Ethology

Push or Pull: Imitation vs. Emulation in Great Apes and Human Children

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Abstract

All four species of great apes and young human children (12–24 mo of age) were administered an imitation task designed to distinguish between results learning (emulation) and action learning (imitation). Some subjects were exposed to a demonstrator either pushing or pulling a door to open a box, whereas others simply saw the door of the box opening itself in one of the two directions (the ghost control). Most of the apes successfully opened the box in both experimental conditions, as well as in a baseline condition, but without being influenced either by the demonstrator's actions or by the door's motions. In contrast, human children over 12 mo of age were influenced by the demonstration: the 18-mo-olds were influenced by the demonstrator's actions, and the 24-mo-olds were influenced both by the demonstrator's actions and by the door's motions in the ghost control. These results provide support for the hypothesis that human children have a greater propensity than great apes for focusing either on a demonstrator's action or on the result of their action, as needed, in social learning situations.

Introduction

Whether apes 'ape' (Tomasello 1996) as a means for problem-solving remains a controversial issue. While some studies seemingly show that apes copy novel behavioral variants of demonstrators (Whiten et al. 1996; Whiten 1998; Stoinski et al. 2001; Stoinski & Whiten 2003; but see Custance et al. 2001), others find no such evidence (Nagell et al. 1993; Call & Tomasello 1994, 1995; Myowa-Yamakoshi & Matsuzawa 1999; Custance et al. 2001; Call et al. 2005). The discrepancy between those sets of studies can partly be attributed to the type of information that apes may gather from demonstrators. Call & Carpenter (2001), see also Carpenter & Call 2002) noted that observers can witness at least two types of information from the behavior of a demonstrator: actions and results. Actions represent the motor patterns used by the demonstrator to achieve his/her goal whereas results are the changes produced in the environment as a consequence of the demonstrator's actions. These environmental results can be further sub-divided into: endstates, affordances of objects and object movements. Hence, an observer may reproduce a demonstrated result by reproducing endstates, by learning about and reproducing affordances, or by reenacting object movements (for an overview see Huang & Charman 2005). Whiten et al. (1996) have argued that apes copied actions in the artificial fruit task, while others have suggested that apes have a greater tendency to copy results, not actions (e.g. Call & Carpenter 2003).

The distinction between copying actions and results is important because all previous great ape studies reporting evidence of imitation in problem solving situations (Whiten et al. 1996; Whiten 1998; Stoinski et al. 2001; Stoinski & Whiten 2003) have not distinguished the influence of the demonstrator's actions from the results produced by those actions (Tomasello 1996; Heyes & Ray 2000). For instance, in the artificial fruit task used by Whiten and colleagues, when a demonstrator removes a bolt by twisting, the bolt also moves in a particular direction, in this case toward the body of the demonstrator.

Similarly, when a demonstrator pokes the bolt, the bolt also moves away from the demonstrator. Additionally, certain results are more likely to be associated with certain actions than with others. Thus, as the bolts fit tightly into the holes, twisting the bolt is a more natural action if one is to remove the bolt in a pulling motion, whereas poking the bolt is more natural if one is to push the bolt out. If one is focused on the result (e.g. 'bolt away from the subject'), one is also more likely to use a poking action than a twisting action. Conversely, if one is focused on bringing the bolt 'toward the subject' one is also more likely to use the twisting action. It is therefore unclear whether this confound has led to a misinterpretation of the data as evidence that subjects are attending to and copying actions, rather than results.

