Comprehension of iconic gestures by chimpanzees and human children

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A B S T R A C T

Iconic gestures—communicative acts using hand or body movements that resemble their referent—figure prominently in theories of language evolution and development. This study contrasted the abilities of chimpanzees ($N = 11$) and 4-year-old human children ($N = 24$) to comprehend novel iconic gestures. Participants learned to retrieve rewards from apparatuses in two distinct locations, each requiring a different action. In the test, a human adult informed the participant where to go by miming the action needed to obtain the reward. Children used the iconic gestures (more than arbitrary gestures) to locate the reward, whereas chimpanzees did not. Some children also used arbitrary gestures in the same way, but only after they had previously shown comprehension for iconic gestures. Over time, chimpanzees learned to associate iconic gestures with the appropriate location faster than arbitrary gestures, suggesting at least some recognition of the iconicity involved. These results demonstrate the importance of iconicity in referential communication.

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Introduction

The communicative abilities of humans are remarkably flexible. Both adults and children are able to communicate a wide variety of messages even when the necessary linguistic abilities are lacking.

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Intuitively, they create gestures on the spot to make themselves understood. The pointing gesture is most often used to single out referents in the immediate perceptual context. In contrast, iconic gestures are often used to single out displaced referents outside of the immediate perceptual context. For example, one might request a glass of water (across a noisy room) by pretending to hold a glass and drink from it. Thus, iconic gestures may be considered "natural" acts of reference because they *re*-present the intended referent and thereby induce the recipient to imagine the gesturer's communicative intention (Tomasello, 2008). Importantly, this does not require that the gesture is part of a shared and conventional communicative system among the interlocutors. Therefore, this natural referential potential of iconic gestures has been recognized in theories on the development of linguistic abilities (Perniss & Vigliocco, 2014; Piaget, 1951; Werner & Kaplan, 1963) and more recently in several theories of language evolution (Arbib, Liebal, & Pika, 2008; Armstrong & Wilcox, 2007; Corballis, 2011; Donald, 1991; Sterelny, 2012; Tomasello, 2008). These evolutionary theories assume some kind of continuity in the communicative abilities of humans and their ancestors. Comparing human children and their closest living relatives, the great apes, might help us to get a more fine-grained understanding of the evolutionary foundations as well as the development of human communication (Liebal & Haun, 2012). If we find evidence for similar abilities in apes and humans, the biological and genetic foundations enabling the development of these abilities most likely evolved at an earlier point in time. To understand the evolutionary history of human communication it is crucial to specify which abilities are unique to humans and which are shared with our closest living relatives.

Large-scale observational studies in captivity and in the wild find no evidence for the use of iconic gestures in chimpanzees (*Pan troglodytes*) or other great apes (Call & Tomasello, 2007; Genty, Breuer, Hobaiter, & Byrne, 2009; Hobaiter & Byrne, 2011). Nevertheless, there are some studies that report production and comprehension of iconic gestures in great apes. Russon and Andrews (2011) reanalyzed observational data collected with forest-living rehabilitant orangutans (*Pongo pygmaeus*) over 20 years and reported a total of 18 anecdotes of communicative pantomiming toward humans and conspecifics. More systematically, Tanner and Byrne (1996) described a number of seemingly iconic gorilla gestures. In a captive group at the San Francisco Zoo, a male gorilla indicated iconically to a female playmate the action he wanted her to perform or the direction he wanted her to move. For example, he swung his arm under his body and tapped his genitals. The authors interpreted this gesture as an invitation to come to the indicated location for sexual contact. Call and Tomasello (2007) suggested that these gestures could also be ritualized intention movements and that the iconicity could be an interpretation by the human observer. In another recent study, these same gestures were found in other groups of gorillas and have been interpreted as belonging to the genetically predisposed natural repertoire of gorilla gestures (Genty et al., 2009).

In a similar way, Genty and Zuberbühler (2014) observed a beckoning gesture in bonobos that could be interpreted iconically as indicating the way in which a conspecific should move her body. However, the authors emphasized that they could not claim with confidence that the iconicity of the gesture was clear to the gesturer. In addition, Pika and Mitani (2006, 2009) argued that high-ranking chimpanzee males used a so-called "directed scratch" in mutual grooming sessions to request grooming of certain body parts. One chimpanzee performed a loud and exaggerated scratch on a part of his body while his partner was watching. This led to increased grooming of the scratched spot. But it is also possible that the scratcher was really scratching and that the groomer then searched for fleas there.

Thus, although a few observational studies have reported rare instances of iconic gesture use in great apes, the iconicity of these gestures is debated. In the only existing experimental study, Grosse, Call, Carpenter, and Tomasello (2015) found no evidence for the production of iconic gestures in chimpanzees and bonobos. They created a situation in which a knowledgeable participant had the opportunity to instruct a naive experimenter how to operate an apparatus that delivered a reward to the participant. Whereas 2- and 3-year-old children readily used iconic gestures to instruct the experimenter, only 1 of 13 apes produced a bodily movement that was somehow related to the corresponding action (not a hand movement but rather a head tilt in the direction the apparatus needed to be turned). This individual had been extensively trained in imitation previously (Hribar, Sonesson, & Call, 2014). However, when participants had access to a duplicate of the apparatus, they showed some signs of comprehending the correspondence between the two by manipulating the corresponding

apparatus more often than an alternative apparatus. To our knowledge, there are no experimental studies of the comprehension of iconic gestures in great apes.

In the case of human children, Piaget (1951) viewed the ability to recognize iconic relations between signs and their referents as a stepping stone toward the acquisition of the arbitrary symbols of language. But empirically there seems to be little temporal advantage for the acquisition of iconic over arbitrary signs in human ontogeny (Bonvillian, Orlansky, & Novack, 1983; Namy, Campbell, & Tomasello, 2004; but see Thompson, Vinson, Woll, & Vigliocco, 2012), suggesting that iconicity is not fundamental to the comprehension of symbolic relations in general. Throughout ontogeny, the absolute number of iconic gestures increases, whereas their relative frequency compared with deictic gestures and words decreases (Iverson, Capirci, & Caselli, 1994). This divergence might be due to a difference in input as, for example, mothers "translate" children's gestures into appropriate words during early communicative interactions (Goldin-Meadow, Goodrich, Sauer, & Iverson, 2007).

