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Interaction-Mediated Tool Use Differently Enhances Physical and Social Cognition in Macaques (*Macaca fascicularis*)

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Abstract

In primates, learning to use a tool modulates cognitive functions related to the physical properties of objects. However, the impact of tool-use learning on social aspects of cognition has not been explored. We addressed this question via a training paradigm by using six, adult, long-tailed macaques (*Macaca fascicularis*), who were born in captivity and housed in the animal facility of the Department of Neuroscience and Rehabilitation of the University of Ferrara, Italy. We tested the effects of interaction-mediated tool use on overall cognitive performance in an experimental group ($n = 2$ males and $n = 1$ females). To evaluate changes in cognitive performance, we applied the Primate Cognition Test Battery at different stages of the training procedure that involved an interaction between the animal and an experimenter and the macaque using a rake to retrieve food items. As a control, we evaluated the performance of an age- and sex-matched group performing an interactive, manual grasping task. Several parameters related to the recognition of the position and noise of specific objects (i.e., space and causality in physical cognition), and those related to image-object association and object pointing to draw the attention of experimenter (i.e., communication aspects of social cognition) showed a significant improvement in the interaction-mediated tool-use group after the training period. The effects were transient, but the enhancement related to the noise and object pointing persisted for 35 days without further training. The control group showed no changes in cognitive performance. Our results show that interaction-mediated tool use enhances cognitive performance in both physical and social cognition domains.

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Introduction

Various factors modulate cognitive skills in nonhuman primates, such as the opportunity to develop in a socio-communicatively rich environment (Russell *et al.*, 2011), enrichment of the physical environment (Celli *et al.*, 2003; Schub & Eisenstein, 2003; Ventura & Buchanan-Smith, 2003), and previous experience of a reward (Bujold *et al.*, 2021). Tool use behavior, which is generally present across taxa (Fayet *et al.*, 2020), is a central concept in animal cognition research in both the laboratory and the wild (St Amant & Horton, 2008). Tool use can be defined generally as the exertion of control over a freely manipulable external object (the tool) with the goal of altering the physical properties (e.g., form or position) of another object, substance, surface or medium (i.e., the target, which may be the tool user or another organism) via a dynamic mechanical interaction, or mediating the flow of information between the tool user and the environment or other organisms in the environment (St Amant & Horton, 2008). Animals use tools for several purposes, mainly related to feeding, defense, aggression, social displays, or physical maintenance (Shumaker *et al.*, 2011). We can distinguish between "true" tool use, which requires manipulation of an object detached from the substrate, and "borderline" tool use, in which the tool remains part of the substrate (Beck, 1980). In an experimental context, tool use can be more easily defined as in the classic (albeit limited) interpretation, as the use of an external object as a functional extension of a body part (mouth, hand, foot) to help attain a desired outcome, including obtaining food and water, grooming, or protecting themselves (van Lawick-Goodall, 1970).

Tool use can result from different mechanisms, such as genetic predispositions (Hopkins *et al.*, 2015) or trial-and-error learning (Tebbich *et al.*, 2010). Furthermore, some great ape tool-use behaviors may develop independently of observation of, or interaction with, another animal (Bandini & Tennie 2019). These latent solutions are behavioral forms that can (re)emerge even in the absence of observational opportunities, via individual (re)innovations, as the Zone of Latent Solution hypothesis states (Tennie *et al.*, 2020). Tool use appears to be related to cognitive skills, including the ability to understand the physical properties of objects, and the spatial relations between the tool and the targets of its use (Seed & Byrne, 2010). This leads to the development of novel and complex abilities (Iriki & Sakura, 2008) that may affect a wide range of situations. Learning to use new tools may augment and enhance the processing of visual stimuli, as well as modify causal reasoning and multisensory spatial attention (Fujita *et al.*, 2011; Hihara *et al.*, 2003; Holmes *et al.*, 2007; Seed & Byrne, 2010; Macellini *et al.*, 2012; Sabbatini *et al.*, 2012).

Among wild Afro-Eurasian monkeys, spontaneous and customary use of tools has only been observed in macaques (Ottoni, 2015). Lion-tailed macaques (*Macaca silenus*) and long-tailed macaques (*Macaca fascicularis*) use leaves or rocks to clean food before ingesting it (Chiang, 1967; Hohmann, 1988; Tan *et al.*, 2016). Some long-tailed macaque populations use tools habitually to obtain food (e.g., populations in several regions of Thailand; *Macaca fascicularis aurea*; Malaivijitnond *et* *al*., 2007; Gumert *et al*., 2009, 2011; Tan *et al*., 2016; Tan, 2017). For example, they use stones and shells to crack gastropods in coastal environments (Malaivijitnond *et al*., 2007) and employ axe- or pounding-hammering techniques (Gumert et al., 2009). Wild Nicobar long-tailed macaques (*Macaca fascicularis umbrosus*) use both natural and synthetic materials as tools and modify tools before use for extractive foraging (Pal *et al*., 2018). Tooth flossing using human hair and coconut shell fiber is a further tool-aided behavior recorded in Thai long-tailed macaques (Watanabe *et al*., 2007). Japanese macaques use fur for the same purpose (Leca *et al*., 2010). Tonkean macaques (*Macaca tonkeana*) showed several cases of spontaneous tool use, including using sticks to obtain food or to clean parts of their own body, or leaning a log against a wall to climb it (Anderson, 1985; Bayart, 1982; Ueno & Fujita, 1997). However, they did not learn to use a tool, such as a wooden pole, to retrieve food, despite repeated opportunities to observe a demonstrator. They succeeded in this task only after individual learning trials (Ducoing & Thierry, 2005).

In a captive group of long-tailed macaques, raking behavior by a single competent individual had a significant positive effect on the synchronous manipulative behavior of naïve animals (Zuberbühler *et al*., 1996). In general, macaques require several weeks of training to learn skillful tool use (Ishibashi *et al*., 2000). In contrast, Japanese monkeys (*Macaca fuscata*) spontaneously stood a pole against a wall and climbed it (Machida, 1990). This species also can build on known techniques to create new variants (Kawai *et al*., 1992; Tokida *et al*., 1994), an ability also observed in wild bonnet macaques (*Macaca radiate*) (Sinha, 1997). Japanese monkeys often are used in tool-use experiments to study the anatomical and functional properties of the brain activity associated with specific tool-use tasks. For example, positron emission tomography scans highlighted activation of different cortical and subcortical areas during a task that required monkeys to reach a pellet by using a rake (Obayashi *et al*., 2001, 2003) and during a task that consisted of poking a pellet with a rake out of a tube and then reaching it with a second rack (Obayashi *et al*., 2002). These brain recordings were performed during a comparatively abstract task, such as retrieving an unreachable pellet by operating a joystick (Obayashi *et al*., 2004) or a pair of dials (Obayashi *et al*., 2007) that remotely controlled a shovel. Magnetic resonance imaging scans highlighted expansion of the grey matter in the temporal and parietal cortices after intensive tool-use training that required monkeys to correctly place a rake behind a food item and to pull it within reach (Quallo *et al*., 2009).

Using a tool as an extension of the body may have consequences for psychological processes, such as perception, attention, and cognition, because it changes the mechanical and sensory capabilities of the periphery of the body (Seed & Byrne, 2010). Whether tool use can influence the social aspect of cognition is an unexplored question. Cognitive processes in Afro-Eurasian monkeys have been successfully assessed by the Primate Cognition Test Battery (PCTB), a large battery of behavioral tests, originally designed for great apes, including humans (Herrmann *et al*., 2007). This testing procedure assigns a score to the performance in a series of tasks that pertain to physical and social aspects of cognition. The PCTB was later adapted and used for testing other species, such as macaques and corvids (Schmitt *et al*., 2012; Tia *et al*., 2018; Pika *et al*., 2020). Studies of long-tailed macaques show that their sociocognitive performance is comparable with that of great apes (Schmitt *et al*., 2012) and that tool-use learning may affect their physical-cognitive skills (Tia *et al*., 2018).

Macaques trained to use a rake to reach food showed improved PCTB performance (i.e., the proportion of successful attempts at performing a task) related to recognition of the physical properties of objects (Tia *et al*., 2018). Specifically, training enhanced the monkeys' spatial, numerical, and causal skills, whereas those relating to social cognition remained unaffected. This finding is an example of how sustained daily training in a specific task that is not frequently used otherwise can enhance other skills. The finding also suggests that a specific learning experience modulated specific aspects of cognition rather than affecting the entire spectrum of cognitive performance. The structure of tool-use training is a crucial influence on cognitive performance and how animals solve different problems (Neves Filho *et al*., 2016).

The purpose of our study was to assess whether a tool-use training procedure that involves a simple social element, i.e., an interaction between two individuals (macaque and experimenter), can modulate both physical and social aspects of cognitive performance. We used the PCTB at five time points: before, during, and after we trained macaques to use a rake to obtain food. We subjected another group of macaques to repeated grasping tasks involving interactions between macaque and experimenter, as a control, to evaluate whether any performance changes are associated with interaction with the experimenter or with repeated testing for a simple motor task. Our hypothesis is that sustained exposure to a social element accompanied by tool-use training increases both physical and social cognitive abilities (i.e., those in which the rake use alone is ineffective; Tia *et al*., 2018). We tested the prediction that animals trained to use a tool by means of an interaction with the experimenter would improve their performance on PCTB tasks related to both physical and social cognitive skills, while animals that only experienced the interaction would not change their performance in any PCTB task.