Hence, we believe that it is crucial to disentangle the use of the actions and results produced by others, as both are potential sources of information in problem solving situations. Call & Tomasello (1995) used an opaque box that would deliver food pieces if a protruding stick was moved in a certain way. Hence, the causal relationship between the movements of the stick and the release of food was blocked from the observer's view. In order to gain the food reward, observers needed to reproduce either the exact actions involving the stick, or the movements of the stick. Call and Tomasello did not find any copying in this task. Recently, Horner & Whiten (2005) tried a seemingly related method on chimpanzees. They used a box with two holes, only one of which led to a reward that could be retrieved with the help of a stick. During the demonstration, a human demonstrator inserted a stick into both holes. Later, observer apes would also insert the stick into both holes, significantly more often if they had seen demonstrations with an opaque box. On the contrary, when demonstrations were given using a clear box, the apes primarily inserted the stick into the baited hole. Also the study was comparable with the artificial fruit studies mentioned above, as the apes produced some target behavior on an extra door defence (that was either slid open or pulled open during demonstrations). The authors concluded that the apes imitated in the opaque box condition, but emulated in the clear box condition and that the latter was due to the causal knowledge that the apes gained by seeing 'into' the clear box (which, just like the opaque box, had a barrier behind the 'non-baited' hole). However, we cannot see why Horner and Whiten's findings necessarily resulted from imitation. The copying of the door defence (slide vs. pull) information suffers from the same problem as the artificial fruit studies, by mixing action with results information. Concerning the stick-use, the chimpanzees acted differently in the clear condition vs. the opaque condition. This simply may have resulted from causal information overriding local enhancement effects (Thorpe 1963) in the clear-box condition. The problem is that the chimpanzees did not learn a new skill in the stick-task (they were supposedly adept at using sticks to probe holes), they were only shown *where* to probe (local enhancement).

What is missing from the ape-literature are studies that withhold action-information from the observers to see how they perform. Note that apes can be trained to imitate novel actions on command (e.g. Hayes & Hayes 1952; Custance et al. 1995; Miles et al. 1996; Call 2001). So the question here is not whether apes are *capable* of copying novel actions, but whether they spontaneously do so to solve problems. Recently, Call et al. (2005) reported that chimpanzees reproduced an outcome without witnessing its transformation. If chimpanzees found a broken tube in its center as opposed to a tube with its lids off, they were more likely to break an intact tube than to remove the lids. Conversely, those chimpanzees that found the tube with the lids off were more likely to remove its lids than to break the tube. However, nothing is known about how apes use information about the online transformation of objects, particularly in comparison with when a demonstrator produces the same information.

The aim of our study was to test whether ape observers as well as human children would benefit from observing a conspecific demonstrator and if so, whether showing the transformations experienced by the apparatus in the absence of the demonstrator's actions would have the same effect on the observer's responses (a form of emulation called 'object movement re-enactment' (Custance et al. 1999; Whiten et al. 2004, see also above). To counter the critique of the task being too demanding and ecologically irrelevant, we borrowed the task that Bugnyar & Huber (1997) had previously used with common marmosets, (*Callithrix jacchus*). It consisted of a box with food inside that could be accessed by pulling or pushing a swing door located on one of the sides of the box. In that study the level of difficulty was high for the marmosets (T. Bugnyar pers. comm. 2003), so it seemed to be a good starting point for great apes. Moreover, the method looked promising, since in Bugnyar & Huber's (1997) study marmosets indeed showed some signs of copying actions on a fine-grained level, but see Caldwell & Whiten (2004) for different results with a different paradigm. We presented different groups of subjects with the three conditions. In the full-model condition, the ape demonstrators pushed or pulled to open a door. In the ghost condition, we moved the door in- or outward with the help of nylon strings (Fawcett et al. 2002 (see also Heyes et al. 1994)). In the baseline condition, we provided no information on how to open the door to the subjects.

Methods

Subjects

We tested three subject groups: chimpanzees (study 1), non-human great apes (study 2), and human children (study 3). Thirty chimpanzees (*Pan troglodytes*) belonging to two different groups participated in study 1. They were housed at the Yerkes Primate Center Field Station in Lawrenceville (GA), USA. We tested 14 adults (older than 15 yr), 10 adolescents (between 15 and 8 yr) and six juveniles (younger than 8). There were 10 males and 20 females. Ten chimpanzees were human-reared, 16 were mother-reared and four had unknown rearing histories. Two subjects had participated in a previous study on social learning in 1990–1991. Eleven other subjects had participated in a social learning study in 1994–1995. Both groups were housed in an indoor–outdoor area equipped with climbing structures and various fixed and movable objects scattered throughout the enclosure. They were fed a diet of fruit and vegetables twice a day and they were neither food nor water deprived during testing.

