findings highlight how the introduction of random modifications can favor the understanding of often poorly understood dimensions, which can, in



Fig. 3. Links between the wheel speed and the understanding scores and increase of intrageneration similarity and exploration scores over generations. (A and B) Links between the wheel speed [(A) the best speed of the first two trials; (B) the best speed of the last two trials] and the understanding scores (total). (C) Intrageneration similarity scores over generations (Within condition: Speed-Only condition, gray; Configurations+Speed+Noise condition, orange; Between condition: green). (D and E) Exploration scores [(D) center of mass; (E) inertia] over generations. Error bars indicate standard errors.

turn, lead to specific innovations. The presence of a decrease in the center-of-mass exploration score suggests that these innovations did not result from lucky errors or occasional experiments but from the direct contribution of random modifications introduced along with the canalizing effect. This is telling with respect to our hypotheses because if participants were using a strategy in which they introduced random modifications and selected the best outcomes, (i) participants in both conditions would mostly explore the center-of-mass dimension (favored by random modifications) and (ii) transmission chains in the two conditions would converge toward the same outcome (but see Fig. 3C).

The present study extends previous findings, which have questioned the crucial role of copying mechanisms (46, 47) and/or emphasized the importance of causal understanding/inductive biases (48–50) and innovative skills in CTC (51, 52). In this experiment, participants with very little or randomly transformed social information managed to improve and converge toward similar outcomes compared to participants with complete information [(13, 53) see also (54, 55)]. This is remarkable and demonstrate the importance

of technical reasoning in producing CTC: Technical reasoning is a reconstruction mechanism that allows us to recover from partial or degraded information obtained through social learning and therefore guarantees the high-fidelity transmission of advantageous technologies (i.e., the high similarity between the wheel configurations). Said differently, technical reasoning can be viewed as a potential cognitive mediator of CTC that allows individuals to filter information acquired either through their own experience (asocial learning) or through social learning, by extracting relevant information and rejecting irrelevant information, irrespective of the origin of this information (25). Technical reasoning might participate in both the innovative component and the high-fidelity component of CTC, thus implying that the distinction between these two components might be of convenience rather than of cognitive distinctness.

The use of microsociety paradigms has provided important insights into the origin of CTC. As stressed by Miton and Charbonneau (56), participants in microsociety paradigms "are adept inventors, capable of innovating in a matter of minutes" (p. 4). Consistent with this fact, our participants were able to improve a multidimensional technology, which is not obviously intuitive as shown by the results, as well as the understanding of it in only about 20 min and five trials. Showing that technical reasoning can play a reconstruction role in such paradigms can also renew the question of how technologies have evolved in early hominins. For instance, the Oldowan industrial complex emerged at around 2.6 million years ago. This industry comprises mainly sharp-edged flakes and the cores from which they were removed (57). There is no clear tradition within the Oldowan before 2 million years ago (58). The Acheulean industry, which appeared around 1.75 million years ago, corresponds to bifacially shape stone tools used as handaxes and cleavers. This industry is characterized by a notable homogeneity, which persisted for around 1.5 million years (59, 60). This shift may reflect the emergence of high-fidelity transmission in our lineage. Several proposals have been made for interpreting this shift at a cognitive level, with a particular focus on social cognitive skills (61, 62). The findings reported here provide an alternative interpretation in suggesting that technical reasoning could have also contributed to the emergence of high-fidelity transmission. Of course, this interpretation must be taken with caution because other aspects can also be fundamental to maintain the stability of technologies over long periods of time, such as the-perhaps presupposed-lesser cost of copying compared to understanding the technical behavior of conspecifics and the interaction of this learning cost with environmental conditions (7, 63), the different social learning strategies [e.g., prestige bias and conformity bias (20, 64)], or the superiority of some social learning conditions over others in the transmission process [e.g., superiority of communication over reverse engineering (65, 66)]. Regardless, our results show that CTC and the high-fidelity transmission of technology between individuals should not be systematically interpreted as evidence of cognitive mechanisms capable of copying coupled to the random retention of useful modifications.

