

Gestures: A Developmental and Evolutionary Perspective

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Abstract

Cumulative cultural learning has been argued to rely on high-fidelity copying of other individuals' actions. Iconic gestures of actions have no physical effect on objects in the world but merely represent actions that would have an effect. Learning from iconic gestures thus requires paying close attention to the teacher's precise bodily movements—a prerequisite for high-fidelity copying. In three studies, we investigated whether 2- and 3-year-old children (N = 122) and great apes (N = 36) learn novel skills from iconic gestures. When faced with a novel apparatus, participants watched an experimenter perform either an iconic gesture depicting the action necessary to open the apparatus or a gesture depicting a different action. Children, but not great apes, profited from iconic gestures, with older children doing so to a larger extent. These results suggest that high-fidelity copying abilities are firmly in place in humans by at least 3 years of age.

Keywords

cultural learning, imitation, evolution, gesture, iconicity, open data, open materials, preregistered

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The social-learning mechanisms enabling human children to absorb the cultural world around them have been extensively studied in the past two decades (Legare & Nielsen, 2015). These abilities are often contrasted with those of great apes in order to explain the different levels of complexity of animal and human cultures (Dean, Kendal, Schapiro, Thierry, & Laland, 2012; Horner & Whiten, 2005; Van Leeuwen, Call, & Haun, 2014). An intense debate has arisen around whether children and great apes focus on the same aspects of other individuals' actions when observing them; children may focus on means (precise bodily movements) as well as ends (effects on the world), whereas apes focus predominantly on the ends (Hecht et al., 2013; Kaneko & Tomonaga, 2012). Focusing on the means of other people's actions supposedly results in a more faithful transmission and thereby enables innovations and traditions to accumulate over time-the ratchet effect (Dean et al., 2012; Legare & Nielsen, 2015; Tennie, Call, & Tomasello, 2009). Yet no consensus has been reached, in part because the two different learning mechanisms are difficult to tease apart in studies looking at learning based on observing other individuals' behavior, especially when actions on objects are involved.

One way to directly address this issue is to compare children's and apes' ability to learn from iconic gestures. Iconic gestures can comprise bodily movements that have no effect on objects in the world but only represent actions that would have such an effect (Cartmill, Beilock, & Goldin-Meadow, 2012). To learn a novel skill

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through an iconic gesture, the learner must pay close attention to the precise bodily movements of the teacher to later translate them into their own actions. Although research on apes' ability to learn novel skills from iconic gestures is, to our knowledge, absent, a recent study found suggestive evidence of this ability in 2- and 3-year-old children (Novack, Goldin-Meadow, & Woodward, 2015). However, this evidence is partly inconclusive because the actions that children had to learn were familiar (e.g., putting a ring over a peg), and there was no motivational incentive for children to perform these actions in a control condition.

In the current studies, participants had to learn a novel skill to achieve a desired outcome: retrieving a reward from an unfamiliar apparatus. The actions required to open the apparatus involved a coordinated bimanual movement. In the *iconic* condition, the experimenter produced an iconic gesture that mimicked the action necessary to open the apparatus. In the *arbitrary* condition, the experimenter also produced a gesture, but the depicted action was unrelated to the task. Aside from the relation between the gesture and apparatus, the two conditions were identical, ensuring similar levels of motivation to perform the target action.

Study 1a

Method

Participants. Thirty-six 2-year-olds (18 girls; age: M = 2.14 years, range = 1.78-2.24) and thirty-six 3-year-olds (18) girls; age: M = 2.99 years, range = 2.73–3.24) participated in the study. Additionally, one 2-year-old and two 3-yearolds started participating but had to be excluded because they became uncomfortable with the test situation. The sample size for each age group was preplanned and matched to the number of apes available for testing in Study 2. Children came from an ethnically homogeneous, midsize German city (~550,000 inhabitants, median income €1,767 per month as of 2017); were mostly monolingual; and had mixed socioeconomic backgrounds. Two-year-olds were recruited from a database of children whose parents volunteered to take part in studies on child development. Three-year-olds were recruited from local kindergartens. The study was approved by an internal ethics committee at the Max Planck Institute for Evolutionary Anthropology. Data collection took place between February 2017 and May 2017.