Even if iconicity plays a less fundamental role in language development than previously imagined, it is an important source of information during language acquisition (Goodrich & Kam, 2009; Imai & Kita, 2014; Laing, 2014; Mumford & Kita, 2014; Perniss & Vigliocco, 2014). Perniss and Vigliocco (2014) argued and reviewed evidence that children are sensitive to iconicity in spoken and signed languages from an early age onward. According to their view, recognizing the resemblance between the signal and its referent reduces referential ambiguity by linking children's own experience of the world with the communicative signals used to communicate about the world. A range of studies on the emergence and development of signed languages supports this view. Deaf children of hearing parents as well as deaf children living among each other spontaneously start to use iconic gestures to communicate in the absence of a conventional signed language (Goldin-Meadow & Feldman, 1977; Senghas, Kita, & Ozyurek, 2004). Furthermore, the fact that also hearing children start to produce iconic gestures during the months following their first birthday shows that they are an important means of communication during times when children's use of language to convey more complex messages is still rudimentary (Goldin-Meadow & Alibali, 2013). This is especially important for communication about actions and the function of objects (Acredolo & Goodwyn, 1988; Özçalışkan, Gentner, & Goldin-Meadow, 2014). For example, Behne, Carpenter, and Tomasello (2014) showed that 27-month-old children creatively used iconic gestures to instruct a naive puppet on how to operate an apparatus. Some 21-month-old children also created iconic gestures but to a lesser extent. In this study, verbal descriptions fulfilling the same function as the gestures were absent and most likely beyond children's linguistic ability. Another important domain of language development in which iconicity plays a facilitating role is the development of graphical symbol systems (Garrod, Fay, Lee, Oberlander, & MacLeod, 2007; Simcock & DeLoache, 2006).

The communicative potential of iconic gestures lies in the resemblance between gesture and its referent. It requires the spontaneous encoding of the perceptual properties of objects and actions during non-communicative episodes. Recognizing the resemblance between, for example, gesture and object helps to single out the referent in a subsequent communicative interaction. Of course, this is true only if the gesture is understood because it re-presents the referent. This is important because other processes such as ontogenetic ritualization and associative learning can produce seemingly iconic gestures when in reality their iconicity does not play a role in how they are understood (Liszkowski, 2010). Earlier studies on iconic gestures in children did not distinguish between these different ways in which a gesture could be comprehended (Namy, 2008; Namy et al., 2004; Tolar, Lederberg, Gokhale, & Tomasello, 2008; Tomasello, Striano, & Rochat, 1999). For example, in Namy (2008), participants were introduced to a novel object and taught a certain way of handling the object. Later, this way of handling was used as an iconic gesture to refer to the object. In this study, the experimenter explicitly taught and also modeled the action on the novel object in a way that is similar to the teaching of a verbal object label. It is conceivable that children associated the action with the object as a kind of conventional label and the iconic properties of the gesture did not play a role in identifying the meaning of the gesture (see also Liszkowski, 2010). Therefore, earlier studies did not directly address the question of whether children comprehended novel iconic gestures as referential acts. To test experimentally that an iconic gesture is comprehended because of its iconicity, it should be derived from an action that was established as shared in a non-communicative functional context.

The current study, therefore, focused on the question of whether human children and chimpanzees comprehend novel iconic gestures. Chimpanzees, together with bonobos, are our closest living relatives among the great apes and can be used as a model to infer the communicative abilities of the last common ancestor of apes and humans. The gestures we used were derived from functional actions that were part of a joint activity. To make the response as simple as possible, the task was simply to go to the location where the experimenter and the participant had previously manipulated an apparatus in the way he was now gesturing. These gestures were not accompanied by any directional cues that could have helped the participant to single out the referent spatially. We contrasted the ability to comprehend iconic gestures as making reference to a location with the ability to associate arbitrary gestures with a location in the same context. We tested chimpanzees and 4-year-old children with a similar setup. A human experimenter performed the gestures for both species. We did not use a conspecific model for chimpanzees for two reasons. First, chimpanzees are very competitive over food and, therefore, are unlikely to inform one another about a potential food source. Moreover, the chimpanzees who participated in the study interact and communicate with humans on a daily basis and are used to receiving food from them. Second, earlier studies showed that chimpanzees do not benefit from a conspecific compared with a human demonstrator in communicative studies (Tempelmann, Kaminski, & Liebal, 2013). Even though earlier studies suggest that children might be able to comprehend iconic gestures from an earlier age, we tested 4-year-old children in our study to be able to use the same experimental setup for both species. Younger children did not have the physical capacity to operate the apparatuses involved. As a result, we hoped to ensure the comparability of the results. The aim of the study, therefore, was not to pinpoint the youngest possible age at which children are able to comprehend iconic gestures but rather to find out about the role that iconicity plays in spontaneously identifying the referent of a novel gesture. Compared with chimpanzees, children experience referential communication including iconic gestures from a very early age. This exposure might make it easier for children to interpret novel gestures in a referential way. However, by contrasting how the same children comprehend iconic gestures compared with arbitrary gestures, we hoped to understand the role that iconicity plays in identifying the referent of a signal. Furthermore, potential differences between the species might inform us about the role that more general expectations about communicative interactions play in comprehending iconic gestures. We predicted that children would spontaneously recognize the resemblance between the iconic gestures and the corresponding actions and would interpret the gesture as communicative, whereas chimpanzees would not.

Experiment 1a

In the first experiment, we investigated whether chimpanzees differed in their comprehension of iconic and arbitrary gestures. The participant was centered between two locations, one of which yielded a reward. The experimenter informed the participant about the correct location by performing a gesture that was paired with one of them. In the *iconic condition*, the relation between the gesture and the location of the reward was iconic; that is, the gesture mimed the action that was needed to make the reward available. In the *arbitrary condition,* the gesture and action needed to retrieve the reward did not resemble each other.

