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Chimpanzees, *Pan troglodytes*, recognize successful actions, but fail to imitate them

David Buttelmann [a,b,*], Malinda Carpenter [b], Josep Call [b], Michael Tomasello [b]

[a] Research Group 'Kleinkindforschung in Thüringen', University of Erfurt, Germany
[b] Department of Developmental and Comparative Psychology, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany

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Cultural transmission, by definition, involves some form of social learning. Chimpanzees and other nonhuman primates clearly engage in some forms of social learning enabling some types of cultural transmission, but there is controversy about whether they copy the actual bodily actions of demonstrators. In this study chimpanzees recognized when a human actor was using particular bodily actions that had led to successful problem solving in the past. But then when it was their turn to solve the problem, they did not reproduce the human actor's bodily actions themselves, even though they were clearly capable of producing the movements. These results help us identify more precisely key reasons for the differences in the social learning and cultural transmission of humans and other primates.

Learning by observing others interacting with the environment enables organisms to acquire important information without engaging in the slower and less efficient process of trial-and-error learning (Laland 2004; Boyd et al. 2011). There are many different forms of social learning, mainly differing in terms of exactly what is learned or replicated (e.g. the action, the result of the action, etc.), practised by many different species, from fish to birds to primates (see Galef & Laland 2005). Much of human cultural behaviour is socially acquired by imitation, that is, the copying of the precise bodily movements of others (Tomasello 1999; see Caldwell et al. 2012 for an alternative view). Although some researchers consider human and chimpanzee cultures to be homologous (Whiten et al. 2003, 2005; Horner et al. 2006), it is unclear whether action copying plays an important role in chimpanzee social learning. Indeed, most of the examples of chimpanzee cultural behaviour involve some form of tool use, whose acquisition may be based on copying the effect of the tool on the environment (emulation learning) rather than the actual bodily actions of the tool user (Tomasello 1996). Even studies suggesting that chimpanzees copy bodily actions (Whiten et al. 2005; Hopper et al. 2008) have different interpretations (Tennie et al. 2009), and have not been replicated in different chimpanzee groups (Hopper et al. 2007) or in different tasks (Tennie et al. 2006). When chimpanzees and human children are directly compared in tool use situations, children copy bodily actions much more often than chimpanzees (Nagell et al. 1993; Horner & Whiten 2005; Dean et al. 2012). Furthermore, in more social instrumental situations, that is, communicative situations in which bodily gestures are used for social ends, both observational and experimental research has found little evidence of chimpanzees acquiring new gestures by copying them (Tomasello et al. 1997; Tennie et al. 2012), although there is positive evidence for this in even very young human children (e.g. Williamson et al. 2013).

However, after extensive training chimpanzees can learn to copy some bodily actions (Hayes & Hayes 1952; Custance et al. 1995). Moreover, some chimpanzees recognize when a human is copying their actions as well (Nielsen et al. 2005; Haun & Call 2008; for imitation recognition in monkeys see Paukner et al. 2005, 2009). So the question arises why chimpanzees do not copy the actions of others more readily in instrumental situations such as tool use and communicative gestures. Perhaps in instrumental (problem-solving) situations, they simply do not attend at all to the actions of others (they need training or special situations such as someone copying them to attend to actions). While many animals can pay attention to even very subtle behavioural cues (see e.g. Pfungst

* Correspondence: D. Buttelmann, Research Group 'Kleinkindforschung in Thüringen', University of Erfurt, Nordhaeuser Strasse 63, D-99089 Erfurt, Germany.
E-mail address: david.buttelmann@uni-erfurt.de (D. Buttelmann).

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1911), in some circumstances chimpanzees apparently find it very difficult to use information from human actions to obtain rewards (e.g. Tomasello et al. 1997; Itakura et al. 1999), so this is a real possibility. Alternatively, they may attend to the actions, but cannot or do not translate them into their own actions. Previous research cannot determine which of these hypotheses might be correct because the studies in which chimpanzees were trained to mimic bodily actions involved different individuals and different actions from the studies in which they failed to copy actions in instrumental contexts.

To investigate these hypotheses directly, we designed the current study with three aims in mind. First, we investigated whether chimpanzees attend to the actions of humans closely enough to recognize these actions and respond appropriately to them later (recognition test). Second, we investigated whether, when subsequently given the opportunity to solve the same problem themselves, individuals who attended to the actions would then use that information to imitate the actions (imitation test). Finally, we additionally investigated whether prior self-experience on the task would increase individuals' ability to recognize the human's actions in the first place (self-experience condition).