Methods

Experimental Protocol

We recruited six, long-tailed macaques (*Macaca fascicularis*; two females and four males), who were housed at the Department of Neuroscience and Rehabilitation (University of Ferrara), in mid-2020. Five of these animals had experienced similar training procedures in mid-2016 (Tia *et al*., 2018). The animals in this study were born in captivity (two in our animal facility, four acquired as young adults from external commercial suppliers). They have been living in cages in the same room since 2014.

The macaques were naïve to any experimental procedures until a study in 2016 when they all experienced the PCTB; two macaques were trained on a task that involved similar rake use as the present study (Tia *et al*., 2018). They underwent no further training after 2016 until the beginning of the tool-use training in mid-2020. Reuse of the same animals after a 3-year resting period is consistent with the ethical and legal requirements that apply to our laboratory. The reuse does not affect our study, because we tested all macaques at baseline. Baseline performance in this study was like that observed at baseline during the 2016 PCTB sessions. Furthermore, the last 2016 PCTB session showed that that any tool-use effect had vanished after 35 days without rake use, which is much shorter than the 3-year time interval that separates the two studies (Tia *et al*., 2018). As a further precaution, we assigned different subjects to the two groups in the two studies. We moved one male and one female from the control group of the 2016 study (Tia *et al*., 2018) to the trained group (this study) and one female from the trained group in the 2016 study (Tia *et al*., 2018) to the control group of this study.

The macaques were cared for daily (cleaning and feeding; 2 h/day) by technical staff who are not authors of this work. The monkeys become acquainted with the experimenter (who is male) with whom they interacted during the training about a month before the start of the training itself, when the experimenter spent approximately 30 min/day in the same room. We housed two animals in each cage (1.8 m × 1.3 m × 1.9 m) with full contact between pairs. During experimental sessions, we housed each animal alone in the cage. To maintain motivation during the tasks, we subjected the macaques to mild food deprivation. They received their daily food intake (pellets, vegetables, and fruits) only at the end of each testing session. Water was always available to the animals. We defined a session as the time during which we collected data for a macaque, including tool-use training and PCTB evaluation.

We divided the macaques into two groups (Fig. 1). Animals in the interaction-mediated tool-use group (one female and two males; age mean ± SEM: 15.3 ± 2.4 years) were involved in the tool-use training program, involving four stages, in which they interacted with the experimenter to obtain and use a rake to retrieve out-of-reach food items. Animals in the interaction-mediated grasping group (one female and two males; age mean ± SEM: 13.3 ± 3.5 years) were involved in the grasping task, where they had to grasp food items with the help of the experimenter.

To evaluate performance, we used the PCTB (Herrmann *et al*., 2007; Schmitt *et al*., 2012; Tia *et al*., 2018) at five time points (Fig. 1): 1) before the start of training procedures (baseline); 2) after completion of the first period of training (stages a and b; interaction-mediated, tool-use group) or 35 grasping sessions (interaction-mediated grasping group); 3) after completion of the second period of training (stages c and d) or 35 additional grasping sessions; after 4) the first resting period, 35 days from last

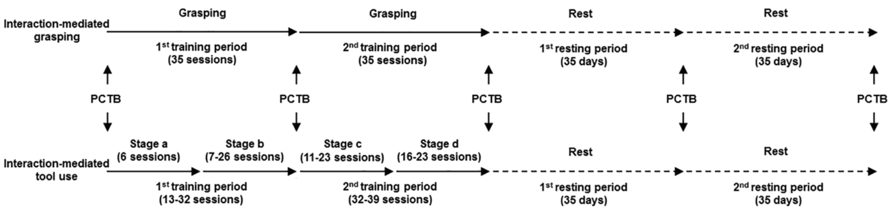

Fig. 1 Time-course of an experiment to test the cognitive performance in macaques. We studied long-tailed macaques at the Department of Neuroscience and Rehabilitation, University of Ferrara, Italy, 2020

training or grasping session, and 5) after the second resting period, 70 days from the last training or grasping session.

Interaction-Mediated Tool-Use Training

We trained macaques to interact with the experimenter to obtain and use a rake-shaped tool to retrieve out-of-reach food items, such as raisins, peanuts, and small pieces of fruit and vegetables (Fig. 2). To keep the macaques' motivation high during sessions, we used a new kind of food when we observed signs of distraction, or

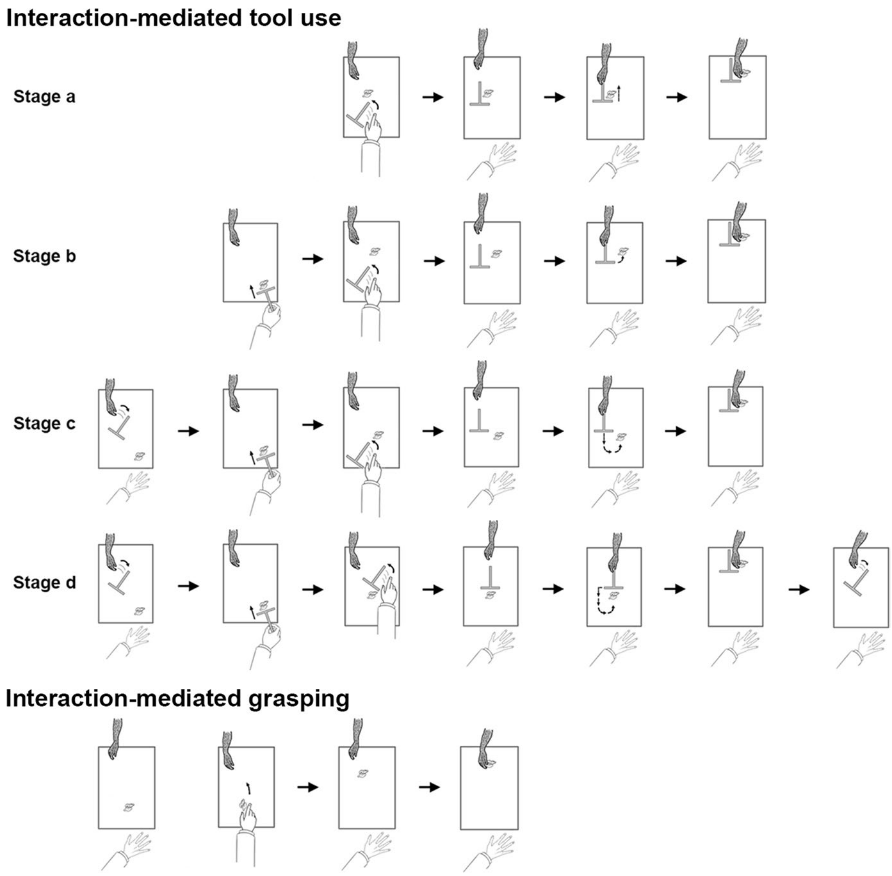

Fig. 2 Training procedure. We trained macaques in an interaction-mediated tool-use group to interact with the experimenter to obtain and use a rake-shaped tool to retrieve out-of-reach food items presented in different locations on a tray. The protocol involved four stages (stages a-d) of increasing difficulty corresponding to different locations of the food items relative to the tool, and different degrees of interaction with the experimenter. Macaques in the interaction-mediated grasping group interacted with the experimenter who pushed the food items to different locations on a tray, to allow macaques to reach the food items. We studied long-tailed macaques at the Department of Neuroscience and Rehabilitation, University of Ferrara, Italy, 2020

they appeared unmotivated. We chose foods to match each subject's individual taste and did not use food types for which animals had showed dislike.

We conducted all training sessions (trials/session mean ± SEM: 20.0 ± 0.5; 1 session/day; 5 days/week) with the monkeys in their individual cages. Each session lasted 20–30 min, based on the time during which a macaque remained in front of the experimenter, paying attention to the task performed, and motivated to collaborate to obtain the food. This time varied by session and animal. The experimenter never forced the animals to participate. The experimenter presented the food and tool on a tray (length, 60 cm; width, 50 cm) attached to a sliding table that we could easily move horizontally from cage to cage. The rake tool was composed of an aluminium plate (16.5 cm × 7.8 cm × 0.05 cm) attached to a handle (diameter, 1.5 cm; length, 38 cm). The experimenter adjusted the tray at cage ground level so that the animals could see the food item from above; this prevented the rake from obstructing the line of sight from the animals to the food. The step-by-step training protocol comprised four stages, corresponding to different locations of the food item relative to the tool (Tia *et al*., 2018; Yamazaki *et al*., 2011) and to different degrees of interaction between macaque and experimenter.

Stage a: The experimenter placed the food item in an unreachable position on the tray in front of the animal. After a few attempts (usually 5–10) in which the monkey tried unsuccessfully to reach the food item, the experimenter presented the rake, by pushing it slowly toward the monkey. To retrieve out-of-reach food items, the monkey had to pull the rake.

Stage b: We introduced the fact that the experimenter also used the rake, who used it to push food items toward the monkey but out of its reach. Then, the procedure continued as in stage a, but the monkey had to move the tool to the left or right in addition to pulling it.

Stage c: The rake was first presented to the monkey, who had to push it toward the experimenter, before the experimenter initiated the training trial. In the first days of this stage, the monkey tried to use the rake to reach food, then pushed it toward the experimenter after some attempts. In the following days, the monkey passed the rake to the experimenter immediately during the most interactive aspect of the training protocol. Then, the procedure continued as for stage b but involved a more complex movement; the monkey moved the rake forward from the original position to retrieve the food item.