MATERIALS AND METHODS

Ethics

The Ethics Committee of the University of Lyon Department of Psychology approved the study, and the procedure was carried out in accordance with the ethical standards of the 1964 Declaration of Helsinki. Informed consent was obtained from all participants after the nature and possible consequences of the study were explained [see (41)].

Participants

One hundred and forty-six students at the University of Lyon took part in the study ($M_{age} = 20.84$, $SD_{age} = 2.91$; 102 women). The participants were nonselectively recruited through advertisements posted on social media websites [see (41)].

Experimental apparatus

The wheel system used in the present study was the same as the one used by Osiurak *et al.* (41) (for an illustration, see https://osf.io/m3d7q/). A description is provided in fig. S5.

Procedure

The procedure was basically the same as in (41). The experiment took place in an experimental room at the University of Lyon (around 30 min in duration). The participants sat at a table placed

2 m from the experimental apparatus. Before the experiment, the participants completed a consent form. After the experiment, they indicated whether they had an academic background in engineering or physics.

Experimental design Building phase

This phase was similar in both conditions. Instructions were similar to those of Osiurak et al. (41) (see https://osf.io/m3d7q/). The participants had five trials to optimize the speed of a wheel that descended a 1-m-long inclined track. They could move four weights to any of 12 discrete positions along each spoke and were free to choose their own configuration (from 1 to 12, with 1 being the closest position to the center of the wheel and 12 being the farthest position from the center of the wheel). After the participants used a marker pen to indicate the positions of the four weights on the wheel (i.e., a paper version of the configuration), the experimenter positioned the weights on the physical wheel accordingly. The participants were not allowed to move the weights on the physical wheel themselves to prevent damage due to potential repeated awkward manipulations. The wheel also needed to be placed correctly in its initial position and the release had to be accomplished without any abrupt movements to avoid a modification of the trajectory of the wheel. Nevertheless, the participants could scrutinize the experimenter moving the weights and releasing the wheel as well as the wheel descending the track. The time it took the wheel to travel down the track was automatically recorded by a computer program (see https://osf.io/m3d7q/). The wheel speed and the associated configuration were then displayed to the participants, who had as much time as they needed to consult their last two configurations and choose the next one. As explained above, we used a paper-andpencil method to display the wheel speeds and the associated configurations (see https://osf.io/m3d7q/). After three trials, the experimenter reminded the participants in the Speed-Only condition that the wheel speeds of their last two trials would be transmitted to the next participant in the chain. In the Configurations+Speed+Noise condition, the experimenter reminded the participants that their last two configurations and the associated speeds would be transmitted to the next participant in the chain. In this condition, a random noise was introduced by the experimenter into the wheel configurations before transmission, by moving the four weights six positions closer to or farther from the center of the wheel (i.e., the absolute sum of the modifications equaled 6). Thus, if the configuration of the wheel of a participant on their fourth trial was, for instance, Position_{Top Weight}: 9; Position_{Front Weight}: 9; Position_{Bottom Weight}: 5; Position_{Back Weight}: 5, a random modification of six positions was applied (e.g., +1;-3;+2;0), which modified the configuration of the wheel (i.e., $Position_{Top Weight}$: 9 + 1 = 10; $Position_{Front Weight}$: 9-3 = 6; Position_{Bottom Weight}: 5 + 2 = 7; Position_{Back Weight}: 5 + 0 = 5). The configurations thus modified and their associated speeds were then transmitted by the experimenter to the next participant. The computer program used to generate these random positions is available at https://osf.io/m3d7q/. The introduction of this random noise frequently generated wheels that did not descend (i.e., speed of 0 m hour^{-1}). Sometimes, the program could generate two configurations with null speed for the same participant. To ensure that the participants in the second-to-fifth generations received at least one configuration with a wheel that descended, we reran the program until we obtained a wheel with a

non-null speed for the second configuration when the speed associated with the first configuration was already null. There were 28 chains of five participants each (i.e., 14 chains in the Speed-Only condition and 14 chains in the Configurations+Speed+Noise).

