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ORIGINAL PAPER

How to crack nuts: acquisition process in captive chimpanzees (*Pan troglodytes*) observing a model

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Abstract Stone tool use for nut cracking consists of placing a hard-shelled nut onto a stone anvil and then cracking the shell open by pounding it with a stone hammer to get to the kernel. We investigated the acquisition of tool use for nut cracking in a group of captive chimpanzees to clarify what kind of understanding of the tools and actions will lead to the acquisition of this type of tool use in the presence of a skilled model. A human experimenter trained a male chimpanzee until he mastered the use of a hammer and anvil stone to crack open macadamia nuts. He was then put in a nut-cracking situation together with his group mates, who were naïve to this tool use; we did not have a control group without a model. The results showed that the process of acquisition could be broken down into several steps, including recognition of applying pressure to the nut, emergence of the use of a combination of three objects, emergence of the hitting action, using a tool for hitting, and hitting the nut. The chimpanzees recognized these different components separately and practiced them one after another. They gradually united these factors in their behavior leading to their first success. Their behavior did not clearly improve immediately after observing successful nut cracking by a peer, but observation of a skilled group member seemed to have a gradual, long-term influence on the acquisition of nut cracking by naïve chimpanzees.

Keywords Chimpanzees · Tool use · Nut cracking · Combinatory manipulation

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Introduction

Tool use for nut cracking is one of the most complex skills in which non-human primates engage. Non-human animals use a variety of tool types, and many tool-using behaviors require relating two objects, such as drawing a banana closer with a stick, inserting a grass stem into a hole, pulling a rake to draw something closer, and stepping on a box to reach a banana on a ceiling (e.g., Köhler 1925; see Beck 1980; Tomasello and Call 1997 for a review). In contrast, tool use for nut cracking requires relating three objects, i.e., nut, anvil, and hammer, which has greater cognitive requirements than relating just two objects (Matsuzawa 1996). The behavior consists of placing a hard-shelled nut onto a stone or wooden anvil and then cracking the shell open by pounding it with a stone or wooden hammer to get at the kernel.

Two non-human primate species use tools to crack nuts in the wild: capuchin monkeys and chimpanzees. Researchers recently discovered that wild bearded capuchin monkeys (*Cebus libidinosus*) in Brazil use tools to crack open palm nuts (Moura and Lee 2004; Fragaszy et al. 2004). The monkeys place a palm nut on a rock and then hit the nut with a 250-g to 2-kg stone to crack it open (Visalberghi et al. 2007). Part of the background to this tool use is that pounding is a very common behavior in capuchins (Izawa and Mizuno 1977). Wild capuchins can crack nuts by hitting them on a hard surface (Izawa 1979). Moreover, in the laboratory, tufted capuchin monkeys (*C. apella*) cracked nuts by hitting them on a hard surface or produced stone flakes by hitting a stone on a hard surface (Anderson 1990; Westergaard and Suomi 1995; Pouydebat et al. 2006; Schrauf et al. 2008). Using hammers and anvils to crack nuts was reported in captivity or a semi-free environment before the discovery of the same behavior in the wild (Ottoni and Mannu 2001; Ottoni et al. 2005). Visalberghi (1987) reported the acquisition of hammer use for nut cracking by two tufted capuchin monkeys among 42 individuals. During a free manipulation period before the formal test, in which the monkeys were given only hammer objects, all 42 monkeys pounded the hammer on a surface, and 12 individuals pounded one hammer on another, suggesting that capuchins commonly perform pounding actions. During the formal test, 11 subjects used the tool incorrectly, e.g., pounding the nut on the tool or next to the tool, while six of them showed correct but unsuccessful use of the tool, i.e., they hit a nut with a hammer, but the blows were insufficient to crack the nut open. Of these six individuals, two males used the tool correctly and successfully.

The other non-human primate species that engages in nut cracking in the wild is the chimpanzee (e.g., Anderson et al. 1983; Boesch and Boesch 1983; Boesch and Boesch 1990; Matsuzawa 2001; Sugiyama and Koman 1979). Researchers have investigated this behavior longer in chimpanzees than in capuchin monkeys and have accumulated knowledge about this type of tool-using behavior in chimpanzees. In the wild, tool use for cracking nuts is specific to certain populations, and this cannot be explained by ecological factors (Whiten et al. 1999). Nut cracking was thought to have been developed by individuals somewhere in West Africa, and then transmitted socially from one generation to the next, with expansion based on the individual emigration and immigration (Whiten et al. 2001; Biro et al. 2003). Regarding the acquisition of nut cracking in these areas by infant chimpanzees, reports from two sites consistently illustrate that it takes 3–7 years for the infants to master the skill (Matsuzawa 1994; Boesch and Boesch-Achermann 2000). Therefore, learning nut cracking is a longer process than for other types of simpler tool use (Matsuzawa 2001).