Stage d: The procedure was conducted as in stage c but to reach the food the monkey had to move the rake by drawing a circular trajectory or lifting it vertically. Moreover, after consuming the food items, the animal had to push the rake toward the experimenter. This final action corresponds to an interaction with the experimenter to facilitate the beginning of the next trial and occurred in the absence of food on the tray, unlike the initial handover of the rake.

To assess learning across the different training stages, we calculated the success rate over the number of training sessions for each animal. A monkey completed a training stage when it executed at least 80% successful trials in five successive sessions.

Interaction-Mediated Grasping Task

We familiarised macaques in the interaction-mediated grasping group with grasping food items placed at different locations on a tray, helped by the experimenter, who moved the food to within the monkey's reach (Fig. 2). Macaques used their preferred hand. Like the interactive tool-use training procedure, we conducted all sessions (trials/session mean ± SEM: 21.2 ± 0.2; 1 session/day; 5 days/week) with macaques in their individual home cage. Each session lasted 15–20 min, based on the time during which a macaque remained in front of the experimenter, paying attention to the task performed, and motivated to collaborate to obtain the food. This allowed us to perform a similar number of trials as for the interaction-mediated tool-use group. We used the same tray and food items as for the interaction-mediated tool-use group. The experimenter presented food in front of the macaque in an unreachable location of the tray. In the first sessions, the monkey tried to reach the food, whereas in the following sessions, the monkey waited for the experimenter to transfer the food to within the reach of the animal at six possible locations (10 cm or 20 cm away from the animal, and at the midpoint or at 15 cm to its left or right). In this interaction-mediated grasping task, the interaction consisted in waiting for help and the actual provided by the experimenter (placing the food in an accessible position). While waiting, the monkey watched the experimenter and the food intently, and often requested the food by pointing at it or attempt to reach it.

Primate Cognition Test Battery

We conducted the PCTB testing procedure (Tia *et al.*, 2018) with macaques in their individual home cage. The PCTB involves different tasks that define physical and social cognition skills (Appendix 1 in Supplementary Material). Each subject repeated each task a fixed number of times (trials), with one session per task.

Physical Domain This domain consists of three scales: Space (four tasks), Quantities (two tasks), and Causality (four tasks). The Spatial cognition scale assesses the ability of each macaque to remember object locations and infer the location of an object after an occluded lateral displacement or spatial rotation. It comprises four tasks: Spatial Memory (six trials), Object Permanence (18 trials), Rotation (18 trials), and Transposition (18 trials). The Quantities scale evaluates each monkey's ability to distinguish between different amounts and leverages two tasks: Relative Numbers (16 trials) and Addition Numbers (14 trials). Finally, the Causality scale tests the monkeys' understanding of causal relations between objects with four different tasks: Noise (12 trials), Shape (12 trials), Tool Use (one trial), and Tool Properties (30 trials).

Social Domain In this domain, we identified three scales: Social Learning (one task), Communication (three tasks), and Theory of Mind (two tasks). The Social

Learning scale consists of testing whether macaques can learn to reproduce actions by observing an experimenter (three trials). The Communication scale assesses the ability to understand and produce communicative cues related to the experimenter, using three tasks: Comprehension (18 trials), Pointing Cups (eight trials), and Attentional State (four trials). The Theory of Mind scale evaluates the macaques' aptitude for acknowledging mental states of the experimenter through two tasks: Gaze Following (nine trials) and Intentions (12 trials).

Following a correct response (i.e., when the animal performed the task correctly and, thus, understood how to acquire the food), the experimenter rewarded the monkey with a small food item (raisins, peanuts, pieces of fruits, and vegetables) and recorded a score of 1. Following an incorrect response, we scored the trial as 0 and gave no food as a reward. At each of the five timepoints, each animal performed the tasks in a fixed sequence: Spatial Memory, Object Permanence, Rotation, Transposition, Relative Numbers, Addition Numbers, Noise, Shape, Tool Use, Tool Properties, Social Learning, Comprehension, Pointing Cups, Attentional State, Gaze Following, and Intentions. We used a fixed sequence to reduce the variability among different timepoints and animals, which could influence the outcome. Macaques completed the PCTB in six to 12 sessions. To ensure that each macaque's performance was maintained throughout all PCTB sessions, both groups went through a 10-min training/grasping period at the beginning of each PCTB session. We filmed the testing sessions with a digital video camera (Carl Zeiss Tessar HD 1080 p, Logitech, Switzerland). A second observer, who was not blind to the experiment, independently scored videotapes to evaluate interobserver agreement; this reached 98% for all the tasks combined (reliability coefficient Cohen's $k = 0.9601$). We performed video analysis using VLC Media Player, a free and open-source platform (www.videolan.org).

Statistical Analysis

The figures show the mean ± SEM of the scores obtained by each animal in the different tasks, scales, and domains of the PCTB procedure. For all statistical results, we considered $p < 0.05$ to be statistically significant.

Quantification of PCTB Scoring We calculated the proportion of correct responses in each PCTB task (spatial memory, object permanence, rotation, transposition, relative numbers, addition numbers, noise, shape, tool use, tool properties, comprehension, pointing cups, attentional state, gaze following, intentions) for each animal and then for each session. Then, we calculated the mean of the scores across tasks for each scale (space, quantities, causality, social learning, communication, theory of mind) and across scales for each domain (physical cognition, social cognition) for each animal. To assess changes in cognitive performance at the domain level, we analysed scores related to physical and social cognition separately. To dissect out the contribution of single tasks to the global effects, we conducted further statistical analyses for each task in the physical and social cognition domains.

Statistical Evaluation of PCTB Scoring We calculated the baseline PCTB score for each animal using the scores obtained from the PCTB sessions before training. To explore whether tool use induced significant changes in PCTB performance with respect to the baseline level, we fitted a generalized linear mixed model (GLMM) to the binary outcome (success/failure) of each trial. We assumed a Bernoulli distribution for the response variable, the expected value of which was assumed to be linked through a logistic link function to the sum of fixed effects (predictors) and random effects (categorical variables representing correlations introduced by the nested structure of the dataset). We assumed that the distribution for the random effects was multivariate Gaussian. We included the following five fixed effects in the GLMM: the first and second training periods, the first and second resting periods, and one fixed intercept. To assess the significance of the overall model, we used a likelihood-ratio test to compare the full model to a null model, which included only the random effects and the intercept. The choice of the random effects depended on which level of the PCTB was considered. We performed the GLMM analysis at three levels: tasks, cognitive scales, and cognitive domains. In the analysis of individual PCTB tasks, we took each subject's identity as a random effect. In the analysis of scales and domains, we added a categorical variable that represented each task of the considered cognitive scale or domain. For instance, when we considered the space scale, the categorical variable could take four values, representing the four tasks that belong to it (spatial memory, object permanence, rotation, transposition). This accounted for both the variability introduced by the experimental subjects and the hierarchical structure of the dataset. As a rough model check, we compared the variance predicted by the model to that observed in the data and found no clear indication of overdispersion. The software implementation used the Python interface of the GPBoost library (www.github.com/fabsig/GPBoost).

Chance Level To test for individual performance that exceeded chance level, we used a binomial test. Chance level for each task was the probability of correctly executing each trial/attempt (Tia *et al.*, 2018; see also Appendix 2 in Supplementary Material). We did not use the binomial test when we could not calculate chance level, i.e., on tasks without alternatives (tool use, social learning, attentional state, and gaze following).

Ethical Note

We used six, long-tailed macaques (*Macaca fascicularis*; two females and four males), which were housed at the Department of Neuroscience and Rehabilitation (University of Ferrara). The methods agree with the 3Rs principle originally formulated by Burch and Russel (Griffin *et al.*, 2014). We performed all procedures in accordance with the Animal Care Ethics Committee of the University of Ferrara, authorized by the Italian Ministry of Health (permission n. 1139/2016-PR) and complied with the ARRIVE guidelines and European laws on the use of laboratory animals (EU Directive 2010/63/EU).

Data Availability We uploaded the raw data supporting this study to the Figshare repository: https://doi.org/10.6084/m9.figshare.22709974.v1.

Conflict of Interest The authors declare that they have no conflict of interest.

Results

Interaction-Mediated Tool Use Learning

Overall, each macaque performed 20.0 ± 0.5 trials (mean ± SEM) per session in the interaction-mediated tool-use group. The three monkeys needed similar times to succeed in stage a (Fig. 3a) but showed different learning times in the subsequent three training stages (Fig. 3b-d).

Animals in the interaction-mediated tool-use group performed a total of 56.0 ± 7.5 (mean ± SEM) sessions. The increased difficulty of the training is consistent with the fact that animals performed stages a and b successfully in 21.0 ± 5.7 sessions but performed stages c and d in 35.0 ± 2.1 (mean ± SEM) sessions. Animals in the interaction-mediated grasping group performed a total of 70 grasping sessions: 35 sessions during the first period and 35 sessions during the second period.