Method

Participants

We tested 11 chimpanzees (*P. troglodytes*) from two different groups at the Wolfgang Köhler Primate Research Center (Leipzig, Germany) (see Table S1 in the online supplementary material for details). Originally, 4 more chimpanzees participated in the experiment but needed to be excluded because they lost interest (*n* = 3) or moved to another zoo (*n* = 1). The final sample consisted of 6 females and 5 males with an age range from 7 to 36 years (*M* = 18.4). We tested each participant individually on a voluntary basis. All participants either had experience with experimental studies or were currently participating in other studies. Chimpanzees were never food or water deprived at any time, and all rewards for participation were in addition to their usual diet.

Apparatus

Participants were tested in a familiar rectangular enclosure that consisted of two adjacent cages with a small booth between them (see Fig. 1). The door between the two cages was open during the entire test so that the participant could roam freely between the cages. The experimenter sat on a small stool inside the booth. The front wall of the booth consisted of a large window with a small mesh underneath it. On the left- and right-hand sides of the booth, we installed transparent Plexiglas testing windows (69 × 48 cm) with a hole in the bottom (8.5 × 2.5 cm). These windows allowed us to attach the needed apparatus to the each side in the *iconic condition*. In addition, a juice dispenser mechanism was installed in order to release small amounts of diluted grape juice through a Plexiglas tube attached to a small mesh panel underneath the large front window. This mechanism allowed the experimenter to center the participant in front of the window at the beginning of each trial.

We used two pairs of apparatuses (Pair A: app1 and app2; Pair B: app3 and app4; see Fig. 2), which we attached to the left and right windows of the booth, depending on the condition. All apparatuses consisted of a Plexiglas box (50 × 25 × 17.5 cm) and two identical releasing mechanisms (one accessible to the ape and the other accessible to the experimenter). Executing a distinct action that varied depending on the apparatus (app1: "pull down"; app2: "push in"; app3: "turn crank"; app4: "push left to right") released a reward to the participant through the hole at the bottom of the Plexiglas panel. The same action needed to be performed by the participant and the experimenter simultaneously. Operating the apparatus alone did not yield a reward. The participant experienced the corresponding action visually and behaviorally by operating the apparatus together with the experimenter.

Design

The gestures used to inform the participant about the location where to obtain a reward were functionally ineffective versions of the actions needed to operate the corresponding apparatuses.
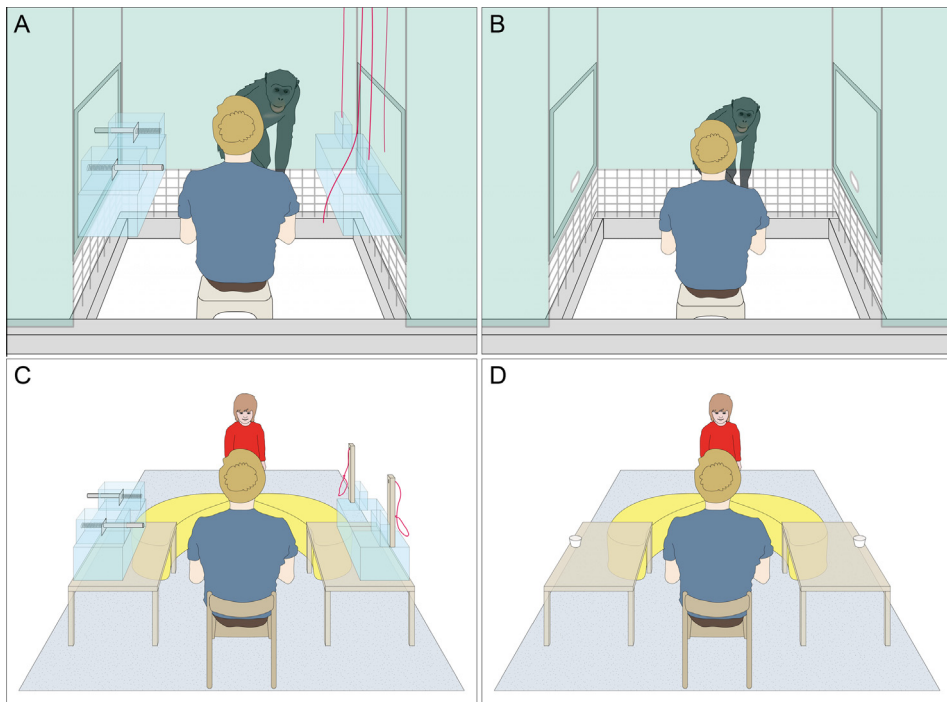

Fig. 1. Schematic drawings of the experimental setups in *iconic condition* chimpanzees (A), *arbitrary condition* chimpanzees (B), *iconic condition* children (C), and *arbitrary condition* children (D). Panel C also shows the modified child apparatus for action "pull down."
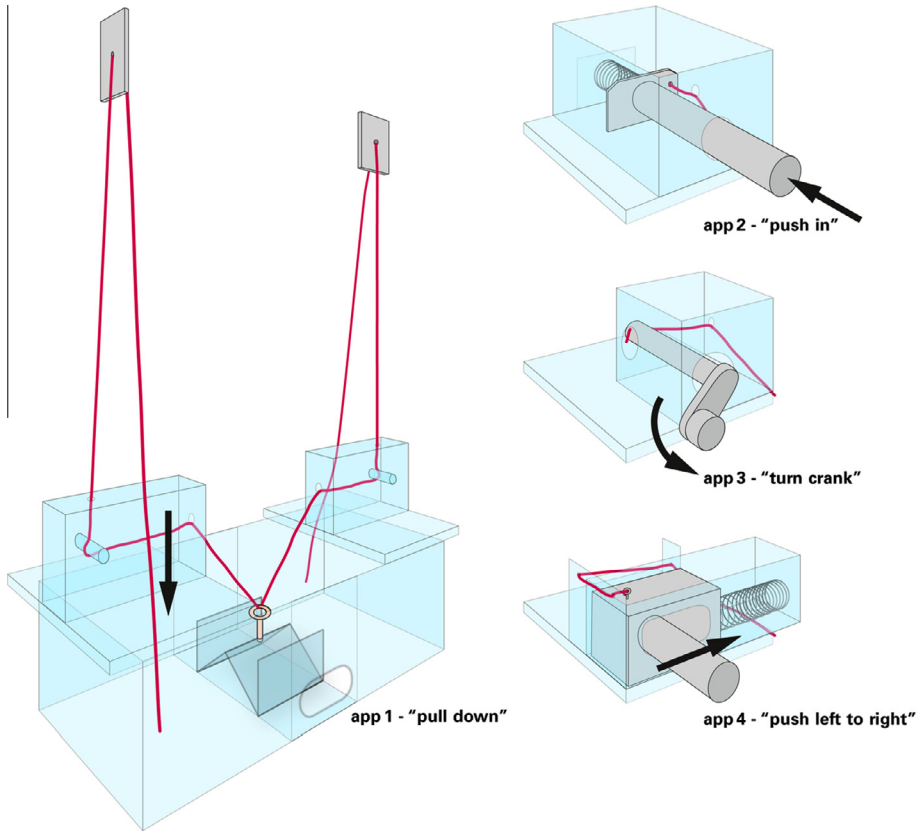
Fig. 2. Schematic drawings of the apparatuses and releasing mechanisms used with both species in the *iconic condition*. App1 ("pull down") needed to be modified for the child study (see Fig. 1).