Setup and design. Two-year-olds were tested in a testing room within a child laboratory. Parents were present in the room but were instructed to remain passive and at a distance. Three-year-olds were tested in a familiar room within their kindergarten.

Statement of Relevance

Human cumulative culture rests on the ability to learn from other people. To explain the different levels of complexity in human compared with animal culture, researchers have argued that human children possess especially powerful social-learning abilities. In this research, we tested whether 2- and 3-year-old children show one such ability, namely, learning from iconic gestures, such as moving one's fist up and down to indicate the action of hammering. Understanding these gestures requires paying close attention to the bodily movements of the teacher-a skill that has been suggested to be foundational to many forms of social learning. We compared learning from iconic gestures in 2- and 3-year-old children with that of great apes. In our studies, 3-year-olds, but not younger children and great apes, learned from iconic gestures. These results add to a growing literature suggesting that there may be uniquely human forms of social learning that emerge in the third year of life.

There were two distinct apparatuses, each operated in a different but comparable way. The apparatuses were screwed to a small children's chair so that children could easily operate them while standing. Both apparatuses were opened by simultaneously moving two handles in opposite directions (see Fig. 1). Moving the handles released the reward (marbles) locked inside the apparatus. Operating only one of the handles was not sufficient. Moreover, the handles moved back to their original starting positions automatically after participants let go of them. Therefore, the two complementary actions could not be carried out sequentially. The first apparatus (Apparatus 1; $34 \text{ cm} \times 12 \text{ cm} \times 7.5$ cm; see Fig. 1, left) released the marbles when the two handles were pulled away from each other simultaneously for 4.5 cm each. The second apparatus (Apparatus 2; 25 cm \times 20.5 cm \times 21 cm; see Fig. 1, right) opened when the two handles, which were positioned parallel to each other, were moved in opposite directions simultaneously for 5 cm (left side) and 4 cm (right side).

Children were tested in a between-subjects design and received a single test trial in the condition to which they were randomly assigned. Random assignment was constrained to yield 18 children (nine girls) per condition and age group. Half of the children per age group and condition were tested with Apparatus 1 and the other half with Apparatus 2.



Fig. 1. Functional depictions of the two apparatuses used in Studies 1 and 2. Apparatus 1 (left) released the reward when the two handles were pulled apart simultaneously. Apparatus 2 (right) opened when the two handles were moved in opposite directions simultaneously.

Procedure. The test was framed as a game in which the child had to collect marbles to play with a marble run. On entering the test room, the child found a couple of marbles lying on the floor. After placing them on the marble run, the experimenter introduced the child to two boxes that contained additional marbles. The experimenter showed the child how the boxes were opened and then encouraged the child to try on their own. No gestures were used at this time. We introduced these boxes after pilot testing because children were very hesitant to approach and operate the test apparatus. After retrieving the marbles from the boxes, children were again encouraged to place them on the marble run.

Up to that point, the test apparatus had been covered by a large blanket. The experimenter kneeled behind the apparatus so that she was facing the child and removed the blanket. This marked the beginning of the test trial. Next, she called the child's attention, briefly touched the apparatus's two handles, and then started gesturing. The gesture for Apparatus 1 went as follows: The experimenter pretended to hold the handles and then simultaneously moved her hands outward. For Apparatus 2, she again pretended to hold the handles (same hand shape as for Apparatus 1) and simultaneously moved the right hand forward and the left hand backward. Both gestures were performed with hands next to the handles and depicted the exact action that participants had to carry out in order to open the apparatus. Note that the gestures were symmetric in that

they looked the same from the experimenter's and the participant's perspective. Implementing the represented action therefore did not require additional perspective taking.