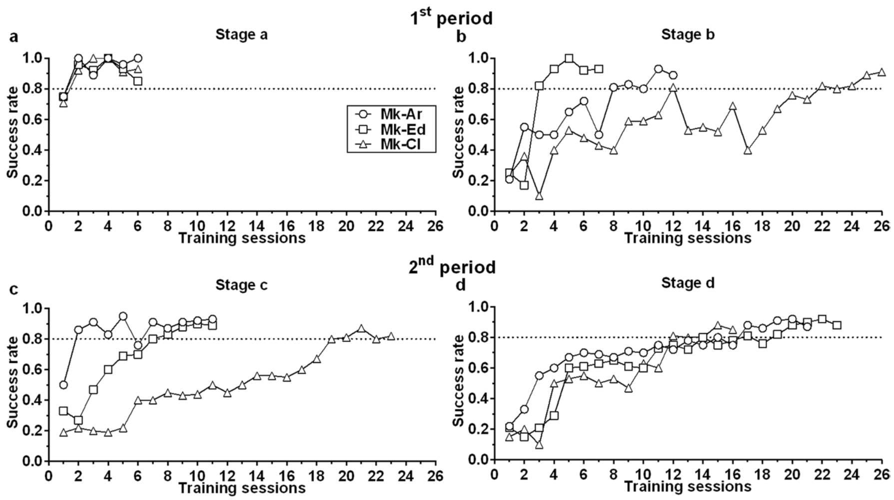

Fig. 3 Proportion of successful attempts at four stages of interaction-mediated tool-use training. We studied three trained long-tailed macaques (Mk-Ar, Mk-Ed, and Mk-Cl). We studied long-tailed macaques at the Department of Neuroscience and Rehabilitation, University of Ferrara, Italy, 2020

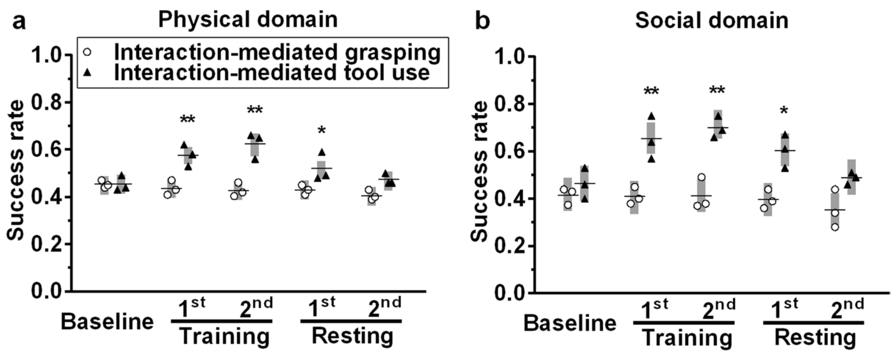

Fig. 4 Effect of interaction-mediated tool-use training on performance in two cognitive domains in long-tailed macaques at the Department of Neuroscience and Rehabilitation, University of Ferrara, Italy, 2020. Proportion of correct responses relative to the physical (**a**) and social (**b**) domains. White circles and black triangles represent individual animals. Horizontal black lines indicate the mean for each group. Gray stripes indicate the predicted mean ± standard deviation based on a GLMM. $*p<0.05$, $**p<0.01$, different from their own baseline (GLMM analysis in Table I)

Effect of Interaction-Mediated Tool-Use Training on PCTB Domains

The training changed the cognitive performance at the domain level (Fig. 4; Table I).

Physical Cognition Domain The overall model for the interaction-mediated, tool-use group was significant (Table I). Macaques trained in interaction-mediated tool use showed increased performance after the first and second training periods with respect to baseline (Fig. 4a; Table I). The increase persisted, albeit weakened, after the first resting period. By contrast, the interaction-mediated grasping group showed no significant differences in performance (Table I).

Social Cognition Domain For the interaction-mediated, tool-use group, the overall model was significant (Table I). Interaction-mediated tool use enhanced cognitive performance with respect to the baseline, following the first training period (Fig. 4b; Table I). After the second training period, the difference with baseline performance was even more pronounced, and a robust effect was still detectable following the first resting period (Table I). The interaction-mediated grasping group showed no significant differences (Table I). We excluded the social learning scale from this analysis because all animals obtained null scores.

Effect of Interaction-Mediated Tool-Use Training on PCTB Scales

The training changed the cognitive performance at the scale level (Fig. 5; Table II).

Space Scale The overall model for the interaction-mediated, tool-use group was significant (Table II). Animals trained in interaction-mediated tool use showed a significant increase in performance after both the first and second training periods, which vanished following the first resting period (Fig. 5a; Table II). We found no

Table I Results of GLMM testing the effect of interaction-mediated tool-use training on performance in two cognitive domains in long-tailed macaques at the Department of Neuroscience and Rehabilitation, University of Ferrara, Italy, 2020. Numbers indicate the chi-square value (χ^2), the degrees of freedom (df), the log-odds regression coefficient (β), the standard deviation (σ), and the *p* value

	Interaction-mediated grasping			Interaction-mediated tool use		
Physical						
Likelihood-ratio test	χ^2	df	*p*	χ^2	df	*p*
Overall model	1.505	4	0.8257	36.732	4	< 0.0001
Fixed effects	β	σ	*p*	β	σ	*p*
Intercept	-0.213	0.163	0.1925	-0.192	0.175	0.2739
1st training	-0.047	0.138	0.7309	0.613	0.139	< 0.0001
2nd training	-0.047	0.138	0.7309	0.643	0.140	< 0.0001
1st resting	-0.076	0.138	0.5819	0.274	0.138	0.0466
2nd resting	-0.162	0.138	0.2411	0.076	0.137	0.5825
Random effects	β	σ	*p*	β	σ	*p*
Subject	-	0.001	-	-	0.003	-
Task	-	0.157	-	-	0.188	-
Social						
Likelihood-ratio test	χ^2	df	*p*	χ^2	df	*p*
Overall model	1.577	4	0.8130	28.498	4	< 0.0001
Fixed effects	β	σ	*p*	β	σ	*p*
Intercept	-0.298	0.250	0.2338	-0.078	0.290	0.7880
1st training	-0.082	0.234	0.7262	0.740	0.241	0.0022
2nd training	-0.054	0.233	0.8155	1.130	0.251	< 0.0001
1st resting	-0.082	0.234	0.7262	0.503	0.238	0.0343
2nd resting	-0.276	0.235	0.2408	0.110	0.235	0.6386
Random effects	β	σ	*p*	β	σ	*p*
Subject	-	0.001	-	-	0.015	-
Task	-	0.168	-	-	0.251	-

significant effect in the performance for the interaction-mediated grasping group (Table II).

Quantities Scale We found no significant difference between the performance at the different time-points in any group (Fig. 5b; Table II). Thus, the training did not modulate the quantities scale.

Causality Scale For the interaction-mediated, tool-use group, the overall model was significant (Table II). Interaction-mediated tool use enhanced the cognitive performance following the first training period with respect to baseline (Fig. 5c; Table II). An effect also was present after the second training period, and it persisted after the first resting period (Table II). Analysis of the interaction-mediated grasping group showed no significant differences (Table II).

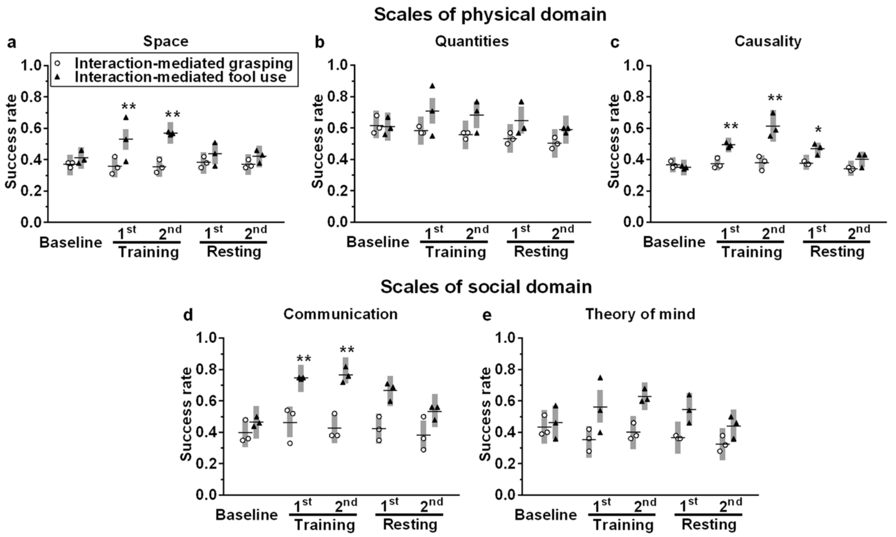

Fig. 5 Effect of interaction-mediated tool-use training on performance in cognitive scales in long-tailed macaques at the Department of Neuroscience and Rehabilitation, University of Ferrara, Italy, 2020. Proportion of correct responses relative to the space (**a**), quantities (**b**), causality (**c**), communication (**d**), and theory-of-mind (**e**) scales. White circles and black triangles represent individual animals. Horizontal black lines indicate the mean for each group. Gray stripes indicate the predicted mean ± standard deviation based on a GLMM. $*p<0.05$, $**p<0.01$, different from their own baseline (GLMM analysis in Table II)

Communication Scale For the interaction-mediated, tool-use group, we found that the overall model was significant (Table II). Macaques showed a large performance increase with respect to baseline following the first and second training periods in the interaction-mediated, tool-use group (Fig. 5d; Table II). Following the first resting period, the difference to baseline was no longer significant (Table II). As before, the interaction-mediated grasping group showed no significant differences in performance (Table II).

Theory of Mind Scale The overall model for the interaction-mediated, tool-use group was not significant (Table II). At the individual predictor level, the cognitive performance of interaction-mediated, tool-use group did not increase significantly after the first training period but did increase significantly after the second training period (Fig. 5e; Table II). We found no significant differences in performance for the interaction-mediated grasping group (Table II).