Thirty-two great apes participated in study 2 (14 chimpanzees; four bonobos, *Pan paniscus*; 6 gorillas, *Gorilla gorilla gorilla*; 8 orangutans, *Pongo pygmaeus abelii*). There were 16 adults (10 yr and older), 9 adolescents (6–9) and 7 juveniles (five and younger). There were 11 males and 21 females. All species were group-housed at the Wolfgang Köhler Research Center, Leipzig Zoo, Germany. They had access to large outdoor and indoor enclosures containing climbing structures and natural vegetation. Testing took place in observation rooms while subjects were separated from the rest of their group. Prior to this study all apes had participated in various cognitive experiments, but none on social learning. Moreover, to the best of our knowledge, none of the study animals had ever before manipulated apparatus comparable to the one in this study. Subjects were fed a diet of fruit and vegetables and were not food- or water-deprived during testing.

For study 3, we recruited eighty-one 12-mo-old infants (±2 wk), seventy 18-mo-old infants (±4 wk) and fifty 24-mo-old infants (±4 wk). All participants were typically developing infants from the Leipzig area (Germany). We tested equal numbers of girls and boys. We excluded a number of infants for the following reasons: being too old, acting on the door after one demonstration, accidentally kicking the door with the foot, or parents influencing the children's responses. For the 12-mo-olds, this resulted in four exclusions in the full-model condition, two exclusions in the ghost condition and one exclusion in the baseline. For the 18-mo-olds, it resulted in eight exclusions in the full-model condition and one exclusion in the ghost condition. Following these exclusions, 74, 61, and fifty 12-, 18-, and 24-mo-old children, respectively, remained in our sample.

Apparatus

Following Bugnyar & Huber (1997), we constructed wooden boxes for all three studies. We used a similar box in each of the three studies, with minor variations for each subject group. In study 1, the box (20-cm wide; 15-cm deep; 15-cm high) had an opaque swinging door whose hinges allowed for an outward (PULL) and an inward (PUSH) motion. A metal ring mounted near the bottom of the door allowed pulling actions. No special devices were installed to facilitate pushing actions because this could be accomplished by simply moving the door inward. The door was not kept in its resting (closed) position by any device other than its own weight. Therefore, the door could easily be opened by pulling or pushing actions with minimum effort. A hole on the top of the box allowed the experimenter to bait the box with banana or apple slices during the experiment in full sight of the animals. The apparatus was mounted inside the cage and rebaited during testing by inserting rewards through the fence and into the hole. For the ghost control condition, two inconspicuous nylon-strings were attached to the box so that the door could be opened by the experimenter via a pull or push movement.

In study 2, we used a slightly larger wooden box (26-cm wide, 18-cm deep and 16.5-cm high) that had several improvements to facilitate use by the apes. First, we replaced the door ring used in study 1 with a protruding screw to prevent subjects from inserting their fingers in the ring and accidentally moving the door. The screw allowed apes to grasp the door thus facilitating the execution of pulling motions. Secondly, to prevent apes from getting their hands stuck under the door once they pushed it in to get the food, we attached a weighted wire to the back of the box that kept the door from swinging back out once it was opened. Thirdly, a small device was attached to the bottom of the door preventing it from opening when the box was accidentally touched (the force needed to open the door was approx. 30 N for the push-motion and approx. 20 N for pull-motion). Fourthly, the entire box could be moved back and forth within a transparent Plexiglas tunnel that was mounted on a table and attached to a Plexiglas research panel on the front of the cage. This latter feature allowed us to move the box within or out of reach of the subject by pushing or pulling a metal rod attached to the back of the box. Moreover, a Plexiglas guillotine-door separated the tunnel from the research panel and allowed the experimenter to control the exact moment when apes accessed the box. The research panel on the front of the cage had a hole large enough to allow the apes free access to the box door. Finally, the apparatus was mounted on the experimental cage so that it could be seen from an adjacent cage through a window (see Fig. 1).

For the children tested in study 3, we used a box similar to those used with the ape groups. This box (30 cm × 21 cm × 19 cm) was painted in colors with a rectangular opening on the top (12 cm × 6.5 cm), through which the box could be baited with one of five toys (a rattle, a red car, a yellow crane, a green finger-toy and a red finger-puppet). Nylon strings were used to open the door in the ghost condition. One of the strings was attached to the back of the door from the inside while the other ran through a straw that was glued on top of the box. Moreover, in the ghost control condition, a black curtain partly covered the back part of the box thus concealing the second experimenter who operated the strings.