METHODS

Participants

Eighteen chimpanzees (mean age = 18.1 years, range 3.8–33.0 years, 12 females, six males) participated in this study. Additionally, two female chimpanzees began the information phase (see below) but were not tested because they were unwilling to approach the apparatuses. The apes were housed socially in two groups of at least six individuals at the Wolfgang Köhler Primate Research Center in the Leipzig Zoo, Germany. Each group had access to an indoor area (230 and 430 m^2) and an outdoor area (1680 and 4000 m^2) furnished with various climbing structures, shelter and natural vegetation. At night, the apes sleep in several series of cages (40 and 50 m^2). In addition to experiments, the animals are provided with a special enrichment programme, including various kinds of tools and foraging containers. Several times per day, the chimpanzees are fed a diet consisting primarily of vegetables, fruits and cereals with regular additions of eggs and meat. Test sessions took place in a familiar enclosure (approximately 30 m^2). The subjects were used to being separated in adjacent enclosures from their group members for testing. They were not food deprived for testing, and water was available throughout all test periods. They were not distressed and were free to stop participating at any time. German law on animal rights and ASAB/ABS guidelines (ASAB/ABS 2012) were followed throughout.

Apparatus

Test materials consisted of two plastic tables (80 × 40 cm), placed in front of Plexiglas windows opposite each other with a distance of 20 cm between them. There were two identical apparatuses (modelled after Horner et al. 2006): opaque boxes (43 × 40 cm and 16.5 cm high) with a transparent Plexiglas door (10 × 10.5 cm) with a small knob (4.5 × 2 cm) on the front (see Fig. 1a). This door could be opened in two different ways: it could either be slid to the (right) side (see Fig. 1b) or lifted (see Fig. 1c) to give access to a small container inside the box. Within each box there was a circular reward holder on top of this container (not visible through the Plexiglas door) that could hold up to six rewards (grapes used throughout the experiment), by means of which the experimenter could drop rewards into the container to bait the box (see Fig. 1d).

Procedure

The procedure consisted of an information phase, in one of two conditions, and two test phases.

Information phase

The information phase consisted of four consecutive sessions of 12 trials per day (for a total of 48 trials). During this phase, chimpanzees were provided with information about one of two techniques ('sliding' or 'lifting') for opening the apparatuses to extract the food inside. This information was provided in two different ways: it was demonstrated by E1 in one condition, and subjects learned it through direct experience in the other condition. That is, after baiting the boxes out of the chimpanzees' view and setting up the test equipment, E1 stood behind one of the two boxes in front of the Plexiglas window, called the chimpanzees to attract their attention and released the first reward into the container, so that it was visible through the Plexiglas door. The subsequent procedure differed according to the experimental condition (with subjects randomly assigned to one of these two experimental conditions, with age and sex matched as well as possible). Ten subjects participated in the modelled condition and eight participated in the self-experience condition (10 were assigned to the latter condition but two dropped out; see Participants section).

Modelled condition. In this condition, the apparatuses stood on the tables facing the Plexiglas windows, approximately 20 cm from the windows (see Fig. 2a). E1 demonstrated to the subjects how to use one of the actions to open the door successfully (see Fig. 2a). After he ensured that subjects were paying attention (i.e. were sitting behind the Plexiglas window, facing the apparatus), he slowly opened the door of the first box by either lifting or sliding (depending on which action had been assigned to the subject). For lifting, he bent over the apparatus, grasped the knob on the door with his right hand, and lifted it as high as possible (90°), then took the reward with his left hand, slowly closed the door, and handed the reward to the subject through a hole at the bottom centre of the Plexiglas window. For sliding, he bent over the apparatus, grasped the knob with his left hand, slid the door open as far as possible (8.5 cm), took the reward with his right hand, closed the door slowly, and handed the reward to the subject through the same hole as in the other action. After a reward was handed over, he released the next reward into the container. Each trial lasted about 5 s with an additional 10 s delay between the trials. Four of the chimpanzees in this condition saw the human open the door of the box by lifting it and six saw the human open the door of the box by sliding it (the numbers are not equal because two more chimpanzees were planned to observe the lifting action but they declined to participate in the information phase).

Self-experience condition. In this condition both apparatuses were attached to the Plexiglas windows. Cut into the windows was a rectangular hole, such that the knob of the doors protruded into the chimpanzees' enclosure, and the doors could easily be opened by the subjects (see Fig. 2c). During the information phase in this condition, subjects did not witness a human acting on the apparatuses but instead were given experience in opening the apparatus themselves, for the same amount of time as the chimpanzees in the modelled condition had observed the successful human. For each individual the box was fixed so it could open in only one way. Five of the chimpanzees in this condition opened the apparatus by lifting and three opened it by sliding. Once a reward was obtained from the apparatus, E1 waited approximately 10 s, and then released the next reward into the container. Already in their first trial, all subjects managed to obtain the reward very quickly (means: 4 s for lift and 6 s for slide).