Effect of Interaction-Mediated Tool-Use Training on PCTB Tasks

Training increased the cognitive performance at the task level (Figs. 6 and 7; Tables III and IV).

Table II Results of GLMM testing the effect of interaction-mediated tool-use training on performance in cognitive scales in long-tailed macaques at the Department of Neuroscience and Rehabilitation, University of Ferrara, Italy, 2020. Numbers indicate the chi-square value (χ^2), the degrees of freedom (df), the log-odds regression coefficient (β), the standard deviation (σ), and the *p* value

	Interaction-mediated grasping			Interaction-mediated tool use		
Physical						
Space						
Likelihood-ratio test	χ^2	df	*p*	χ^2	df	*p*
Overall model	0.219	4	0.9944	19.423	4	0.0006
Fixed effects	β	σ	*p*	β	σ	*p*
Intercept	0.493	0.155	0.0014	-0.353	0.167	0.0345
1st training	-0.096	0.219	0.6615	0.653	0.214	0.0023
2nd training	-0.048	0.218	0.8270	0.630	0.214	0.0032
1st resting	-0.024	0.218	0.9129	0.136	0.213	0.5226
2nd resting	-0.024	0.218	0.9129	0.000	0.214	1.0000
Random effects	β	σ	*p*	β	σ	*p*
Subject	-	0.000	-	-	0.002	-
Task	-	0.001	-	-	0.016	-
Quantities						
Likelihood-ratio test	χ^2	df	*p*	χ^2	df	*p*
Overall model	3.111	4	0.5394	3.897	4	0.4202
Fixed effects	β	σ	*p*	β	σ	*p*
Intercept	0.499	0.219	0.0225	0.458	0.255	0.0720
1st training	-0.185	0.305	0.5429	0.454	0.319	0.1553
2nd training	-0.276	0.304	0.3637	0.295	0.314	0.3480
1st resting	-0.366	0.303	0.2279	0.144	0.310	0.6418
2nd resting	-0.499	0.303	0.0994	-0.094	0.306	0.7596
Random effects	β	σ	*p*	β	σ	*p*
Subject	-	0.001	-	-	0.049	-
Task	-	0.001	-	-	0.002	-
Causality						
Likelihood-ratio test	χ^2	df	*p*	χ^2	df	*p*
Overall model	1.073	4	0.8985	17.279	4	0.0017
Fixed effects	β	σ	*p*	β	σ	*p*
Intercept	-0.578	0.575	0.3152	-0.506	0.516	0.3268
1st training	0.074	0.222	0.7390	0.656	0.227	0.0038
2nd training	0.074	0.222	0.7390	0.844	0.230	0.0002
1st resting	0.025	0.222	0.9115	0.501	0.225	0.0260
2nd resting	-0.124	0.223	0.5778	0.249	0.224	0.2648
Random effects	β	σ	*p*	β	σ	*p*
Subject	-	0.001	-	-	0.011	-
Task	-	1.098	-	-	0.866	-
Social						
Communication						
Likelihood-ratio test	χ^2	df	*p*	χ^2	df	*p*

Table II (continued)

	Interaction-mediated grasping			Interaction-mediated tool use		
Overall model	0.860	4	0.9303	21.226	4	0.0003
Fixed effects	β	σ	*p*	β	σ	*p*
Intercept	-0.315	0.337	0.3491	-0.038	0.214	0.8584
1st training	0.137	0.302	0.6509	0.892	0.312	0.0043
2nd training	0.000	0.303	1.0000	1.298	0.330	0.0001
1st resting	0.046	0.302	0.8800	0.544	0.303	0.0727
2nd resting	-0.138	0.303	0.6495	0.223	0.299	0.4558
Random effects	β	σ	*p*	β	σ	*p*
Subject	-	0.001	-	-	0.001	-
Task	-	0.189	-	-	0.003	-
Theory of mind						
Likelihood-ratio test	χ^2	df	*p*	χ^2	df	*p*
Overall model	2.251	4	0.6896	8.483	4	0.0754
Fixed effects	β	σ	*p*	β	σ	*p*
Intercept	-0.270	0.345	0.4330	-0.206	0.630	0.7443
1st training	-0.409	0.371	0.2698	0.514	0.385	0.1820
2nd training	-0.133	0.365	0.7156	0.902	0.394	0.0220
1st resting	-0.269	0.367	0.4642	0.439	0.384	0.2527
2nd resting	-0.481	0.373	0.1968	-0.073	0.382	0.8487
Random effects	β	σ	*p*	β	σ	*p*
Subject	-	0.001	-	-	0.144	-
Task	-	0.105	-	-	0.552	-

Spatial Memory, Object Permanence and Rotation Tasks The analysis demonstrated no significant effect in either group (Fig. 6a-c; Table III). The training did not affect these tasks.

Transposition Task The overall model for the interaction-mediated, tool-use group was significant (Table III). The performance of the interaction-mediated, tool-use group was clearly and significantly enhanced after the first and second training periods (Fig. 6d; Table III). The positive effect did not persist after the resting periods (Table III). The interaction-mediated, grasping group showed no significant effects (Table III).

Relative Numbers Task We found no significant effect for both groups (Fig. 6e; Table III). Thus, the training did not lead to an effect.

Addition Numbers Task We found that for neither group the overall model was significant (Table III). Although a mild performance enhancement following the second training period was observed in the interaction-mediated, tool-use group, the

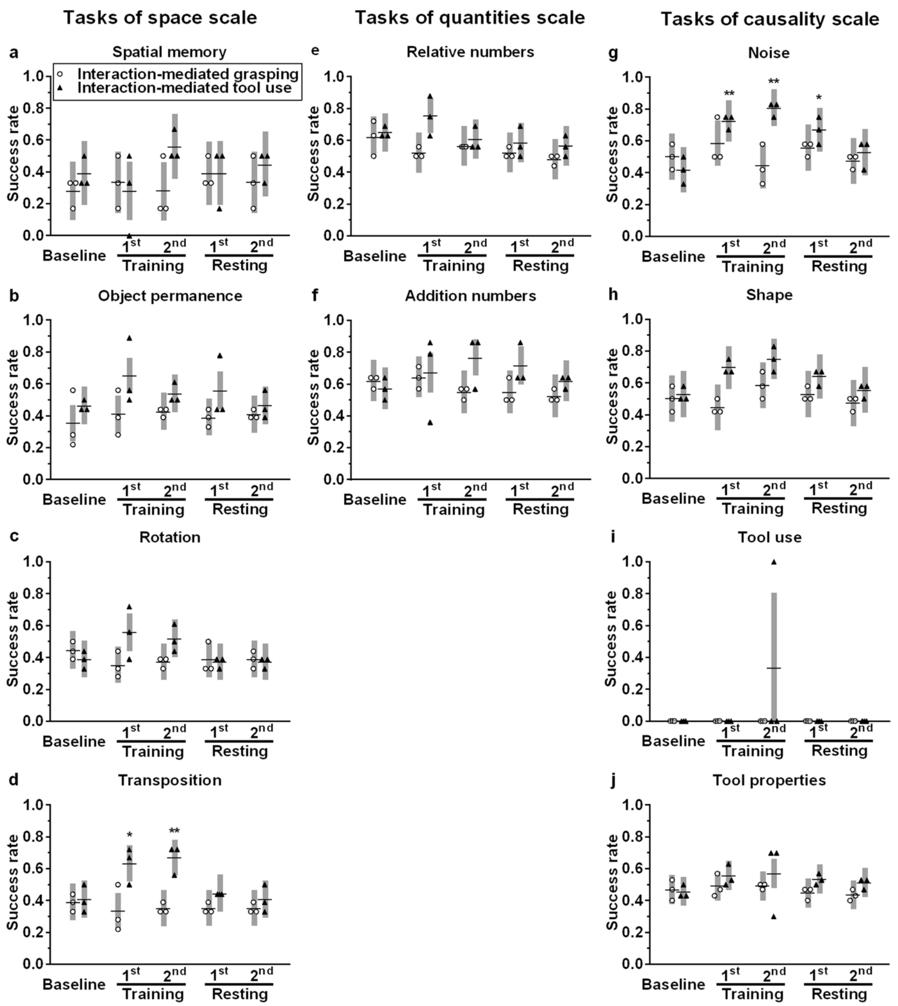

Fig. 6 Effect of interaction-mediated tool-use training on performance in tasks of physical domain in long-tailed macaques at the Department of Neuroscience and Rehabilitation, University of Ferrara, Italy, 2020**.** Proportion of correct responses relative to the spatial memory (**a**), object permanence (**b**), rotation (**c**), transposition (**d**), relative number (**e**), addition numbers (**f**), noise (**g**), shape (**h**), tool use (**i**), and tool properties (**j**) tasks. White circles and black triangles represent individual animals. Horizontal black lines indicate the mean for each group. Gray stripes indicate the predicted mean ± standard deviation based on a GLMM. *$p < 0.05$, **$p < 0.01$, different from their own baseline (GLMM analysis in Table III)

change was close but did not exceed the significance criterion (Fig. 6f; Table III). Hence, training hardly affected this parameter (Table III).