Inoue-Nakamura and Matsuzawa (1997) studied the developmental change in nut-cracking behavior in wild chimpanzees at Bossou, Guinea. They started observing three chimpanzees as 6-month-old infants and continued their observations once every year for about 1 month for 4 years. Their observations revealed the following. First, only one object was manipulated at the age of 0.5 years, either a nut or a stone. As the animals matured, they began to manipulate several nuts or stones, as well as combinations of nuts and stones. At the age of 2.5 years, the chimpanzees could perform five basic behaviors necessary for nut cracking: (1) picking up a nut, (2) putting a nut on a stone, (3) holding a stone, (4) hitting a nut on an anvil stone with a hammer stone, and (5) eating the kernel of a cracked nut. Nevertheless, the 2.5-year-old chimpanzees could not combine these elements in the appropriate order. Two of the three infants began to crack nuts by themselves when they were 3.5 years.

Three studies have focused on the emergence of nut cracking in chimpanzees in captivity or a semi-natural environment. Hannah and McGrew (1987) observed previously captive chimpanzees that were released on an island in Liberia. When a group of three females was added to the original group, one of these three females was observed using a hammer and an anvil as tools to crack open oil palm nuts. Before that event, no other animal had been observed engaging in nut-cracking behavior. Within 1 month of the first observation of a female cracking nuts, 13 of 19 individuals began to use tools to crack nuts. However, the history of each individual before its release on the island was not known in many cases, hence, it was impossible to determine whether they learned this behavior during the period of observation, or if they had acquired the skill previously, and it reappeared on the island.

Sumita et al. (1985) investigated the learning of nut-cracking behavior in captive chimpanzees. They presented model actions of nut cracking, performed either by a human experimenter or a skilled chimpanzee, to five chimpanzees individually. Three of the five chimpanzees succeeded in cracking nuts. In another group, situation where skilled chimpanzees stayed with naïve chimpanzees, one of 14 naïve chimpanzees acquired the skill. Among individuals who did and did not acquire the behavior in single-subject conditions, differences were evident in their responses to model actions and to nuts. In addition, differences were evident in the responses to stones among individuals who did and did not acquire the behavior in group conditions.

Hayashi et al. (2005) investigated the behavior of three human-raised captive chimpanzees after observing a human model performing the correct sequence of nut cracking. Two of the three chimpanzees placed a nut on an anvil stone and hit it with a hammer stone in the first session. One of them succeeded in cracking the nut open in the first session, and the second individual first succeeded in the following training session. The third chimpanzees never performed the correct sequence of nut-cracking behavior. The subject that failed did not perform a hitting action and rarely manipulated stones, while the two successful individuals manipulated stones in various ways.

Together, these data show that both capuchins and chimpanzees are able to acquire the use of a hammer and anvil to crack open nuts both in the wild and in captivity.

The question arises as to what kind of understanding of the tools and actions will lead to the acquisition of this type of complex tool use. No study has investigated this aspect of nut cracking, although Visalberghi et al. provided a comparative perspective based on the experimental studies of another kind of tool use in capuchin monkeys and chimpanzees (Visalberghi and Trinca 1989; Visalberghi and Limongelli 1994; Visalberghi et al. 1995; Limongelli et al. 1995). They presented various types of tube task, in which an appropriate tool must be used to push a piece of food out of a tube. In some variations of the task, the tool needed to be modified, while in other variations, the food needed to be pushed in a certain direction to avoid a trap. The authors interpreted the results as indicating that the capuchins had little understanding of the causal structure of the task, while chimpanzees had more foresight than capuchins. However, there is controversy as to whether chimpanzees have a deeper understanding of causality in tool use than monkeys (Tomasello and Call 1997).