Gestures were executed in bouts of four gestures every 30 s; each bout was preceded by calling the child's attention and briefly touching the two handles. From the first gesture onward, the trial lasted 2 min or until the child opened the box. In the iconic condition, the gesture corresponded to the action that was necessary to open the apparatus. In the arbitrary condition, the gesture corresponded to the action that was necessary to open the respective other apparatus. For example, in the iconic condition, Apparatus 1 was present, and the experimenter gestured in a manner indicating how Apparatus 1 was opened. In the arbitrary condition, Apparatus 2 was present, but the experimenter gestured in a manner indicating how Apparatus 1 was opened. Therefore, in both conditions, children saw the exact same gestures. The only difference between conditions was whether or not the gesture corresponded to how the apparatus was opened. This ensured that children were equally attracted (or distracted) by the experimenter's movements in the two conditions.

Coding and analysis. We coded whether or not children opened the apparatus within 2 min after the experimenter's first gesture. For 2-year-olds, we additionally coded whether they performed components of the successful

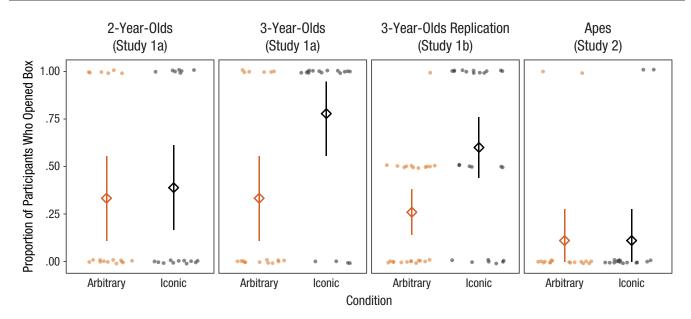


Fig. 2. Proportion of participants who successfully opened the apparatus per gesture type (condition), separately for each group. Circles show data from individual participants. Diamonds represent means, and error bars are 95% confidence intervals based on a nonparametric bootstrap of the data.

actions. The decision to code these behaviors was made post hoc, after the results were known. Our rationale behind this additional coding was that 2-year-olds might have understood the gesture but were unable to implement it because of its complexity. This should have led to more partial actions in the iconic condition compared with the arbitrary condition. For this coding, we divided successful actions into four partial actions: (a) moving the left handle, (b) moving the right handle, (c) performing a bimanual action on the apparatus (not necessarily on the handles), and (d) putting the components together (successful opening). We counted how many of the partial actions (types) each child performed, resulting in a score between 0 (none of the partial actions) and 4 (successful opening). For example, if a participant moved the left handle and the right handle independently, they received a score of 2. A second coder blind to the purpose of the study coded 25% of trials. Coders reached an agreement of 100% for opening, partial action left, partial action right, and bimanual manipulation.

We used logistic general linear models and a Bayesian inference scheme to analyze whether opening the box (yes/no) was influenced by the relation between gesture and action. All models were fitted in the R programming environment (Version 3.5.1; R Core Team, 2018) using the function *brm* of the R package *brms* (Bürkner, 2017) and default priors. Following McElreath (2016), we used widely applicable information criterion (WAIC) scores and weights to compare models. The WAIC score is an indicator of a model's out-of-sample predictive accuracy; models with smaller scores are preferred. WAIC weights are an estimate of the probability that this model will make the best predictions on new data compared with all other models considered (weights add up to 1). In addition, we inspected the posterior distribution for the key parameters in the model via their means and 95% credible intervals (CrIs). Detailed results of the model comparisons are reported in the Supplemental Material available online. All models included apparatus type as a control predictor. Data and supplementary information about the analysis along with the R scripts are available online at https:// osf.io/x5493.

Results

Both age groups opened both apparatuses at least once, and the majority of 2-year-olds also performed the partial actions (see Fig. S2 in the Supplemental Material). Figure 2 shows the proportion of participants who opened the box in each condition and group.