Noise Task For the interaction-mediated, tool-use group, we found that the overall model was significant (Table III). We found a clear enhancement in the cognitive

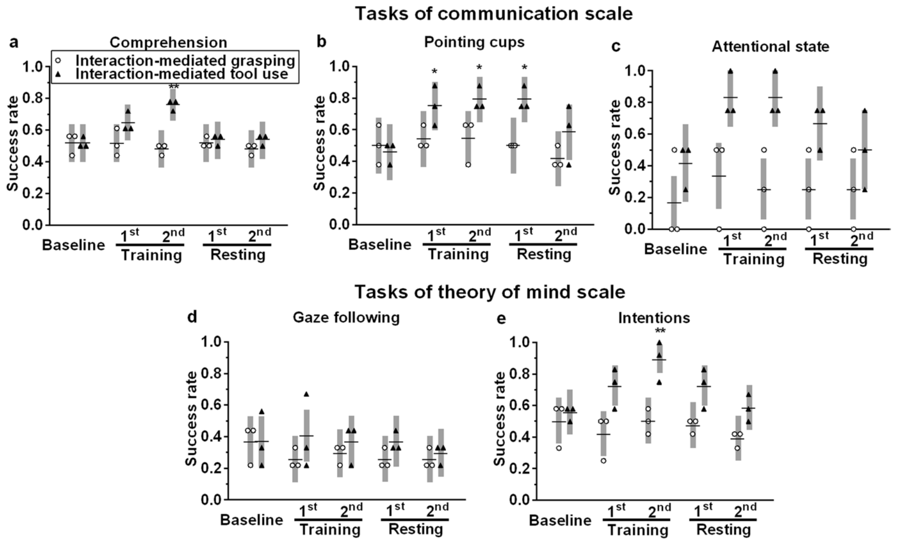

Fig. 7 Effect of interaction-mediated tool-use training on performance in cognitive tasks of the social domain in long-tailed macaques at the Department of Neuroscience and Rehabilitation, University of Ferrara, Italy, 2020. Proportion of correct responses relative to the comprehension (**a**), pointing cups (**b**), attentional state (**c**), gaze following (**d**), and intentions (**e**) tasks. White circles and black triangles represent individual animals. Horizontal black lines indicate the mean for each group. Gray stripes indicate the predicted mean ± standard deviation based on a GLMM. *$p<0.05$, **$p<0.01$, different from their own baseline (GLMM analysis in Table IV)

performance of the animal trained to the interaction-mediated tool use both after the first period, which and the second period, and persisted after the first resting period (Fig. 6g; Table III). Analysis pertaining to the interaction-mediated grasping group showed no significant effect (Table III).

Shape Task For neither group, the overall model was significant (Table III). At the single predictor level, for the interaction-mediated tool-use group, a mild performance increase after the second training period barely reached the significance (Fig. 6h; Table III).

Tool Use and Tool Properties Tasks We found that for neither group the overall model was significant. We conclude that training did not modulate these features (Fig. 6i-j; Table III). Only a macaque performed the tool use task correctly after the second training period, a mentionable but too mild effect.

Comprehension Task The overall model for the interaction-mediated, tool-use group was significant (Table IV). Training induced a transient increase of the score with respect to baseline, since the effect was significant after the second training period, whereas it vanished following the resting periods (Fig. 7a; Table IV). Analysis

Table III Results of GLMM testing the effect of interaction-mediated tool-use training on performance in cognitive tasks of the physical domain in long-tailed macaques at the Department of Neuroscience and Rehabilitation, University of Ferrara, Italy, 2020. Numbers indicate the chi-square value (χ^2), the degrees of freedom (df), the log-odds regression coefficient (β), the standard deviation (σ), and the *p* value

	Interaction-mediated grasping			Interaction-mediated tool use		
Space						
Spatial memory						
Likelihood-ratio test	χ^2	df	*p*	χ^2	df	*p*
Overall model	0.710	4	0.9502	3.062	4	0.5475
Fixed effects	β	σ	*p*	β	σ	*p*
Intercept	-0.591	0.317	0.0618	-0.282	0.300	0.3469
1st training	0.152	0.439	0.7298	-0.307	0.435	0.4796
2nd training	-0.013	0.446	0.9759	0.422	0.422	0.3168
1st resting	0.305	0.435	0.4837	0.000	0.424	1.0000
2nd resting	0.152	0.439	0.7298	0.143	0.422	0.7353
Random effects	β	σ	*p*	β	σ	*p*
Subject	-	0.003	-	-	0.001	-
Object permanence						
Likelihood-ratio test	χ^2	df	*p*	χ^2	df	*p*
Overall model	0.717	4	0.9492	5.170	4	0.2703
Fixed effects	β	σ	*p*	β	σ	*p*
Intercept	-0.382	0.176	0.0296	-0.093	0.172	0.5880
1st training	0.148	0.246	0.5477	0.474	0.245	0.0530
2nd training	0.196	0.245	0.4241	0.186	0.242	0.4414
1st resting	0.099	0.246	0.6870	0.233	0.242	0.3358
2nd resting	0.148	0.246	0.5475	0.000	0.242	1.0000
Random effects	β	σ	*p*	β	σ	*p*
Subject	-	0.001	-	-	0.001	-
Rotation						
Likelihood-ratio test	χ^2	df	*p*	χ^2	df	*p*
Overall model	1.085	4	0.8967	6.973	4	0.1373
Fixed effects	β	σ	*p*	β	σ	*p*
Intercept	-0.139	0.172	0.4175	-0.283	0.173	0.1030
1st training	-0.241	0.245	0.3246	0.423	0.243	0.0822
2nd training	-0.192	0.244	0.4325	0.329	0.243	0.1753
1st resting	-0.143	0.243	0.5563	-0.049	0.245	0.8426
2nd resting	-0.143	0.243	0.5571	-0.049	0.245	0.8423
Random effects	β	σ	*p*	β	σ	*p*
Subject	-	0.000	-	-	0.000	-
Transposition						
Likelihood-ratio test	χ^2	df	*p*	χ^2	df	*p*
Overall model	0.386	4	0.9836	14.072	4	0.0071
Fixed effects	β	σ	*p*	β	σ	*p*
Intercept	-0.282	0.173	0.1039	-0.235	0.177	0.1842

Table III (continued)

	Interaction-mediated grasping			Interaction-mediated tool use		
1st training	-0.150	0.247	0.5427	0.567	0.245	0.0208
2nd training	-0.099	0.246	0.6876	0.667	0.247	0.0069
1st resting	-0.099	0.246	0.6885	0.095	0.243	0.6960
2nd resting	-0.099	0.246	0.6885	0.000	0.244	0.9996
Random effects	β	σ	*p*	β	σ	*p*
Subject	-	0.000	-	-	0.005	-
Quantities						
Relative numbers						
Likelihood-ratio test	χ^2	df	*p*	χ^2	df	*p*
Overall model	2.366	4	0.6688	4.692	4	0.3203
Fixed effects	β	σ	*p*	β	σ	*p*
Intercept	0.321	0.185	0.0827	0.374	0.187	0.0447
1st training	-0.269	0.258	0.2984	0.305	0.271	0.2589
2nd training	-0.163	0.259	0.5284	-0.109	0.261	0.6756
1st resting	-0.269	0.258	0.2985	-0.163	0.260	0.5310
2nd resting	-0.373	0.258	0.1483	-0.217	0.260	0.4029
Random effects	β	σ	*p*	β	σ	*p*
Subject	-	0.000	-	-	0.001	-
Addition numbers						
Likelihood-ratio test	χ^2	df	*p*	χ^2	df	*p*
Overall model	1.844	4	0.7644	4.523	4	0.3398
Fixed effects	β	σ	*p*	β	σ	*p*
Intercept	0.304	0.197	0.1233	0.182	0.229	0.4260
1st training	0.064	0.279	0.8180	0.263	0.282	0.3505
2nd training	-0.184	0.276	0.5058	0.550	0.291	0.0587
1st resting	-0.184	0.276	0.5062	0.395	0.284	0.1651
2nd resting	-0.244	0.276	0.3766	0.124	0.277	0.6557
Random effects	β	σ	*p*	β	σ	*p*
Subject	-	0.001	-	-	0.043	-
Causality						
Noise						
Likelihood-ratio test	χ^2	df	*p*	χ^2	df	*p*
Overall model	1.918	4	0.7509	15.113	4	0.0045
Fixed effects	β	σ	*p*	β	σ	*p*
Intercept	0.000	0.209	1.0000	-0.210	0.211	0.3185
1st training	0.210	0.297	0.4780	0.800	0.306	0.0090
2nd training	-0.140	0.296	0.6369	1.072	0.319	0.0008
1st resting	0.140	0.296	0.6368	0.641	0.302	0.0336
2nd resting	-0.070	0.296	0.8136	0.280	0.297	0.3451
Random effects	β	σ	*p*	β	σ	*p*
Subject	-	0.000	-	-	0.000	-

Table III (continued)

	Interaction-mediated grasping			Interaction-mediated tool use		
Shape						
Likelihood-ratio test	χ^2	df	*p*	χ^2	df	*p*
Overall model	1.650	4	0.7997	5.425	4	0.2664
Fixed effects	β	σ	*p*	β	σ	*p*
Intercept	0.000	0.209	1.0000	0.070	0.210	0.7395
1st training	-0.140	0.296	0.6368	0.439	0.303	0.1472
2nd training	0.210	0.297	0.4780	0.605	0.309	0.0500
1st resting	0.070	0.296	0.8136	0.286	0.299	0.3391
2nd resting	-0.070	0.296	0.8136	0.070	0.296	0.8130
Random effects	β	σ	*p*	β	σ	*p*
Subject	-	0.000	-	-	0.001	-
Tool use						
Likelihood-ratio test	χ^2	df	*p*	χ^2	df	*p*
Overall model	0.000	4	1.0000	3.536	4	0.4725
Fixed effects	β	σ	*p*	β	σ	*p*
Intercept	-34.539	n.c	n.c	-4.259	24.217	0.8604
1st training	0.000	n.c	n.c	-0.291	48.234	0.9952
2nd training	0.000	n.c	n.c	3.782	24.228	0.8760
1st resting	0.000	n.c	n.c	-0.291	48.234	0.9952
2nd resting	0.000	n.c	n.c	-0.291	48.234	0.9952
Random effects	β	σ	*p*	β	σ	*p*
Subject	-	1.000	-	-	0.222	-
Tool properties						
Likelihood-ratio test	χ^2	df	*p*	χ^2	df	*p*
Overall model	0.930	4	0.9202	2.818	4	0.5887
Fixed effects	β	σ	*p*	β	σ	*p*
Intercept	-0.084	0.133	0.5225	-0.112	0.144	0.4364
1st training	0.056	0.187	0.7646	0.253	0.188	0.1778
2nd training	0.056	0.187	0.7645	0.283	0.188	0.1330
1st resting	-0.056	0.187	0.7643	0.196	0.187	0.2946
2nd resting	-0.084	0.187	0.6534	0.140	0.187	0.4538
Random effects	β	σ	*p*	β	σ	*p*
Subject	-	0.000	-	-	0.010	-

conducted on the interaction-mediated grasping group showed no significant effect (Table IV).