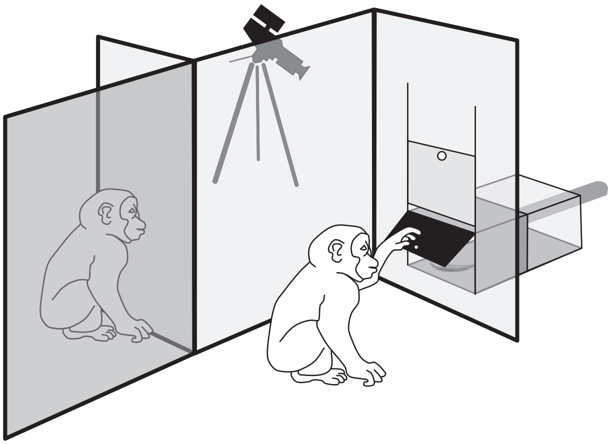

Fig. 1: Sketch of the full-model condition (here 'pull') in study 2

Procedure

The procedure was matched as closely as possible across the ape and children studies. In study 1, the chimpanzees were distributed among three conditions counterbalanced as much as possible for age and sex. Two-fifths were distributed to the full-model condition, two-fifths to the ghost control condition, and one-fifth to baseline.

Full Model (N = 12)

Conspecific demonstrators showed observers the opening of the box in their trained style. Observers were required to watch at least one full demonstration (i.e. from first touch of the door until hand insertion) before they were allowed to manipulate the apparatus. Upon fulfilling this requirement, demonstrators left the room, observers were given access to the apparatus and the testing began. Half of the subjects observed the PULL action, while the other half observed the PUSH action. In addition, half of the subjects observed the demonstrator get food from the box, while the other half only saw the demonstrator open the box without getting a reward.

Ghost (N = 12)

The experimenter swung the door in or out by pulling on nylon strings attached to the box. The inward and outward motion corresponded to the PUSH and PULL action respectively. The experimenter ensured that he used the nylon-strings as inconspicuously as possible, out of sight of the apes. The requirements regarding the observation of demonstrated information were identical to the full-model condition (i.e. witnessing one demonstration from beginning to end).

Baseline (N = 6)

Subjects were given access to the apparatus without prior information on how to open it. Some dominant females in this condition later served as demonstrators for the full-model condition.

All subjects were shown the baiting of the box prior to testing and they were encouraged to approach the box, either vocally ('come here'), or by gentle knocking on the box/fence. Subjects received one 10-min trial.

The procedure of study 2 (non-human apes) followed closely that of study 1 with the exceptions noted below. Subjects from the four species were distributed so that they were counterbalanced as much as possible for age and sex among the same three conditions of study 1. Twelve, 12 and eight subjects were assigned to the full-model, ghost control, and baseline conditions, respectively. In both information conditions, observers were required to watch a demonstration a minimum of six times (and a maximum of 10 times) before they were allowed to manipulate the apparatus. Unlike study 1, however, if an ape had seen only part of one demonstration-routine (touching/opening the box and insertion of the hand) it was counted as half a demonstration. We adopted this procedure to provide the apes with high-quality information, whilst still having demonstrations as standardized as possible. Still, all subjects had to see at least one *complete* demonstration from beginning until end (as part of the requirement to see at least six demonstrations). Another difference with study 1 was that subjects always witnessed the ape demonstrator getting food from the box. Each ape received one 5-min trial. Demonstrator training was identical to that of study 1. To enhance comparability across species, we only used adult females as demonstrators, with the exception of the bonobos whose group lacked an adult female.