Model comparison showed that models including condition as a predictor made better predictions, with a slight advantage for the model including the interaction between age group and condition (interaction: weight = .48, main effects: weight = .40, without condition: weight = .12). The model estimate for the interaction term was large and positive, suggesting that 3-year-olds performed better than 2-year-olds in the iconic condition. However, this estimate was associated with some uncertainty because the corresponding 95% CrI overlapped with 0 (β = 1.86, 95% CrI = [-0.25, 4.03]). In the main-effects model excluding the interaction, the estimate for condition was reliably positive ($\beta = 1.14$, 95% CrI = [0.14, 2.18]), and the estimate for age was largely, although not entirely, positive ($\beta = 0.91$, 95% CrI = [-0.09, 1.94]).

When looking at the two age groups separately, we found no effect of condition for 2-year-olds (with condition: weight = .23, without condition: weight = .77; $\beta = 0.27, 95\%$ CrI = [-1.15, 1.71]). On the other hand, we found a positive effect of the iconic condition for 3-year-olds (with condition: weight = .91, without condition: weight = .09; β = 2.15, 95% CrI = [0.63, 3.81]). When analyzing the number of partial actions in 2-yearolds, we found no evidence that more components of the successful actions were performed in the iconic condition (with condition: weight = .27, without condition: weight = .71; β = 0.00, 95% CrI = [-0.41, 0.41]). This pattern of results shows that children were more likely to open the apparatus when presented with an iconic compared with an unrelated gesture. Although both age groups were equally successful in the arbitrary condition, older children were better at using the information provided in the iconic gestures.

Study 1b

Method

Study 1b was a preregistered replication (https://osf .io/8ubsx) of the findings with 3-year-olds from Study 1a. To rule out potential experimenter effects, we showed gestures as videos instead of live demonstrations.

Participants. Fifty 3-year-olds (18 girls; age: M = 2.93 years, range = 2.71–3.39) participated in the study. Five additional children started participating but had to be excluded because they became uncomfortable with the test situation. One additional child had to be excluded because of experimenter error. The sample size was chosen to be slightly larger than in Study 1a because we expected the video demonstration to lead to a smaller effect. Children came from the same general population as in Study 1a. The study was approved by an internal ethics committee at the Max Planck Institute for Evolutionary Anthropology. Data collection took place in November 2019 and December 2019.

Setup and design. The apparatuses used were the same as in Study 1a. Videos were presented on a 21.5-in. computer screen embedded in a black cardboard box. Videos were embedded in a slideshow, and the experimenter could start, stop, and replay them via a hidden remote control in her pocket. Half of the children (n = 25) were tested in the iconic condition and the other half in the

arbitrary condition. Children received two trials, both in the same condition—one with Apparatus 1 and one with Apparatus 2. The order of apparatuses was counterbalanced.

Procedure. The general procedure was the same as in Study 1a. The main alteration was that the gestures were shown by a third person presented in a video instead of by the experimenter in a live demonstration. The experimenter structured the experiment and established a contingent interaction between the child and the person shown on the screen. Details for how this affected the procedure can be found in the Supplemental Material. At test, the demonstrator on the screen used the same gestures as in Study 1a. Importantly, we edited the videos so that children in both conditions saw the exact same gestures. To do so, we filmed each gesture without an apparatus. Later, we edited the movie and placed either the apparatus corresponding to the gesture (iconic condition) or the other apparatus (arbitrary condition) in front of the demonstrator. Videos used during test trials in the study can be found at https://osf.io/x5493.

Coding and analysis. We coded box opening in the same way as in Study 1a. Reliability coding for 25% of trials yielded an agreement of 100% between coders. Data were analyzed in the same way as in Study 1a. However, because children received two trials, models included a random intercept for participant.

Results

Figure 2 shows the proportion of participants who opened the box in each condition. Model comparison clearly favored the model including condition as a predictor (with condition: weight = .86, without condition: weight = .14). The predictor for the iconic condition was large and reliably positive (β = 2.39, 95% CrI = [0.75, 4.77]). Taken together, these results replicate the finding of Study 1a for 3-year-olds.