Pointing Cups Task For the interaction-mediated, tool-use group, the overall model was significant (Table IV). Interaction-mediated tool-use training led to a robust increase in performance with respect to baseline (Fig. 7b; Table IV). The effect was detectable after the first as well as second period, and the difference to baseline

Table IV Results of GLMM testing the effect of interaction-mediated tool-use training on performance in cognitive tasks of the social domain in long-tailed macaques at the Department of Neuroscience and Rehabilitation, University of Ferrara, Italy, 2020. Numbers indicate the chi-square value (χ^2), the degrees of freedom (df), the log-odds regression coefficient (β), the standard deviation (σ), and the *p* value

	Interaction-mediated grasping			Interaction-mediated tool use		
Communication						
Comprehension						
Likelihood-ratio test	χ^2	df	*p*	χ^2	df	*p*
Overall model	0.356	4	0.9859	9.859	4	0.0429
Fixed effects	β	σ	*p*	β	σ	*p*
Intercept	0.046	0.171	0.7861	0.046	0.171	0.7890
1st training	0.000	0.241	1.0000	0.336	0.245	0.1696
2nd training	-0.093	0.241	0.7003	0.661	0.253	0.0091
1st resting	0.000	0.241	1.0000	0.047	0.241	0.8462
2nd resting	-0.093	0.241	0.7003	0.047	0.241	0.8462
Random effects	β	σ	*p*	β	σ	*p*
Subject	-	0.000	-	-	0.001	-
Pointing cups						
Likelihood-ratio test	χ^2	df	*p*	χ^2	df	*p*
Overall model	1.004	4	0.9092	9.583	4	0.0481
Fixed effects	β	σ	*p*	β	σ	*p*
Intercept	0.000	0.257	1.0000	-0.105	0.268	0.6943
1st training	0.105	0.362	0.7726	0.787	0.380	0.0382
2nd training	0.105	0.362	0.7726	0.924	0.387	0.0171
1st resting	0.000	0.362	1.0000	0.924	0.387	0.0171
2nd resting	-0.211	0.363	0.5623	0.318	0.365	0.3831
Random effects	β	σ	p	β	σ	p
Subject	-	0.001	-	-	0.018	-
Attentional state						
Likelihood-ratio test	χ^2	df	p	χ^2	df	p
Overall model	1.053	4	0.9016	7.863	4	0.0967
Fixed effects	β	σ	p	β	σ	P
Intercept	-1.305	0.720	0.0698	-0.211	0.366	0.5649
1st training	0.644	0.634	0.3097	1.179	0.565	0.0367
2nd training	0.353	0.644	0.5834	1.179	0.564	0.0368
1st resting	0.348	0.645	0.5889	0.642	0.523	0.2196
2nd resting	0.353	0.644	0.5834	0.211	0.514	0.6819
Random effects	β	σ	*p*	β	σ	*p*
Subject	-	0.785	-	-	0.002	-
Theory of mind						
Gaze following						
Likelihood-ratio test	χ^2	df	*p*	χ^2	df	*p*
Overall model	1.193	4	0.8793	0.780	4	0.9411
Fixed effects	β	σ	*p*	β	σ	*p*

Table IV (continued)

	Interaction-mediated grasping			Interaction-mediated tool use		
Intercept	-0.333	0.247	0.1771	-0.339	0.262	0.1964
1st training	-0.317	0.358	0.3760	0.098	0.349	0.7776
2nd training	-0.206	0.354	0.5598	0.004	0.349	0.9919
1st resting	-0.315	0.358	0.3797	0.003	0.350	0.9931
2nd resting	-0.317	0.358	0.3760	-0.204	0.355	0.5655
Random effects	β	σ	*p*	β	σ	*p*
Subject	-	0.001	-	-	0.022	-
Intentions						
Likelihood-ratio test	χ^2	df	p	χ^2	df	*p*
Overall model	1.484	4	0.8294	13.351	4	0.0097
Fixed effects	β	σ	*p*	β	σ	*p*
Intercept	0.000	0.209	1.000	0.141	0.235	0.5479
1st training	-0.210	0.297	0.4780	0.459	0.308	0.1358
2nd training	0.000	0.295	1.0000	1.107	0.351	0.0016
1st resting	-0.070	0.296	0.8136	0.459	0.308	0.1358
2nd resting	-0.282	0.298	0.3429	0.072	0.298	0.8092
Random effects	β	σ	*p*	β	σ	*p*
Subject	-	0.001	-	-	0.033	-

persisted after the first resting period. Analysis conducted on the interaction-mediated grasping group showed no significant effect (Table IV).

Attentional State Task The overall model for the interaction-mediated, tool-use group was not significant (Table IV). At the individual predictor level, we observed some enhancement in the performance score of the interaction-mediated, tool-use group after the first training period and second training period, but it declined after the first resting period to a level that was not statistically different from baseline (Fig. 7c; Table IV). There was no significant effect in the interaction-mediated grasping group (Table IV).

Gaze Following Task We found no significant effect in both groups (Fig. 7d; Table IV). Thus, the training did not influence this skill.

Intentions Task The overall model was significant for the interaction-mediated, tool-use group (Table IV). The interaction-mediated tool uses enhanced performance with respect to baseline only after the second training period (Fig. 7e; Table IV). The effect vanished after the resting periods (Table IV). The same analysis conducted on the interaction-mediated grasping group showed no significant effect (Table IV).

Effect of Interaction-Mediated Tool-Use Training on Tasks with Respect to Chance Level

Baseline No animals performed tasks above chance level (Appendix 3 in Supplementary Material).

1st Training Period Individuals in the interaction-mediated, tool-use group scored above chance level in some tasks of the physical domain, namely object permanence, rotation, transposition, relative and addition numbers (Appendix 3 in Supplementary Material). In the social domain, we observed scores above chance level in comprehension, pointing cups and intentions (Appendix 3 in Supplementary Material). For the interaction-mediated grasping group, no score was above chance level.

2nd Training Period Individuals in the interaction-mediated, tool-use group scored above chance level in some tasks of the physical domain, namely object permanence, rotation, transposition, addition numbers, noise, shape, and tool properties (Appendix 3 in Supplementary Material). In the social domain, we observed a score above chance level in comprehension and intentions (Appendix 3 in Supplementary Material). Performance was not above chance levels in the interaction-mediated grasping group.

1st Resting Period Animals of the interaction-mediated, tool-use group revealed a success rate above chance level in some tasks of physical domain, namely object permanence, addition numbers and noise (Appendix 3 in Supplementary Material). In the tasks of social domain, we observed a score above chance level in pointing cups and intentions (Appendix 3 in Supplementary Material). For the interaction-mediated grasping group, no score was above chance level.

2nd Resting Period Individuals belonging to the interaction-mediated, tool-use group showed a score above chance level only in the object permanence task (Appendix 3 in Supplementary Material). In the tasks of the social domain, we detected no score above chance level. For the interaction-mediated grasping group, performance was never above chance level.

Discussion

Our results show that learning to use a tool with interaction between individuals enhances performance in cognitive tests evaluating macaques' comprehension of the physical world and their communication skills. Most specific effects did not persist beyond the period in which we trained the monkeys, although the overall enhancement shown by increased performance with respect to baseline at the domain levels continued for 35 days.

Our findings highlight the importance of the co-presence of tool use and inter-individual interaction in modelling cognitive performance in the social domain. In the physical cognition domain, both simple (i.e., noninteractive; Tia *et al.*, 2018) and interaction-mediated (this study) tool use increase overall performance with respect to baseline. This pattern was mainly due to the large effects observed in the Space and Causality scales. In particular, the tool use procedures of both studies significantly enhanced the success rate in the Transposition task. However, only the interaction-mediated tool use in the present study increased success in the Noise task. In the social cognition domain, animals that learned the interaction-mediated tool use increased their overall PCTB performance, an effect that was not observed when animals were trained only in tool use, without inter-individual interaction (Tia *et al.*, 2018). This difference was largely due to the strong effect observed in the Communication scale. In particular, Comprehension and Pointing cups tasks were enhanced by the interaction-mediated tool use. The same procedure also affected positively the Intentions task.