For example, the gesture derived from app2 ("push in") went as follows. The experimenter lifted his right hand in front of his chest with the palm facing away from the body and the fingers slightly bent inward. Then he moved his hand horizontally forward as if pushing something in. Gestures were never accompanied by any directional cues such as eye gaze, head turning, or pointing. We tested in a within-participant design; that is, each participant received the *iconic condition* and the *arbitrary condition*. We counterbalanced the order of the conditions and gestures used by the experimenter across participants. For each participant and condition, we randomly assigned the gestures derived from one pair of apparatuses to the sides of the booth. In the *iconic condition*, we attached the corresponding apparatus to the Plexiglas windows on the left- and right-hand sides of the booth. In the *arbitrary condition*, we did not attach any apparatus to the windows; instead, the experimenter handed over the reward manually through the hole at the bottom of the left or right window. The task of the participant was to identify the referential connection between the experimenter's gestures and the two locations using associative and/or iconic information. Because the referent of each gesture was a specific location, the relation between gesture and location remained the same for each participant within a condition.

Participant who started with the *iconic condition* and gestures derived from Pair A received the *arbitrary condition* and gestures of Pair B in the next condition and vice versa (see Table S1 for details).

Procedure

To ensure that the chimpanzees knew where to get the reward and how to operate the apparatus, we administered additional training sessions before the actual testing sessions. The general procedure

for both training and testing trials was the same. Each trial started with the participant being centered in the middle of the large window and ended with the participant receiving a reward.

Training. Training trials were administered in sessions with 12 trials each. After the participant was centered, the experimenter turned to one of the two sides and waited for the participant to come to the other side of the window. In the *iconic condition*, there were two apparatuses installed and baited, and the experimenter and participant operated the apparatus together. Thereby, the participant received a reward. In the *arbitrary condition*, there were no apparatuses installed. The experimenter simply turned to one side, offered a reward through the hole in the panel, waited for the participant to move to the same side, and handed over the reward. We pseudo-randomized the sequence of sides to which the experimenter turned, with the same number of turns for both sides and never more than two turns in a row to the same side. Training continued until the participant reliably followed the experimenter and was able to operate the apparatuses in the *iconic condition* or until the participant moved to the side the experimenter had turned to in the *arbitrary condition*. The participant received a minimum of 24 training trials.

Test. The participant received 24 trials per condition split into two sessions across different days with 12 trials each. Each session lasted approximately 10 min. The test trials followed the same general procedure as described above. After the participant was centered, the experimenter called the participant's name and started gesturing as soon as the participant visually attended to him. The gesture always referred to the side to which the experimenter turned afterward. Therefore, the gesture served to inform the participant about what the experimenter would do next and the location at which to obtain the reward. In the *iconic condition*, the gesture matched the action needed to operate the apparatus at the location. In the *arbitrary condition*, no such connection existed between gesture and location.

The experimenter executed the gestures in three blocks of four gestures each (i.e., minimum of 4 gestures and maximum of 12 gestures per trial). Before each block, he made sure that the participant visually attended to him, calling the participant's name if necessary. While gesturing, the experimenter openly looked at the participant, maintaining eye contact whenever possible. As soon as the participant chose one of the sides by moving away from his or her initial position toward one of the panels, the experimenter turned to the side that he indicated with the gesture. If the participant started moving before the experimenter fully executed the first gesture, the trial was repeated. If the participant did not move until the end of the three blocks, the experimenter turned to the indicated side.

One participant refused to move away from her initial position until the experimenter had turned to one of the sides. Therefore, the procedure was changed slightly so that the experimenter waited until the participant made a decision. However, this had no effect on coding (see next section). The sequence of gestures was pseudo-randomized with the same number for each kind of gesture and never more than two of the same kind of gesture in a row. Participants were non-differentially reinforced to ensure their motivation across sessions and conditions. That is, the penalty for making a wrong decision was a short time delay of approximately 5 s in getting the reward.

Coding and analyses

All trials were filmed by a single video camera on a large tripod behind the experimenter, granting a full shot of the experimental setup. We coded the participant's first response after the onset of the experimenter's gesturing. The response was coded as "correct" if the participant moved to the side that matched the side referred to by the experimenter. It was coded as "incorrect" if the participant moved toward the side that was not indicated by the experimenter or did not move at all within the time frame of the onset of the first gesture and 3 s after the last gesture. In the *iconic condition*, 14.4% of trials (38/264 trials) were coded as incorrect because participants did not make a choice. The respective number for the *arbitrary condition* was 18.2% (48/264 trials).

A performance of 18 of 24 or more trials correct was considered as individually above chance (binomial test, $p < .05$). To test whether chimpanzees' performance was influenced by other predictor variables, we used a generalized linear mixed model (GLMM). This model allowed us to determine the effects of the predictor variables on the response variable while accounting for the repeated testing of the same participant. The response variable was defined as the overall proportion of correct trials. We included sex, age, and order of condition (*iconic* or *arbitrary condition* first) as fixed

between-participant factors and included condition as a fixed within-participant factor. Furthermore, we included random effects for chimpanzee group and participant identity as well as random slopes for condition within participants. The first author coded all trials live and again from video. A second coder, unfamiliar with the purpose of the experiment, coded 15% of all experimental trials (together for Experiment 1a and Experiment 1b) randomly selected. There was a very high agreement of 98.9% between the initial and naive coders (κ = .965).