Study 2

Method

Participants. All apes housed at the Wolfgang Köhler Primate Research Center at Zoo Leipzig, Germany, who were old enough to participate were included in the study. This resulted in a total of 36 great apes (age: M = 22.61years, range = 7.46–50.76): 7 bonobos (*Pan paniscus*; 5 females), 20 chimpanzees (*Pan troglodytes*; 13 females), 3 gorillas (*Gorilla gorilla*; 2 females), and 6 orangutans (*Pongo abelii*; 4 females). Research was noninvasive and strictly adhered to the legal requirements in Germany. Animal husbandry and research complied with the European Association of Zoos and Aquaria Minimum Standards for the Accommodation and Care of Animals in Zoos and Aquaria as well as the World Association of Zoos and Aquariums Ethical Guidelines for the Conduct of Research on Animals by Zoos and Aquariums. Participation was voluntary, all food was given in addition to the daily diet, and water was available ad libitum throughout the study. The study was approved by an internal ethics committee at the Max Planck Institute for Evolutionary Anthropology. Data collection took place between September 2016 and January 2017.

Setup and design. Apes were tested in their familiar sleeping rooms. The apparatuses were functionally equivalent to those used in Study 1 (see Fig. 1). However, given that apes substantially differ from children in size and strength, they had to be rebuilt using a more durable material and were adjusted in size (Apparatus 1: 50 cm × 13 cm \times 9 cm; handles had to be pulled apart for 4 cm; Apparatus 2: 30 cm × 15 cm × 15 cm; handles had to be moved in opposite directions for 6 cm each). The apparatus was attached to a mesh panel inside the apes' room so that they could freely access and manipulate it. The experimenter sat on a small stool on the opposite side of the mesh panel facing the ape. Instead of marbles, the apparatus was filled with eight pieces of monkey chow, a highly desirable food item. Participants were highly motivated to open the apparatus.

Like children, apes were tested in a between-subjects design. We created matched pairs for species, age, sex, and rearing history and then randomly assigned each member of a pair to one of the two conditions, resulting in 18 apes per condition.

Procedure. We used a human demonstrator instead of training a conspecific to produce the gestures. This allowed for a precise and controlled presentation of the gestures, ensuring that the participant saw the gesture. Furthermore, previous research has shown that great apes can learn to comprehend iconic gestures produced by a human demonstrator (Bohn, Call, & Tomasello, 2016), are able to learn novel actions demonstrated by a human (Horner & Whiten, 2005), and do not generally perform better in studies that use conspecific demonstrators (Boesch, 2007).

Pilot testing showed that apes were eager to approach and manipulate the apparatus; therefore, pilot boxes were omitted, and the test trial started as soon as the ape entered the room. Because apes have been found to be less likely to spontaneously comprehend communicative signals, we made the following adjustments to the procedure compared with Study 1a: Each trial lasted 5 min instead of 2 min, and participants received a small food reward after 2 min and 4 min to keep them engaged in the task. Furthermore, apes received a maximum number of five such trials per condition or until they opened the apparatus. The gestures were the same as in Study 1a. As for children, before gesturing, the experimenter made sure that the ape was attending to them.

Coding and analysis. We coded the opening of the box and the execution of partial actions in the same way as in Study 1. However, because apes received five trials instead of one trial, we aggregated their performance across trials to have a comparable measure with that of the children. That is, if the participant opened the box in one of the trials, they received an overall score of 1 for opening. Similarly, if the participant performed the partial action on the right side at any time in any of the five trials, they received an overall score of 1 for the right side action, and so on. The rationale behind this coding was the same as for 2-year-olds. Reliability coding of 25% of trials yielded an agreement of 100% for opening, 95.45% $(\kappa = .91)$ for partial action left, 90.91% ($\kappa = .82$) for partial action right, and 88.64% ($\kappa = .76$) for bimanual manipulation. The statistical analysis was analogous to that used in Study 1.