We saw no change in performance in animals that simply had to grasp the food brought by the experimenter (interaction without tool). This observation suggests that a simple interaction alone (without a tool) does not significantly affect cognitive functions. Alternatively, the complexity or duration of the interactive manual grasping exercise may have been insufficient to promote such changes. Sustained interaction with human caregivers during development in apes can improve cognitive abilities (Russell *et al.*, 2011). The macaques' familiarity with humans and their training history may have had an important influence on our findings, affecting their motivation to interact (Pope *et al.*, 2018). Chimpanzees (*Pan troglodytes*), housed at two different captive facilities (a rehabilitation center and a zoo) displayed different cognitive skills when tested in problem-solving tasks (Forss *et al.*, 2020), suggesting the importance of the time spent in captivity and the specific captive setting in defining the level of cognitive performance. Different experiences with humans also caused captive orangutans (*Pongo abelii* and *Pongo pygmaeus*) to vary in curiosity and their understanding of physical problem-solving tasks (Damerius *et al.*, 2017).

Our findings are in line with studies showing that tool-use training promotes skills related to the physical properties of surrounding objects, reflecting abilities related to spatial information processing (Gamberini *et al.*, 2008; Maravita & Iriki, 2004; Zuberbühler *et al.*, 1996) and understanding of causal interactions between objects (Fujita *et al.*, 2011; Macellini *et al.*, 2012). The number of sessions required to correctly perform the task increased progressively with stages, because subsequent stages required a more advanced understanding of the interaction with the experimenter and of the spatial relations needed to adapt the trajectory of the rake to the location of the reward (Yamazaki *et al.*, 2011). The enhancement of the physical cognition performance can be observed in noninteractive (rake use to obtain the reward, without any help from the experimenter; Tia *et al.*, 2018) as well as interactive (this study) contexts, suggesting that learning to manipulate a tool is sufficient to modulate performance on different aspects related to physical, but not social, cognition. In contrast, the lack of effect of this learning on some PCTB tasks may be a result of insufficient training complexity and/or duration, or absence of motivational determinants (Völter *et al.*, 2017).

In contrast to simple noninteractive tool use (Tia *et al.*, 2018), interaction-mediated tool use had a large effect on some skills in the social domain, which strongly reflect the strength of the reciprocal interaction between subjects. Social cognition concerns an individual's ability to interact with others and relies on the animals' ability to recognize social relations among conspecifics, predict their behavior, or create insightful and novel solutions that are not just the result of a trial-and-error approach (Zuberbühler & Byrne, 2006). Genetic predispositions and acquired skills and the various social signals that make it possible to learn about the world are of major importance to social cognition, allowing individuals to take advantage of being part of a group (Frith & Frith, 2007; Firth, 2008). The attention allocated to a social interaction depends on how biologically relevant the interaction is, which is ultimately affected by phylogeny and previous experience (McFarland *et al.*, 2013).

An important interaction is the request for food that is directed by captive primates, including chimpanzees (Hostetter *et al.*, 2001), orangutans, gorillas (Poss *et al.*, 2006), mangabeys (Maille *et al.*, 2012), macaques (Canteloup *et al.*, 2015), and baboons (Bourjade *et al.*, 2015; Meunier *et al.*, 2013) toward humans. We evaluated communication between the macaque and experimenter, but not between conspecifics. Communication during PCTB testing consisted of the behavior that occurred during the task, e.g., when the monkey used a gesture (pointing to the correct cup) or inferred the correct cup following the experimenter's indication. In general, communicative strategies used by nonhuman primates to obtain rewards are similar (Deshpande *et al.*, 2018). If the partner was a conspecific, we speculate that the results may not change significantly, because both nonhuman primates and humans interact by employing body postures, facial expressions, gestures, and vocalisations (Maestripieri, 1997). However, the difficulty of carrying out the training and testing is likely to increase, because two macaques would need to attend to the task at same time, without distraction or competition for the reward (Chancellor & Isbell, 2008).

Monkeys and humans collect information by observing others performing the same actions and then use it in an adaptive manner to predict future actions or scenarios, as well as to guide behavioral choices (Ferretti & Papaleo, 2019). The effect of the interaction-mediated, tool-use training was predominant on the communication scale, which comprised tasks where a communicative approach was required to obtain the reward. This finding is in line with previous reports that tool use and communicative gestures share similar cortical networks (Króliczak & Frey, 2009; Steele *et al.*, 2012). The fact that tool-use ability and brain size are related in primates (Reader & Laland, 2002) supports the hypothesis that interaction between individuals can amplify the effect of tool use on cortical and subcortical brain substrates that play a role in the neural activity specific to a particular situation (Brincat *et al.*, 2018). We cannot assess whether the changes relative to social cognition are directly driven by the interaction-mediated tool use or through effects induced by the physical cognition enhancement. However, the enhancement in the physical domain was not accompanied by similar changes in the social domain when the tool use was not interactive (Tia *et al.*, 2018), a finding that supports our initial hypothesis, i.e., that the interaction-mediated tool use directly drives the social cognition changes.

The training procedures used with the two groups differed not only in terms of the presence or absence of tool use but also in their complexity. We tried to reduce the difference in cognitive challenge between the two conditions in the experimental design. Both protocols required the monkey to observe the experimenter's behavior, request help, and wait for intervention. The goal of the experimenter's intervention was similar in the two protocols: helping the monkey to reach the food. However, the action was performed with different approaches (hand vs. tool). In the control procedure, the main interaction factors were the monkeys' expectation that the experiment would bring the food nearer. In the tool-use training, the interaction occurred when the experimenter handed the rake to the monkey or used it to push the food item (stages a and b), as well as when the monkey slid the rake toward the experimenter (stages c and d).

Despite these efforts to balance the two training procedures, we cannot exclude the possibility that the cognitive enhancement results from a higher degree of cognitive participation or challenge required by the tool-use training procedure rather than from the tool use. Even in this case, however, this interpretation is in line with our hypothesis that the reinforcement of the interaction between individuals facilitates overall cognitive performance enhancement. Our main goal was to test whether all aspects of cognitive performance are increased if tool use is combined with interaction with another individual. In other words, the additional challenge in the training procedure leads to a larger effect on the cognitive performance induced by the training. It is beyond the scope of our study to assess what the minimum amount of interaction is that would lead to the enhancement.

We also found interindividual differences in the time needed to master rake use. This observation echoes previous work showing variability in the level of attention and manual dexterity in long-tailed macaques (Kaeser *et al*., 2014). Furthermore, the success rate in stage a exceeded 70% during the first session for all subjects. The performance observed at the beginning of the 2016 study was similarly high (Tia *et al*., 2018), meaning that the high initial success rate does not necessarily suggest that the monkeys remember the rake manipulation from the earlier study but is more simply explained with the easiness of the exercise: the monkey only had to pull the rake to itself.

As shown by the domain scores, the effects of the interaction-mediated tool-use training on cognition persisted after the first 35-day resting period, a time span similar to the time needed for a single training period. The duration of the effects induced by interaction-mediated tool use depended on the skill tested. One probable reason for these differences is the different degree of plasticity of circuitry that promoted these changes (Kolb & Gibb, 2014). Alternatively, some cognitive tasks may be easier to perform and to recall. By contrast, the combined increase in both physical and social scores vanished by 70 days after training. These results suggest that sustained practice or a longer period of training before resting may be needed to maintain a cognitive enhancement about properties of objects as well as communicative strategies. The disappearance of the enhancement after a resting period suggests that only the specific cognitive skills required by the PCTB tasks were affected, rather than cognition per se.

The PCTB evaluated the possible production of new (simple) strategies to obtain a reward, which is a common motivation for the execution of voluntary actions (Ebel *et al*., 2019). The fact that only the interaction-mediated tool use increased overall performance revealed that animals engaging in both tool use and interaction procedures can achieve new abilities with unfamiliar tools after they have been appropriately stimulated (Macellini *et al*., 2012). In contrast, in our experimental setting, the tools were not completely unknown to the subjects. We repeated the PCTB five times for each animal. The animals had the possibility to see and use the object and tools that were used for the tasks for the duration of a task. Moreover, trained animals understood well the shapes and properties of the simple tools used in the different tasks (e.g., cups, board, plates). The macaques performed PCTB only at five timepoints during this study, because repetition could have reduced curiosity and attractiveness, affecting the outcome. Several studies have previously described habituation, loss of motivation, and decreased activity with new objects (Line *et al*., 1991; Paquette & Prescotte, 1988), suggesting that new materials elicit behavioral changes only for short periods (Celli *et al*., 2003). Capuchins consistently select tools of suitable material and weight to acquire food (Manrique *et al*., 2011; Santos *et al*., 2003; Schrauf *et al*., 2012; Spagnoletti *et al*., 2011; Visalberghi *et al*., 2009), revealing that tool use is promoted, in part, by the overall difficulty of obtaining the reward.

Conclusions

This study of six, adult, laboratory, long-tailed macaques provides evidence of a relationship between an interaction-mediated, tool-use learning protocol and enhancement of a large spectrum of cognitive abilities in both the physical and social aspects. The synergy between interindividual interaction and tool use may play a crucial role in enhancing individual cognition, facilitating the development of novel strategies to find optimal solutions for daily survival problems and to promote aggregation (Sinha, 1998), which represents the basis of cooperative behavior and social evolution in primates. However, caution is needed in the generalization of our conclusions. It is an open question whether the findings that apply to the group of captive macaques studied here would hold true for other individuals, different experimental conditions, or in the wild.

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