In study 3, the procedure followed the ape procedures from studies 1 and 2 as closely as possible. However, some differences were necessary when testing the children. For example, prior to testing, all children underwent a warm-up period in which they played with various toys, different to those used in the actual experiment. Testing only began once the children were comfortable with the testing situation. For the 12-mo-old children and four of the 18-mo-olds who were tested at the Max Planck Institute for Evolutionary Anthropology child laboratory, the warm-up took place in a room adjacent to the testing room. The remaining 18-mo-olds and 24-mo-olds received both the warm-up and the test in the same room at their local kindergartens. All children were tested with their parent present except 24 mo-olds. In the test, older children sat on a carpeted floor; 12 mo-olds sat on their parents' lap in front of a table. Parents were instructed to act neutrally during the test, and to ignore requests for help from their children. Prior to the test, the 18 mo-olds were administered an unrelated task on altruism.

Children of each age group were randomly distributed into the three conditions (full-model, ghost, and baseline) with equal numbers of boys and girls in each condition. During the test, the experimenter baited the box by getting the child's attention, dropping a toy through the top hole in the box and covering this hole with her hand. Then the experimenter acted as a demonstrator by engaging in one of the three conditions. In the full-model condition, the experimenter opened the box by either pulling or pushing the door with her hand while in the ghost condition a second experimenter concealed behind a black curtain pulled or pushed the door open with the help of the nylon strings. In both test conditions, the experimenter took the toy out of the box after each demonstration. Finally, in the baseline condition, children were given no information about how to open the box. The experimenter then said something inviting like, 'Now you get the toy yourself, yes?' without any reference to a particular method the child should use. Sometimes, the children were reluctant to participate so a second toy was inserted through the top hole. Each child received two to three demonstrations of toy retrieval except in the baseline, before they were allowed to act on the box themselves. Children who acted on the door before they received the second demonstration were excluded from the analysis.

Ape Demonstrator Training

In both study 1 and study 2, we selected two dominant females (except for the case of the bonobos) from the baseline group to serve as demonstrators for the full-model condition. Upon completion of their baseline tests, we trained them in the target actions by either reinforcing the method that they had previously used, or by blocking the apparatus so that they were prevented from using their preferred action until they consistently developed the appropriate technique. In both cases, the ape demonstrators developed the appropriate techniques, which became habitual after a few sessions.

Data Analysis and Scoring

All trials were videotaped. We analyzed two dependent variables: (1) whether subjects successfully opened the box and got the food, and (2) whether their opening technique (pull or push) matched what they had witnessed. We scored a pull action when the subjects displaced the door towards themselves and a push action when the subjects displaced the door into the box. However, actions resulting from the accidental displacement of the box door (e.g. if the box door was accidentally moved whilst inserting a finger into the ring) were excluded from the count. A second coder coded all trials from the tapes to assess inter-observer reliability.

In study 1, five subjects that failed to open the box were excluded from the analyses on the matching measure (see Table 1). We excluded two subjects (one in each information condition) whose demonstrator both pulled and pushed the door. Agreement between the two coders for the remaining subjects was perfect (Cohen's kappa = 1.0). We analyzed each of the two dependent variables as a function of experimental condition. We collapsed the independent variable, 'food presence during demonstration' because preliminary analyses showed that it had no effect on the dependent variables (Matching was six out of nine in the food conditions and four out of nine in the non-food conditions). This was considered a sensible strategy because of our modest sample size and the nominal nature of our dependent variables. When the frequency distributions did not meet the requirements for the use of the chi-square test, we collapsed the data into 2 × 2 tables and conducted Fisher's exact test for independent samples. All tests were two-tailed.

In study 2, we scored and analyzed the data in the same way as in study 1. Scoring actions (pull vs. push) was easier than in study 1 because the device attached to the bottom of the door almost completely eliminated the accidental movement of the door. We considered actions with and without outcomes since some animals failed to apply enough force to displace the door and the inter-observer reliability based on a second observer scoring all trials was excellent (Cohen's kappa = 0.85).

In study 3, we scored and analyzed the data in the same way as in the earlier studies, but also analyzed the dependent variables as a function of age. A second observer coded 20% of the trials that were randomly selected from each age class. Inter-observer reliability was perfect (Cohen's kappa = 1.0).

Table 1: Number of subjects who opened the door across conditions

	Pass	Fail
Full demo	10	1
Ghost	8	3
Baseline	5	1
Total	23	5

Results

Success

Table 1 presents the number of successful chimpanzee subjects from study 1 as a function of condition. Eighty-two percent of the subjects successfully opened the door and got the food. There were no significant differences between information conditions (Fisher test: p = 0.57) or between the information conditions combined and the baseline (Fisher test: p = 1.0). In baseline, four of five subjects pulled the door.