Results

Chimpanzees chose the side indicated by the experimenter in 42% of trials in the *iconic condition* and in 40% of trials in the *arbitrary condition* (see Fig. 3). These performances did not significantly differ from chance level (one-sample *t*-test: *iconic condition*, $t(10)$ = −2.06, p = .07; *arbitrary condition*: $t(10)$ = −2.20, p = .052). When considering only the trials in which participants made a choice, participants chose 49% correct in the *iconic condition*, $t(10)$ = 0.05, p = .96, and also 49% correct in the *arbitrary condition*, $t(10)$ = −0.78, p = .45. On an individual level, none of the chimpanzees performed above chance in any of the conditions (binomial test, p < .05).

Furthermore, using the GLMM, we found no significant effect of age (β = −.01, *SE* = .01, z = −1.24, p = .21), sex (β = .21, *SE* = .18, z = −1.14, p = .26), or condition (β = .10, *SE* = .18, z = 0.54, p = .59). The latter shows that chimpanzees did not perform differently in the *iconic* and *arbitrary conditions*. However, we found a significant effect for the order of conditions (β = .48, *SE* = .18, z = −2.67, p = .008). Participants who completed the *iconic condition* first showed a significantly better overall performance compared with participants who completed the *arbitrary condition* first (47% vs. 35% correct). Note that trials in which the participant did not decide for one of the sides were coded as incorrect. Participating in the *iconic condition* did not improve the comprehension of the gestures in the *arbitrary condition* but increased the number of trials in which the participant actively made a choice. As a result, the average
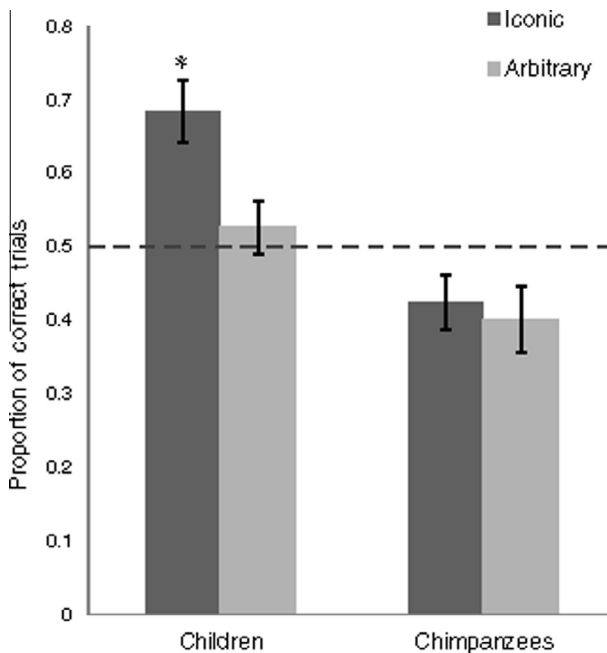

Fig. 3. Experiments 1a and 2: Mean proportions of trials in which the participant chose the side indicated by the experimenter. The dashed line represents the level expected by chance performance. Error bars represent standard errors of the mean. $^{*}p$ < .05.

performance approached a level expected by chance rather than exceeding it. When considering only the trials in which participants made a choice, participants receiving the *iconic condition* first chose correctly in 51% of the trials and participants receiving the *arbitrary condition* first did so in 47% of the trials.

Discussion

Chimpanzees showed no comprehension of informative iconic or arbitrary gestures in the current experiment. These results are in line with previous research showing that chimpanzees have difficulties with the comprehension of communicatively provided informative gestures (Herrmann & Tomasello, 2006; Tomasello, Call, & Gluckman, 1997). However, all previous studies used directional gestures such as pointing. More recent findings suggest that the performance in these tasks can be improved by methodological changes such as increasing the distance between the objects communicated about and enhancing the salience of the experimenter by placing him in a location likely to attract the apes' attention (see Mulcahy & Hedge, 2012, for a review). In the current experiment, we incorporated these suggestions and arranged the apparatus left and right of the experimenter instead of next to each other in front of him and placed the experimenter in front of the participants. Nevertheless, participants performed rather poorly in Experiment 1a, which might reflect a failure to recognize that the experimenter intended to refer to one of the locations using the gesture. Even if the participants recognized the resemblance between the gesture and the corresponding action in one of the locations, they might not have comprehended the gesture as a means used by the experimenter to provide them with information. For example, in studies using pointing gestures to inform, apes sometimes follow the point to a location, suggesting that they understand the directional nature of the gesture but do not search in this location for food, suggesting that they do not interpret the gesture as informative (Tomasello, 2008). Therefore, based on these results it is not possible to tell whether chimpanzees recognized the iconicity of the gestures or not. If chimpanzees failed to recognize the resemblance between the gesture and the action in the *iconic condition*, given more time, they should learn to associate arbitrary and iconic gestures equally fast with the corresponding location. Therefore, to investigate whether chimpanzees recognize iconicity, we conducted a second experiment.

Experiment 1b

In the second experiment, we investigated whether chimpanzees differentiate between arbitrary and iconic gestures over time. That is, we compared the number of sessions it took chimpanzees to associate one type of gesture with a certain location. Experiment 1b took place immediately after Experiment 1a in each of the two conditions. That is, chimpanzees that started with the *iconic condition* completed all experimental trials in this condition (maximum of 300) before moving on to the *arbitrary condition* and vice versa.

Method

Participants
The same 11 chimpanzees that completed Experiment 1a also participated in Experiment 1b. All of them completed both conditions.

Apparatus
Because Experiment 1b immediately followed Experiment 1a, we used the same apparatuses.

Design
Conditions and gestures were the same as in Experiment 1a.

Procedure
The procedure was the same as in Experiment 1a. Again note that participants were not differentially reinforced. That is, whenever they chose the wrong side, they were allowed to correct their

choice and retrieve the reward from the other side. The only penalty for making an incorrect decision was a short delay due to crossing over. This aspect of the procedure might have delayed the overall learning speed but should not affect the two conditions differently.