Byrne (2003) discussed what apes might understand when they acquire complex skills in a social situation. He provided an example of gorillas, which do not use tools in the wild, but engage in elaborate techniques to process plants before they eat them. Mountain gorillas feed on nettles that are defended by powerful stinging hairs. They prepare the plants variously by stripping leaves off stems, accumulating larger bundles of leaves, detaching petioles, picking out unwanted debris, and folding a package of leaf blades within a single leaf before ingestion. Byrne (2003) argued that when an infant gorilla watches its mother performing fluid movements of skilled action, the infant sees the movements as composed of strings of elements that are segmented from the entire sequence. The infants may then recognize the statistical regularities separating a set of essential actions, and become able to perform the same structure of behaviors. In contrast, Gleissner et al. (2000) showed that human children decomposed the perception of manual gestures into different aspects when they were asked to imitate several gestures made by a model. The authors also stated that the children coded the actions of another individual as hierarchically organized goals, and not as physical movements, and that the children reconstructed actions based on their understanding of the decomposed goals with some goals getting more emphasis than others, which led to errors involving skipping some of the goals that were ranked lower by the children. Although there is discrepancy between Byrne's (2003) view on gorillas and the view of Gleissner et al. (2000) on human children regarding how they recognize the goal of other individuals, both decompose a sequence of behaviors into several components.

The correct sequence of nut cracking has several different components and consists of two steps in terms of the actions involved: placing a nut on an anvil and hitting the nut with a hammer. The sequence requires combining three objects in the correct order: an anvil at the bottom, a nut resting on it, and a hammer on top of the nut. The final goal of these actions is to crack open the nut shell and not to crush the edible kernel, which can be achieved by applying necessary force to the nut shell. Hitting is the key action in this regard. Although studies have examined how nut-cracking behavior is learned, no study has provided detailed evidence on how the chimpanzees recognize these different aspects during the process of acquiring nut-cracking skills. In studies conducted in the wild, such as that of Inoue-Nakamura and Matsuzawa (1997), it is virtually impossible to follow the entire process by which infants acquire nut cracking; the researchers made observations for 1 month, once a year, in four consecutive years; therefore, we do not know what happened during the other 11 months of each year. Hannah and McGrew (1987) did not know whether the chimpanzees acquired the skill for the first time during their observations. Sumita et al. (1985) did not report on detailed behavior during the acquisition process. In a study by Hayashi et al. (2005), two of the adult chimpanzees tested performed the correct sequence in the first session, but the process before their first success was not reported in detail.

We were interested in whether chimpanzees foresee the necessary components of nut-cracking behavior before their first success. Two different scenarios are possible. In the first scenario, the chimpanzees do not understand the necessary components at all before their first success. In this case, the first success is an accidental occurrence of the correct sequence of behaviors; appropriate sequences of behaviors or behaviors that are close to the correct one will appear randomly among many irrelevant behaviors before the accidental first success. In the second scenario, the chimpanzees understand some of the necessary components before their first success. In this case, the frequency of appropriate behavior reflecting a necessary component will increase before the first success.

In this study, we tracked the acquisition of tool use for nut cracking in captive chimpanzees who could observe a skilled conspecific model to address the above-mentioned issue. First, one member of a group of five chimpanzees was assigned as the model and was trained separately to use tools to crack nuts with human modeling and teaching. Along with the four other group members, the model chimpanzee was then put in a situation where abundant nuts, hammer stones, and anvil stones were provided. We analyzed the behavioral changes in each chimpanzee from the start of the study until their first success to clarify the process by which naïve chimpanzees acquire nut-cracking behavior in the presence of a skilled model. The test situation was not designed to clarify a specific social learning mechanism; rather, we attempted to simulate a natural setting in which individuals acquire the skill through social interaction with the skilled individual.

Methods

Subjects and housing conditions

The subjects were five young chimpanzees (*Pan troglodytes*) cared for at the Great Ape Research Institute (GARI) of Hayashibara Biochemical Laboratories (Bril et al. 2009; Idani and Hirata 2006). The subjects and their age and sex at the onset of the group test in June 2003 were as follows: Loi (male, 7 years and 10 months), Zamba (male, 7 years and 10 months), Tsubaki (female, 7 years and 3 months), Mizuki (female, 6 years and 5 months), and Misaki (female, 4 years and 4 months). All individuals were born in captivity at another institution. All but Mizuki were reared by their mother before they were moved to GARI, while Mizuki was hand-reared from several days after birth. Loi, Zamba, Tsubaki, and Mizuki were moved to GARI in January 1999 when they were 2–3-year-old and formed a group. Misaki joined the group in January 2001. The chimpanzees lived in a group in a facility consisting of a large outdoor compound covering approximately 7,400 m^2 containing natural forest, a pond, and a 13-m high climbing structure with attached indoor rooms and a smaller compound. The subjects had previously participated in several types of cognitive tasks (Morimura 2006; Hirata and Fuwa 2007); for example, they had used plant stems to fish for honey (Hirata, unpublished data) and drank juice with a straw sponge (Morimura 2003). The chimpanzees were fed various fruits and vegetables 3–10 times a day. Water was available freely, and the chimpanzees were never food deprived.