Results

Both apparatuses were opened twice in the two conditions. Furthermore, most apes performed the partial actions (see Fig. 2; see also Fig. S3 in the Supplemental Material). However, the opening of the box and the performance of the partial actions were not influenced by the relation between the gesture and the apparatus: For box opening, the model comparison favored the model without condition as a predictor (with condition: weight = .16, without condition: weight = .84), and the predictor for the iconic condition was essentially zero $(\beta = -0.03, 95\% \text{ CrI} = [-2.44, 2.27])$. Similarly, we found no condition effect in the model looking at partial actions (with condition: weight = .50, without condition: weight = .50; β = -0.09, 95% CrI = [-0.51, 0.32]). Thus, great apes in our study did not profit from the information provided by the iconic gestures.

Discussion

We investigated whether 2- and 3-year-old children and great apes would be more likely to learn a novel skill when observing iconic gestures than when observing unrelated gestures. For 3-year-olds—but not 2-year-olds and apes—observing bodily actions without any physical effect on the world was sufficient to learn a novel skill. From a developmental perspective, this suggests that the cognitive abilities that enable learning novel skills from iconic gestures emerge during the third year of life. From an evolutionary perspective, this suggests that at least some of these abilities might be uniquely human.

The results for apes might be explained by the fact that apes, at least the ones tested by humans in captivity, are less likely to attend to a demonstrator's bodily movements without a direct effect on the world (e.g., Tennie, Call, & Tomasello, 2012). This led them to ignore the representational nature of the gesture. On the other hand, 2-year-olds understand that gestures can be representational (Bohn, Call, & Tomasello, 2019; Novack et al., 2015). Yet our findings suggest that younger children might have difficulties translating a representational gesture into a bodily action. Research on overimitation also shows that from 2 years onward, children-in contrast to apes (Clay & Tennie, 2018)increasingly imitate (and therefore translate) causally irrelevant actions (Hoehl et al., 2019; Nielsen & Tomaselli, 2010). Further research is needed to determine whether the current findings are culturally or species specific (Nielsen, Haun, Kärtner, & Legare, 2017).

In sum, children below the age of 3 as well as great apes appear limited in their ability to learn from other individuals if their actions have no direct effect on objects in the world. By the age of 3, children have developed the cognitive abilities to engage in this form of learning, thereby broadening their repertoire of cultural-learning techniques.

Transparency

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Author Contributions

M. Bohn, J. Call, and M. Tomasello conceptualized the studies. C. Kordt and M. Braun collected the child data. M. Bohn collected the ape data, performed the statistical analysis, and drafted the manuscript. All the authors revised and approved the final manuscript for submission.

Declaration of Conflicting Interests

The author(s) declared that there were no conflicts of interest with respect to the authorship or the publication of this article.

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Open Practices

Data for all studies have been made publicly available via the Open Science Framework and can be accessed at https://osf.io/x5493. The video demonstrations used in Study 1b are also available at https://osf.io/x5493 (Studies 1a and 3 involved live interactions, so no materials were available to post). The design and analysis plans for Study 1b were preregistered at https://osf.io/8ubsx. The other studies were not preregistered. The complete Open Practices Disclosure for this article can be found at http://jour nals.sagepub.com/doi/suppl/10.1177/0956797620921519. This article has received the badges for Open Data, Open Materials, and Preregistration. More information about the Open Practices badges can be found at http://www.psy chologicalscience.org/publications/badges.