Table 2 presents the number of successful subjects in each condition from study 2 (non-human apes). Eighty-eight percent of the subjects opened the door. However, there were no significant differences between information conditions (Fisher test: p = 1.0) or between the information conditions combined and the baseline (Fisher test: p = 1.0). Additionally, there were no significant differences across species (Fisher test: ns in all cases).

Table 3 shows the number of successful children from study 3 as a function of condition and age. Eighty-four percent of the subjects successfully opened the door and retrieved the toy. There were no significant differences across conditions [χ^2 (2) = 0.08, p = 0.96] or age groups [χ^2 (2) = 4.08, p = 0.13].

Table 2: Number of subjects who opened or failed to open the door across species and conditions

	Chimpanzees		Bonobos		Gorillas		Orangutans		Total	
	Pass	Fail	Pass	Fail	Pass	Fail	Pass	Fail	Pass	Fail
Full demo	4	1	2	0	1	1	3	0	10	2
Ghost	6	0	1	0	2	0	2	1	11	1
Baseline	2	1	1	0	2	0	2	0	7	1
Total	12	2	4	0	5	1	7	1	28	4

Table 3: Number of subjects who opened the door across age and conditions (including failed attempts)

	12-mo-old		18-mo-old		24-mo-old		Total	
	Pass	Fail	Pass	Fail	Pass	Fail	Pass	Fail
Full demo	24	9	21	3	19	1	64	13
Ghost	24	5	20	3	17	3	61	11
Baseline	10	2	10	4	10	0	30	6
Total	58	16	51	10	46	4	155	30

Matches

Table 4 presents the number of chimpanzees from study 1 that matched or mismatched the observed door action in the information conditions. There were no significant differences between the Full demonstration and ghost conditions (Fisher test: $p = 1.0$).

Although subjects across conditions were significantly more likely to pull (87%) than to push (13%) the door (χ^2 (1) = 12.56, $p < 0.001$), there were no significant differences between the baseline and the full demonstration (Fisher test: $p = 1.0$) or the ghost condition (Fisher test: $p = 0.36$).

In study 2, great apes showed no significant differences between conditions (Fisher test: $p = 1.0$) and no differences across species (Fisher test: ns in all cases). Table 5 presents the number of subjects that matched or mismatched the observed door action in the information conditions.

However, there were significant differences across species on their door opening styles. Chimpanzees were more likely to push (91.7%) than the other apes species (37.5%), (X^2 (1) = 7.631; $p = 0.014$). Nevertheless, there were no significant differences between the baseline and the information conditions combined for chimpanzees (Fisher test: $p = 1.0$) or the other apes (Fisher test: $p = 0.093$).

In contrast to the ape data from studies 1 and 2, children in study 3 did show matching behavior. Older children matched the observed movement more often than younger ones in both the full demo (Fisher test: $p = 0.012$) and ghost conditions (χ^2 (2) = 8.99, $p = 0.011$). Specifically, 24-mo-olds matched in both the full demo and ghost conditions (18:1/16:1, binomial test: $p < 0.001$ in both cases), whereas 12-mo-old children did not match in either condition (15:9/12:12, binomial test: $p > 0.30$ in both cases). Eighteen-month-old children matched in the full-model (18:3, binomial test: $p < 0.001$) but not in the ghost condition (12:8, binomial test: $p = 0.50$). Table 6 presents the number of children who matched or mismatched the observed door movement in the information conditions as a function of age.