Materials

Macadamia (*Macadamia ternifolia*) nuts in the shell, anvil stones, and hammer stones were used for the experiment. A macadamia nut in the shell is about 25 mm in diameter and weighs about 6 g. The edible kernel is surrounded by a shell about 3-mm thick, and it is extremely difficult for chimpanzees to crack it with their teeth. Granite stones of two different sizes were provided as anvils in the group test. One was about 35 cm in diameter (large anvil) and the other was 30 cm in diameter (small anvil). Both anvils were 7-cm high. Because macadamia nuts are round to stay on a flat surface, ten artificial depressions were made in each large anvil and eight in each small anvil. Five nut-cracking sites were created in the open enclosure for the group test, and each site had one large and one small anvil (Fig. 1). The five sites were located at the vertices of an equilateral pentagon. The distance between the two sites was 10 m, which was enough to prevent monopolization of the opportunities by dominant individuals. The anvil stones were fixed in the ground to prevent the chimpanzees from carrying the anvil stones to unobservable areas. Natural stones collected at a riverside were used as hammer stones. Fifty stones were selected so that there were five stones in each of ten classes: 100–200, 200–300, 300–400, 400–500, 500–600, 600–700, 700–800, 800–900, 900–1,000, and 1,000–1,100 g. Each stone was numbered for identification.

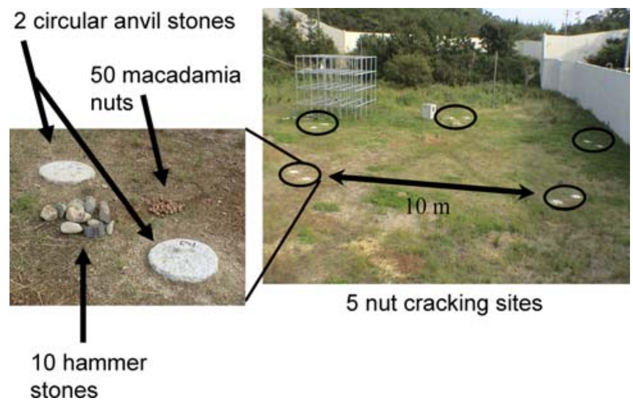

Fig. 1 Experimental arrangement used in the group test

Pre-training the model individual

Loi, the oldest of the five chimpanzees, was selected as the model individual for the subsequent group test. The pre-training started in June 2000 and ended in June 2003, and took place at an experimental room about 8 m^2 and 3-m high, where he was brought individually from the enclosure. The training period was divided into three phases: June 2000–January 2001 (Phase I), June 2002–March 2003 (Phase II), and April 2003–June 2003 (Phase III). During Phase I, 67 sessions (a “session” started when the chimpanzee entered the experimental room and ended when the animal left the room) were conducted in which 20–50 nuts and 13 stones of varying size (a 20-kg stone about 35 cm in diameter and 7-cm high to be used as an anvil, and 12, 400–800 g stones to be used as hammers) were provided and a human experimenter who stayed in the same room demonstrated nut cracking for Loi, except for the first six sessions in which the chimpanzee’s spontaneous behavior with these materials was observed. Artificial nuts were used in these sessions. These “nuts” were made from two small plastic cups and a metal belt; each cup was 2-cm long, 3.3 cm in outer diameter, and 2.5-mm thick, and the belt was 0.3-mm thick, 1.5-cm wide and 3.3 cm in inner diameter. The two cups were combined so that the openings of the cups were joined together, a piece of fruit (e.g., apple, orange, and banana) was put inside, and the halves were joined by the metal belt. When the artificial nut was hit with an appropriate blow, the metal belt slipped off. The strength of the artificial nut could be adjusted by controlling the tightness of the metal belt. From the 37th session onward, the human experimenter asked the chimpanzee to put a nut on an anvil stone, by pointing at a nut until the chimpanzee took it, and then pointing at an anvil until the chimpanzee put the nut on it, while verbally encouraging these actions, and he gave a food reward if the chimpanzee did so. From the 47th session, the human experimenter asked the chimpanzee to hold a hammer stone after putting a nut on an anvil stone, by pointing at a hammer stone, while verbally encouraging holding it, and from the 57th session the experimenter took the chimpanzee's hand, after making the chimpanzee put a nut on the anvil stone and hold a hammer stone, to instruct the nut-cracking action by molding. Loi never hit a nut on an anvil stone with a hammer stone by himself during this period. After a break of about 1.5 years, the pre-training restarted in June 2002 (Phase II). In the first trial of the first session of Phase II, Loi spontaneously hit an artificial nut on an anvil stone with a hammer stone when he was provided with the nut, anvil, and hammer stones. The reason for the sudden emergence of hitting behavior using a hammer was unknown. Initially, the artificial nuts were attached loosely, so that only a weak hit was needed to crack the nuts. The tightness of the belt was increased gradually, until the subject's hitting action became mature and stable. In addition, macadamia nuts were introduced from the 17th session of Phase II, when the subject's hitting action became reliable. Initially, the subject did not tend to crack the macadamia nut and avoided eating its kernel, probably due to neophobia in the food repertoire. To facilitate the consumption of macadamia nuts, honey or maple syrup was injected through a tiny hole made in the macadamia nut shell. During Phase II, 154 sessions were conducted, in which 1–50 artificial or macadamia nuts were provided. During Phase III, which started immediately after Phase II, the training was moved to the open enclosure where the subsequent group test took place, and the training continued until the subject began to crack macadamia nuts reliably in the open enclosure. In total, 11 sessions were conducted during this period. Throughout Phase III, the training sessions lasted for 5–30 min.