We specified a learning criterion and a maximum number of sessions to determine when to stop with one condition and move on to the next condition. Participants who performed above chance in two consecutive sessions (10 of 12 correct; binomial test: $p < .05$) or completed a maximum of 25 sessions (300 trials) moved on to the next condition. One participant received 26 sessions in the *iconic condition* because she performed above chance in the 25th session.

Coding and analyses

Coding was identical to that in Experiment 1a. In addition, we scored the number of sessions it took a participant to perform above chance in two combined sessions for each condition (performance criterion: 18 of 24 correct; binomial test: $p < .05$). If this criterion was not reached within a condition, we assigned the minimum number of sessions it would have taken to reach this criterion if testing had continued. That is, all participants who did not reach the performance criterion within 25 sessions were treated as if they reached it within 27 sessions because it would have taken them at least two more sessions to reach the criterion. Note that this is a rather conservative estimate because it underestimates the real difference between the two conditions. The differences in performance between the two conditions were not normally distributed. Therefore, we used a non-parametric Wilcoxon signed ranks test to compare the performance within participants. Considering the small sample size, exact tests instead of asymptotic tests were used (Mundry & Fischer, 1998). For reliability, see same section of Experiment 1a.

Results

Five participants reached the performance criterion (18/24) in the *iconic condition*, and one participant reached it in both conditions. None of the chimpanzees tested reached the performance criterion in only the *arbitrary condition*. To reach the criterion, chimpanzees needed on average 21.27 sessions (minimum of 13) in the *iconic condition* and 26.27 sessions (minimum of 19) in the *arbitrary condition* (see Fig. 4). We found a significant difference between the two conditions ($z = -2.20$, $p = .031$).
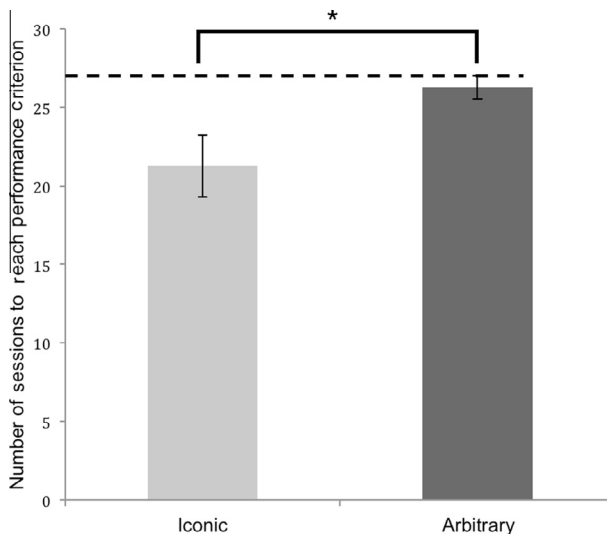

Fig. 4. Experiment 1b: Average numbers of sessions until chimpanzees reached the performance criterion (18/24 trials correct in two combined sessions). The dashed line represents the value that was assigned if the criterion was not reached within the experiment. Error bars represent standard errors of the mean. $^*p < .05$.

Chimpanzees needed significantly fewer sessions to reach the performance criterion in the *iconic condition* than in the *arbitrary condition*.

Discussion

Even though chimpanzees initially failed to comprehend informative iconic gestures, they learned to associate iconic gestures with a certain location faster than arbitrary gestures. This result suggests that they recognized the resemblance between the gestures and the corresponding actions performed at the two locations. There are at least two non-exclusive ways in which chimpanzees could have recognized the iconicity of the gestures. On the one hand, chimpanzees could have recognized that the experimenter's gesture resembles the experimenter's action in one of the two locations. Support for this interpretation comes from a recent study by Buttelmann, Carpenter, Call, and Tomasello (2013), who found that chimpanzees recognized the similarity between a previously functional action and a non-functional version of the same action performed in the same location. In their study, after having observed a human demonstrator successfully manipulating an apparatus in a certain way, chimpanzees spent more time in front of an apparatus that the demonstrator tried to operate in the previously successful way. In the current experiment, the gesture was also a non-functional version of the action, but the execution of the action and the execution of the gesture were spatially separated. On the other hand, chimpanzees could have recognized that the gesture resembles their own action in one of the two locations. To retrieve the reward, the participant and experimenter needed to operate the apparatus in the same way. Therefore, the iconic gestures not only mimed the experimenter's action but at the same time also mimed the participant's action. Earlier studies found that great apes recognized when others were imitating them and spent more time in executing the imitated behaviors (Davila-Ross et al., 2014; Haun & Call, 2008; Nielsen, Collier-Baker, Davis, & Suddendorf, 2005). Whereas imitation and action happened at the same time in these earlier studies, in the current experiment the miming of the action was temporally separated from the execution of the action. Taken together, seeing the iconic gesture might have directed participants' attention toward the corresponding apparatus rather than the other. This shift of attention might have been caused by an automatic activation of the motor program corresponding to the mimed action, potentially mediated by the mirror neuron system (Dunphy-Lelii, 2014; Heyes, 2011). Over time, participants learned that the gesture reliably predicted the experimenter's turn to the same apparatus and, therefore, chose the correct side more often. No such learning took place in the *arbitrary condition* because these gestures failed to activate the corresponding motor pattern and, therefore, also failed to allocate attention to one of the apparatuses in the first place. Interestingly, the only chimpanzee that reached the performance criterion in the *arbitrary condition* had previously been trained to imitate arbitrary bodily actions (Hribar et al., 2014).

Experiment 2

We tested children's comprehension of iconic gestures with an experimental setup that was analogous to Experiment 1a for chimpanzees. We used the same apparatus and the same gestures to ensure the comparability of the results.

Method

Participants

A total of 29 4-year-old children participated in the study (see Table S1 in the supplementary material for details). They came from a middle-sized German city and were recruited from a database of children in kindergartens whose parents volunteered for studies on child development. Some of the children had participated in other studies on cognitive development. They were seen in their regular kindergarten for two sessions that lasted approximately 20 min each and were spread over a maximum of 5 days. Among the original sample, 5 children needed to be excluded from the experiment because they were unavailable for the second session ($n = 4$) or because of experimental error ($n = 1$). We collected complete data for 24 children (12 girls, $M_{age} = 4.58$ years, range = 4.07–4.95).