Table 4: Number of subjects who matched the door's movement across conditions

	Match	Mismatch
Full demo	6	4
Ghost	4	4
Total	10	8

Table 5: Number of subjects who matched the door's movement across species and conditions (including failed attempts)

	Chimpanzees		Bonobos		Gorillas		Orangutans		Total	
	Yes	No	Yes	No	Yes	No	yes	No	Yes	No
Full demo	3	1	0	2	1	0	2	1	6	4
Ghost	3	3	0	1	1	1	2	0	6	5
Total	6	4	0	3	2	1	4	1	12	9

Table 6: Number of subjects who matched the door's movement across conditions and age groups (including failed attempts)

	12-mo-old		18-mo-old		24-mo-old		Total	
	Yes	No	Yes	No	Yes	No	Yes	No
Full demo	15	9	18	3	18	1	51	13
Ghost	12	12	12	8	16	1	40	21
Total	27	21	30	11	34	2	91	34

Children in the baseline condition significantly preferred to pull (81.3%) rather than push (18.7%) the door, [χ^2 (1) = 12.5, $p < 0.001$] and this outcome was independent of age (Fisher test: $p = 1.0$). Specifically, eight out of ten 18- and 24-mo-old children pulled the door. Similarly, ten of the twelve 12-mo-old-children pulled the door. This overall preference for pulling was significantly reduced to 58.5% in the conditions where a door push was demonstrated (Fisher test: $p = 0.029$) and increased to 90.5% in the conditions where a door pull was demonstrated. This latter increase did not significantly differ from the baseline level (Fisher test: $p = 0.21$).

Discussion

Both apes (studies 1 and 2) and children (study 3) solved the task at high levels regardless of whether they received information on how to open the box, so this information conferred no advantage to either species. However, 18- and 24-mo-old children differed from the apes and 12-mo-old children in that they copied the demonstrator's door opening strategy. Previous studies of social learning did not distinguish copying actions from copying results, so we examined whether great apes and human children would also copy results alone (without a demonstrator). We found no evidence that apes copied the information that they had observed; neither the observation of results nor results with actions changed the apes' behavior. This is consistent with past studies showing that children are more adept than apes at matching the actions of others. Older children in our study also copied the door's motion in the absence of the demonstrator, using the necessary actions in order to produce the observed effect. Although our study does not clarify whether observing results alone may account for matching behavior in great apes, it corroborates past experiments finding little or no evidence of imitation (Nagell et al. 1993; Call & Tomasello 1994, 1995; Myowa-Yamakoshi & Matsuzawa 1999; Custance et al. 2001; Call et al. 2005).

In addition to the diffences in action-copying between apes and humans, we also found a developmental increase in action copying in infants. 18-mo-olds matched only the full-demo condition, and younger infants did not match the direction of movement in any condition. This increase in the ability to copy object movement information confirms previous studies (Bellagamba & Tomasello 1999; Call et al. 2005, but see Huang et al. 2002) and also corroborates findings that children younger than our sample (3 to 6-mo-olds) reproduce simple object affordances (Barr et al. 1996, 2005; Learmonth et al. 2004; Campanella & Rovee-Collier 2005; Kressley-Mba et al. 2005).

Although one interpretation of our data suggests that actions may take precedence over results during human development (Call & Carpenter 2001), the current findings may also reflect the fact that children in the full-model condition received information about both actions and results, whereas in the ghost condition they only witnessed information regarding results. Future studies could present actions without results. This would be sufficient information for the children (e.g., Meltzoff 1995; Bellagamba & Tomasello 1999; Call et al. 2005) and would entail observing a demonstrator trying to pull the door but failing to produce any observable result. Nevertheless, our current results with 24-mo-old children question the idea that emulation tasks may be too complex for human infants (Want & Harris 2002; Byrne 2003). It is still possible that end-state information is less likely to foster learning than object transformation information. Indeed, there are several studies suggesting that this may be the case (end state: Bellagamba & Tomasello 1999; Call et al. 2005; object transformation: Huang et al. 2002; Thompson & Russell 2004; Huang & Charman 2005; this study).

Although there are alternative explanations for why apes and younger children failed to copy, we find these explanations to be unlikely. For example, apes and younger children may have known how to open the box on their own. Consequently, they may have ignored the social information provided. Although this may account for the high success rates across conditions, it does not explain the apes and young children's failure to match. Older children also have found the task easy, and they nonetheless copied the strategy of a stranger. Another possibility is that the apes and younger children groups did not utilize the information provided because they had a pre-existing bias for one of the actions. That is, the chimpanzees' strong tendency to produce one action, combined with a potential ceiling effect in all species, may make the push-pull task unsuitable to test social learning in apes. However, older children in study 3 had a high success rate as well as an action-preference (pulling the door) in the absence of demonstration, much like the apes. Indeed, 24-mo-old infants matched the door's movement in both information conditions. Nonetheless, they still copied the information that they had observed, even when 'given by a ghost'. Individual older children who showed a strong bias for one of the actions (see baseline data) also copied the observed result. Thus, action preferences may have precluded copying in the apes, but it did not for human children. As we tested 42 chimpanzees, a sample comparable with that of each group of human children, the apes' failure to match was not because of small sample size.