Testing phase

In both conditions, the participants completed this phase after the building phase [see (41)]. They were instructed that they would be presented with items consisting of four wheels and that they would have to choose which of the four wheels would roll down the rails faster in their opinion. They could take as much time as they needed to complete the test. They received no feedback. All the participants saw the same items in the same order. The understanding test consisted of 24 items (i.e., 12 inertia items and 12 center-of-mass items). The test is available at https://osf.io/m3d7q/. Last, the participants had to write a brief theory (i.e., less than 340 characters long) about the functioning of the wheel system, which always started with "The wheel covers the distance faster when..." [for a similar procedure, see (22)]. The data collected about these theories are not discussed in the present report.

Statistical analyses

One participant in the Speed-Only condition received an incorrect speed from the previous participant because of an experimental error. The data of this participant were removed, and the participant was replaced by a new participant. We checked for the presence of outliers for each condition separately. As our key predictions concerned the increase in wheel speed over generations, we explored whether some chains behaved differently from the others on this aspect. To do so, we computed the slope associated with each chain with x being the position of the participant in the chain and y being the best speed of their last two trials. For each condition, we obtained 14 slopes. We considered as outliers the chains with a slope that did not fall within 2 SDs from the mean. This procedure led us to remove one chain of five participants in the Speed-Only condition, which we replaced with a new chain of five participants. No chain was removed for the Configurations+Speed+Noise condition. In total, the data of six participants were excluded, giving us a final sample of 140 participants (14 chains of five participants for each condition).

Wheel speed corresponded to the best speed of the first or last two trials. Wheels that did not travel down were assigned a speed of 0 m hour⁻¹. To compute the intrageneration similarity score, we first selected the configuration of the wheel that was fastest among the last two trials of each participant. Then, for the within-condition similarity score, we compared this best configuration with the 13 best configurations produced by the other participants of the same generation, and we did so for each participant of each generation. The comparison was based on the sum of absolute differences of the positions of the four weights between two configurations. The positions varied from 1 to 12. Therefore, the maximum absolute differences could be 44 [i.e., (Position₁₂ – Position₁) \times 4 weights]. The sum of absolute differences reflected the dissimilarity between the two configurations. Therefore, we subtracted this sum from 44 to obtain the similarity score. The procedure was the same for the between-condition similarity score except that we compared the best configuration of each participant with the 14 best configurations produced by the participants of the same generation in the other condition. More detail about this intrageneration similarity score is given at https://osf.io/m3d7q/ [for a similar procedure, see

(67, 68)]. The inertia exploration score corresponded to the difference between the smallest and the greatest sum of positions of the four weights on the five trials. The greater this difference, the greater the exploration. The center-of-mass exploration score corresponded to the surface of the convex envelope that contained the centers-of-mass coordinates of the five wheels. For each wheel, the coordinates of its center of mass were computed by subtracting the position of the bottom weight from that of the top weight (*x* coordinate) and the position of the back weight from that of the front weight (*y* coordinate). The greater this surface, the greater the exploration. More details about these two exploration scores are provided at https://osf.io/m3d7q/.

In both conditions, we first explored the wheel speed over generations. Wheel speed corresponded here to the best speed of the last two trials. Wheels that did not travel down were assigned a speed of 0 m hour⁻¹. We used regression modeling in R [(69); lmerTest package (70)] to fit a linear model with "wheel speed" as outcome variable, "generation" as fixed effect, and "chain's identity" as random effect. The same analyses were conducted for the understanding scores (total, center of mass, and inertia), the intrageneration similarity score (within condition and between condition), the exploration scores (center of mass and inertia), and the best speed of the first two trials (two participants in the Speed-Only condition and four participants in the Configurations+Speed+Noise condition were excluded from this analysis because their first two wheels did not descend). We also used regression modeling in R [(69); lmerTest package (70)] to explore the links between the understanding scores (total) and the best speed of the first or last two trials. We fitted a linear mixed model with "understand score (total)" as outcome variable, "wheel speed (the best speed of the first or last two trials)" as fixed effect, and "generation" and "chain's identity" as random effects. Statistical significance was set at P < 0.05 and bootstrapping method was used to estimate 95% CI.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at https://science.org/doi/10.1126/ sciadv.abl7446

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