Apparatus

We tested children in a familiar room in their kindergarten. The experimenter sat on a small stool placed between two wooden tables (50 × 59 × 50 cm and 42 × 54 × 50 cm; see Fig. 1). To separate the participant from the experimenter, we placed two half-moon-shaped pillows (27 × 33 × 95 cm) in front of the experimenter. The participant's starting position was marked by a piece of cardboard with footprints on it. As a reward, children received marbles that they could collect by dropping them into a Plexiglas tube, thereby creating a "Marble Tower." Therefore, a clear Plexiglas tube (height: 59 cm; holding capacity: 39 marbles), vertically glued to a Plexiglas plate, was located behind the participant's starting position.

For the *iconic condition*, we used the same apparatuses as in the chimpanzee study (Experiment 1). One apparatus (app1: "pull down") needed to be modified in order to function under the altered conditions. The top of all apparatuses involved in the study was covered with cardboard to prevent the participant from directly reaching for the marble in it. In the *iconic condition*, we bolted the apparatuses to the wooden tables flanking the experimenter's stool. In the *arbitrary condition*, we placed on the tables two identical bowls into which the experimenter dropped the marbles.

Design

We used the same conditions, gestures, and counterbalancing procedure as in Experiment 1.

Procedure

On entering the experimental room, the participant discovered three marbles on the floor, at which time the experimenter introduced the participant to the Plexiglas tube and the logic of collecting the marbles in order to build the Marble Tower. He asked the child if he or she would want to play a game in order to collect more marbles. If the participant consented to playing the game, the experimenter led him or her to the starting position and sat down on the small stool facing toward the child. On the second day, the child was asked whether he or she remembered the marble game from the day before. The experimenter again allowed the child to put three marbles into the tube, at which time he led the child to the starting position.

For the training and the test, we used the same procedure as in Experiment 1 with some minor adjustments. The training for each condition took place on the same day as the test session. Because all children followed the experimenter's turn from the first trial onward, the number of training trials was fixed to 12 for each child to ensure sufficient experience with the operation of the apparatuses. Furthermore, children received one test session with 24 trials instead of two sessions with 12 trials each.

Verbal instructions were minimal. The experimenter never named the action that was necessary to operate the apparatuses, nor did he instruct the participant verbally on how to operate the apparatuses. The instruction for the child in the beginning of each test trial was "to get the marble," followed by the corresponding gesture without highlighting the gesture as a means of communication. If the participant did not move toward one of the tables by the end of the three blocks of gestures, the experimenter turned to the indicated side for the first 3 trials of each session. During pilot sessions, some children went to the Marble Tower on the verbal instruction or asked the experimenter which marble they should get. Therefore, if children did not spontaneously choose one of the two locations after the first 3 trials, the experimenter pointed to both sides simultaneously and encouraged the child verbally to go to one of the sides without saying which side was correct. This was necessary for 7 children in the *arbitrary condition* and for 2 children in both conditions.

Coding and analysis

We used the same coding scheme as in Experiment 1. In the *iconic condition*, 1.4% of trials (8/576 trials) were coded as incorrect because participants did not make a choice. The respective number for the *arbitrary condition* was 6.1% (35/576 trials). The first author coded all trials live and again from video. A second coder, unfamiliar with the purpose of the experiment, coded 25% of all experimental trials randomly selected. Agreement between the coders was very high (98.7%, κ = .965). We adjusted the GLMM used for the chimpanzee data (see Experiment 1a) to analyze the data obtained for the children in more detail. We defined the response variable as the overall proportion of correct trials. We

included sex, age, and order of condition (*iconic* or *arbitrary condition* first) as fixed between-participant factors and included condition as a fixed within-participant factor. Furthermore, we included random effects for kindergarten and participant as well as random slopes for condition within participants.

Results

Children chose the correct side in 68% of trials in the *iconic condition* and in 53% of trials in the *arbitrary condition* (see Fig. 3). The performance in the *iconic condition* differed significantly from chance (one-sample *t*-test: *iconic condition*, $t(23) = 4.31$, $p = .0003$; *arbitrary condition*: $t(23) = 0.74$, $p = .47$). On an individual level, 5 children performed above chance (minimum of 18 of 24 correct; binomial test: $p < .05$) in the *iconic condition*, and 3 children performed above chance in both conditions. No child performed above chance in only the *arbitrary condition*.

Using the GLMM, we found that children performed significantly better in the *iconic condition* compared to the *arbitrary condition* ($\beta = .93$, $SE = .22$, $z = 4.15$, $p > .001$). Furthermore, we found an effect of order of condition ($\beta = .82$, $SE = .29$, $z = 2.87$, $p = .004$). Children who completed the *iconic condition* first showed a significantly better overall performance than children who started with the *arbitrary condition* (67% vs. 54% correct). In fact, on an individual level, all children who performed above chance in the *arbitrary condition* did so in the *iconic condition* first. Children starting with the *iconic condition* also showed an overall performance significantly better than expected by chance (one-sample *t*-test: *iconic condition* first, $t(11) = 2.79$, $p = .018$; *arbitrary condition* first, $t(11) = 1.44$, $p = .18$). Finally, we found no significant effects of age ($\beta = .08$, $SE = .55$, $z = 0.15$, $p = .88$) or sex ($\beta = -.41$, $SE = .30$, $z = -1.39$, $p = .16$).

Discussion

The results showed that 4-year-old children were able to comprehend informative iconic gestures. That is, children were able to recognize the iconic gesture as making reference to the action that was performed in one of the two locations. These results are in line with earlier studies showing comprehension of ionic gestures in younger children (Namy, 2008; Namy et al., 2004). However, the current experiment provides further important insights. Children were able to comprehend iconic gestures that referred to actions that were established as shared in a *non*-communicative functional context. During the training phase, the actions were part of a joint activity by the experimenter and the participant. During the test phase, children spontaneously recognized the similarity between the gesture and the corresponding action and used this information to infer the communicative goal of the experimenter. As for chimpanzees, the recognition of similarity might have been mediated by an automatic activation of the motor program corresponding to the mimed action (Dunphy-Lelii, 2014; Heyes, 2011). However, children also recognized the experimenter's communicative intention behind the production of the gesture.