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Supplemental Material

Additional supporting information can be found at http://journals.sagepub.com/doi/suppl/10.1177/0956797620921519

References

- Boesch, C. (2007). What makes us human (*Homo sapiens*)? The challenge of cognitive cross-species comparison. *Journal* of Comparative Psychology, 121, 227–240. doi:10.1037/ 0735-7036.121.3.227
- Bohn, M., Call, J., & Tomasello, M. (2016). Comprehension of iconic gestures by chimpanzees and human children. *Journal of Experimental Child Psychology*, 142, 1–17. doi:10.1016/j.jecp.2015.09.001
- Bohn, M., Call, J., & Tomasello, M. (2019). Natural reference: A phylo- and ontogenetic perspective on the comprehension of iconic gestures and vocalizations. *Developmental Science*, 22, Article e12757. doi:10.1111/desc.12757
- Bürkner, P.-C. (2017). brms: An R package for Bayesian multilevel models using Stan. *Journal of Statistical Software*, 80(1). doi:10.18637/jss.v080.i01
- Cartmill, E. A., Beilock, S., & Goldin-Meadow, S. (2012). A word in the hand: Action, gesture and mental representation in humans and non-human primates. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367, 129–143. doi:10.1098/rstb.2011.0162
- Clay, Z., & Tennie, C. (2018). Is overimitation a uniquely human phenomenon? Insights from human children as compared to bonobos. *Child Development*, 89, 1535–1544. doi:10.1111/cdev.12857
- Dean, L., Kendal, R., Schapiro, S., Thierry, B., & Laland, K. (2012). Identification of the social and cognitive processes underlying human cumulative culture. *Science*, *335*, 1114–1118.
- Hecht, E., Murphy, L., Gutman, D., Votaw, J., Schuster, D., Preuss, T., . . . Parr, L. (2013). Differences in neural activation for object-directed grasping in chimpanzees and humans. *The Journal of Neuroscience*, 33, 14117–14134.
- Hoehl, S., Keupp, S., Schleihauf, H., McGuigan, N., Buttelmann, D., & Whiten, A. (2019). 'Over-imitation': A review and appraisal of a decade of research. *Developmental Review*, 51, 90–108.
- Horner, V., & Whiten, A. (2005). Causal knowledge and imitation/emulation switching in chimpanzees (*Pan*

Funding

troglodytes) and children (Homo sapiens). Animal Cognition, 8, 164–181. doi:10.1007/s10071-004-0239-6

- Kaneko, T., & Tomonaga, M. (2012). Relative contributions of goal representation and kinematic information to selfmonitoring by chimpanzees and humans. *Cognition*, 125, 168–178.
- Legare, C., & Nielsen, M. (2015). Imitation and innovation: The dual engines of cultural learning. *Trends in Cognitive Sciences*, 19, 688–699.
- McElreath, R. (2016). *Statistical rethinking: A Bayesian course* with examples in R and Stan. Boca Raton, FL: CRC Press.
- Nielsen, M., Haun, D., Kärtner, J., & Legare, C. H. (2017). The persistent sampling bias in developmental psychology: A call to action. *Journal of Experimental Child Psychology*, *162*, 31–38. doi:10.1016/j.jecp.2017.04.017
- Nielsen, M., & Tomaselli, K. (2010). Overimitation in Kalahari Bushman children and the origins of human cultural cognition. *Psychological Science*, 21, 729–736. doi:10.1177/0956797610368808

- Novack, M., Goldin-Meadow, S., & Woodward, A. (2015). Learning from gesture: How early does it happen? *Cognition*, 142, 138–147. doi:10.1016/j.cognition.2015 .05.018
- R Core Team. (2018). R: A language and environment for statistical computing (Version 3.5.1) [Computer software]. Vienna, Austria: R Foundation for Statistical Computing.
- Tennie, C., Call, J., & Tomasello, M. (2009). Ratcheting up the ratchet: On the evolution of cumulative culture. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364, 2405–2415. doi:10.1098/rstb.2009 .0052
- Tennie, C., Call, J., & Tomasello, M. (2012). Untrained chimpanzees (*Pan troglodytes schweinfurthii*) fail to imitate novel actions. *PLOS ONE*, 7(8), Article e41548. doi:10.1371/ journal.pone.0041548
- Van Leeuwen, E., Call, J., & Haun, D. (2014). Human children rely more on social information than chimpanzees do. *Biology Letters*, 10, Article 20140487. doi:10.1098/rsbl.2014.0487