We also think that it is unlikely that necessary methodological differences between the ape and children studies can account for our results. These differences include: (1) apes watched familiar conspecifics, but children watched unfamiliar humans. (2) Demonstrators for apes left the room following the demonstration, but not for children. (3) In the ghost control condition, no conspecific was present for the apes, while 12- and 18-mo-olds had a parent present. (4) Apes may have seen a different number of demonstrations than children depending on their attention level. These differences should have either improved or not affected the apes' performance, so they probably do not account for our pattern of results.

A final possibility is that additional trials might have increased the apes' likelihood of copying (Custance et al. 2001). However, we were most interested in what subjects did on their first attempt, prior to any individual experience with the box, because data derived from first acts is considered to be maximally informative regarding copying effects (Huang & Charman 2005). Although the apes had previously pushed and pulled objects, they had no experience with hinged doors or puzzle boxes in general. Our boxes, therefore, represent a truly novel behavior, unlike the sticks used in Horner & Whiten's (2005) study. As argued above, we believe that poking sticks into holes is a very natural behavior for chimpanzees, and may have been a relevant part of the apes' environment of evolutionary adaptedness. Nonetheless, two lines of evidence suggest that additional demonstrations would not have altered our results. First, our observations of the trained ape demonstrators indicated that these individuals adopted a particular strategy within a few trials and rarely altered it. Secondly, past studies have revealed matching without such repetition: In the artificial fruit studies, for example, successful matching occurs following only three to five demonstrations (e.g. Whiten et al. 1996).

Our study, therefore, failed to produce robust evidence that apes copy actions. Although some researchers claim that apes readily copy others (e.g. de Waal 2001), other studies indicate that this is not the case (Nagell et al. 1993; Call & Tomasello 1994, 1995; Myowa-Yamakoshi & Matsuzawa 1999; Custance et al. 2001; Call et al. 2005). Those studies that find some action copying have not examined whether subjects copied results rather than the actions that produced those results (Tomasello et al. 1987). This does not mean that apes are *unable* to copy actions. On the contrary, several studies show that apes can be trained to imitate actions on command (e.g. Hayes & Hayes 1952; Custance et al. 1995; Miles et al. 1996; Call 2001), and evidence suggests that chimpanzees are sensitive to when others copy their behavior (Nielsen et al. 2005). Moreover, some enculturated apes seem more attuned to actions than results (Tomasello et al. 1993; Bjorklund et al. 2002). However, non-enculturated apes do not appear to routinely solve problems by copying the actions of demonstrators – a strategy that human children and possibly birds, use more frequently (e.g., Nagell et al. 1993; Call & Tomasello 1995; Atkins & Zentall 1996; Bellagamba & Tomasello 1999; Klein & Zentall 2003). While recent evidence indicates that adult humans copy actions less than children (Horowitz 2003) the tested adults clearly copied *some* actions.

What types of information do apes and young children extract when they watch demonstrations of problem solving? One of the most challenging tasks for future studies is to create tasks with an appropriate level of difficulty to answer this question. An easy task may not engage the subjects' social learning skills, because those skills only appear in challenging situations that surpass the individual's own problem-solving abilities. Conversely, difficult tasks may be too complex to imitate, as Whiten et al. (1996) argued with respect to studies reporting emulation. Call & Tomasello (1995) countered this critique by showing that orang-utans, unlike human children, could not solve a simple reward-box task that required successful action-copying.

Horner & Whiten (2005) suggested that when chimpanzees understand the causal structure of a task they use emulation; whereas, when they lack this understanding they may engage in imitation. Causal understanding may therefore be a main factor determining when imitation occurs. As such, future research should more closely examine the relationship between social learning and causal understanding.

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