Crucially, the iconicity was necessary to infer the referential nature of the experimenter's gesture. The results in the *arbitrary condition* show that the associative contingency between gesture and location alone was not sufficient to do so. Nevertheless, some children were able to comprehend the arbitrary gestures, but only after they showed comprehension of iconic gestures in the previous condition. This finding suggests that only iconic gestures had the potential to resolve the referential ambiguity of the experimenter's gesture and, thereby, establish a communicative interaction between the child and the experimenter that allowed the child to infer the experimenter's communicative goal. Once established, arbitrary gestures were in some cases sufficient to maintain the communicative interaction.

General discussion

In this study, we addressed the question of whether chimpanzees and children are able to comprehend novel iconic gestures in an experimental setting. We used gestures to refer to actions that played an important role in a joint activity in a specific location. The results showed that 4-year-old children,

unlike chimpanzees, spontaneously chose the correct location based on the iconicity depicted in the corresponding gesture. Neither species was able to quickly associate arbitrary gestures with one of the locations. However, over time, chimpanzees learned to use the information provided by the iconic gestures but not by the arbitrary gestures.

In contrast to chimpanzees, children showed comprehension of iconic gestures on an individual level as well as on a group level. As a result, our results confirmed earlier studies (Namy, 2008; Namy et al., 2004). In addition, our results showed that children were able to comprehend iconic gestures because they *re*-presented their referent. The results on gesture comprehension in previous studies were open to various interpretations, including associative learning and ontogenetic ritualization (Liszkowski, 2010; Tomasello, 2008). In the current study, the only way in which to immediately comprehend the iconic gesture was to recognize its resemblance with the corresponding action. Importantly, this iconic information was necessary for children to identify the communicative goal of the experimenter because they failed to comprehend arbitrary gestures in the same way even though they provided the same kind of information; that is, they reliably predicted to which side the experimenter would turn. In fact, some children readily comprehended the arbitrary gestures, but only after they had previously shown comprehension of the iconic gestures. One interpretation of this result is that the iconic information was necessary for children to initially infer that the experimenter was using the gesture to refer to one of the locations.

Theoretically, any behavioral act could be communicative as long as it offers relevant information to the receiver and it is understood as intentionally produced for that purpose (Moore, Liebal, & Tomasello, 2013; Moore, Mueller, Kaminski, & Tomasello, 2015; Sperber & Wilson, 2001). However, only if the information conveyed is relevant for the receiver will the sender's message be understood. The relevance of a signal, on the other hand, depends on the shared knowledge of the interlocutors with respect to the situation they are communicating about (Clark, 1996; Sperber & Wilson, 2001). The more knowledge is shared, the easier it is to interpret any given signal. Therefore, in novel and ambiguous situations, the signal must offer more information about the message the sender intents to convey than in highly structured situations. In the current study, the iconicity of the gestures provided that additional piece of information and helped to disambiguate the referent of the gesture (Perniss & Vigliocco, 2014). Once the child identified the gestures as making reference to one of the locations, the iconic gestures could, at least in some cases, be substituted for arbitrary gestures because the interaction was already structured in a way that allowed only limited interpretation for the new gestures. The importance of shared knowledge for the comprehension of iconic gestures in younger children is a valuable topic for future research. Furthermore, it would be interesting to see whether younger children would show a similar performance to 4-year-olds in a more child-friendly version of the setup used in the current study.

Most likely, chimpanzees did not recognize that the experimenter used the gesture to communicate relevant information to them. This interpretation has been proposed in earlier studies on chimpanzees' comprehension of informative gestures (Herrmann & Tomasello, 2006; Tomasello et al., 1997). However, chimpanzees were susceptible to the resemblance between the gesture and the corresponding action in the *iconic condition*. However, given the rather ambiguous nature of the interaction, this resemblance alone was not sufficient to infer its referential nature. If not comprehended as being communicative, iconic gestures might end up as bizarre acts of random behavior or, at best, as pretense. The latter might have led the chimpanzees to imagine something remotely related to the intended referent but did not lead them to spontaneously interpret the gesture as cooperatively intended by the experimenter to provide information that is relevant in the current context. Instead of immediately comprehending the gesture, chimpanzees gradually became better at choosing the corresponding location in the *iconic condition*. Over time, they learned that the experimenter's iconic gestures reliably predicted a turn toward the corresponding apparatus. Following Grice's (1957) terminology, the gestures came to naturally (as opposed to non-naturally) mean that the experimenter will turn to the respective side because the experimenter's communicative intention played no role in using the information that was conveyed by the gesture. Taken together with the findings of Grosse and colleagues (2015), these results suggest that the so-called iconic gestures reported in the literature (Genty & Zuberbühler, 2014; Pika & Mitani, 2006, 2009; Tanner & Byrne, 1996) are neither comprehended nor produced because they represent a desired action in the moment they occur. More

likely, they are the result of a learning and ritualization process in which the observed iconicity might have had a facilitating effect, as it did in our study.

However, it is conceivable that chimpanzees might show a more flexible comprehension of iconic or informative gestures in situations that are highly structured with respect to the potential referent and informative nature of the gesture. For example, participants could be trained to use one type of gesture to decide between two locations, and then novel iconic gestures could be introduced to refer to the same locations. Within this already established communicative interaction, chimpanzees might immediately comprehend the referential nature of the novel gestures because the training already established that the experimenter is using gestures to provide relevant information.

Our study also has implications for gestural theories of language evolution. Most important, it strengthens the idea that iconic gestures might have been used as a means of communication during a transitional period from ape-like to human communication by showing that iconic gestures are a potential source of information for chimpanzees and human children. Iconic gestures as a source of information about the communicative goal of the sender might have played an important role once early humans were able to intentionally use them for communicative purposes. Chimpanzee communicative signals, as a model for the last common ancestor, usually present detailed information about the sender's message because they have been phylo- or ontogenetically selected for this purpose (Call & Tomasello, 2007; Moore, 2013; Wheeler & Fischer, 2012). However, their meaning is restricted to a very limited context. Iconic gestures, although more ambiguous and cognitively more demanding than ritualized signals, can be used more flexibly and still provide rich evidence for a sender's message. Therefore, they seem especially suitable as an adjustable means of communication during the shift from signal-based to symbol-based communication.

Acknowledgments

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.jecp.2015.09.001.

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