Procedure

Pre-test

Before putting the model and other chimpanzees together, the spontaneous manipulation of the nuts and stones by the four naïve chimpanzees was observed in a free-play situation. Zamba and Mizuki were brought to an experimental room alone, while Tsubaki and Misaki were brought to the room together as Misaki was reluctant to be separated from her companions and preferred to stay with Tsubaki. The experimental room was 8 m^2 and 3-m high. A 20-kg anvil stone about 35 cm in diameter and 7-cm high, a 700-g hammer stone, five artificial nuts, and five macadamia nuts were provided. Each subject's behavior was observed for 5 min, and if a subject continued to manipulate the objects for more than 5 min, the observations were extended until the subject stopped the manipulations for 1 min. Each individual participated in 15 sessions. The behavioral repertoire of each subject converged in subsequent sessions, and no new behavior was observed during the 15th session in any individual.

Group test

The group test in which the four naïve chimpanzees (Zamba, Tsubaki, Mizuki, and Misaki) were put together with the model (Loi) began in June 2003 in the open enclosure. The test started when the five chimpanzees were moved from a waiting area to the open enclosure, and continued for 30 min. The chimpanzees were returned to the waiting area at the end of a session. Two or three sessions were conducted per week, and each session was separated by at least 1 day. Before releasing the chimpanzees into the open enclosure, 50 macadamia nuts and ten stone hammers, one from each of the ten weight categories were put at each of the five sites with a pair of stone anvils (Fig. 1). Because maple syrup was injected in the macadamia nuts during Loi's pre-training, macadamia nuts containing maple syrup were used in the first and second sessions. However, Loi's nut-cracking behavior was stable and reliable during the first two sessions, so plain macadamia nuts in the shell were used from the third session on. After the human experimenters placed the macadamia nuts and stone hammers, the four naïve chimpanzees were released from the waiting area into the open enclosure. Loi was released into the enclosure last. Six video cameras were used to record the behavior of the chimpanzees. Five of the six video cameras were used to follow a target individual such that each of the five cameras followed one chimpanzee. The sixth video camera was used to record the scene including all five sites. At the end of a session, when the chimpanzees were moved to the waiting area, all stone hammers, uncracked macadamia nuts, remaining kernels, and cracked nut shells were removed from the enclosure. Therefore, the chimpanzees had no chance to manipulate these objects outside of the test sessions.

Data analysis

The way in which the chimpanzees manipulated the macadamia nuts, anvils, and hammers was scored from the video recordings. We described the subjects' behaviors in terms of actions, objects involved, and body parts used. We used the lists of actions from the studies of Inoue-Nakamura and Matsuzawa (1997) and Hayashi et al. (2005) on nut cracking in chimpanzees. In this study, we coded the following actions: bite, drop, eat, hit, hold, kick, kiss, mouth, pick, press, put, sit, step, touch, and turn. The definitions of these actions are the same as described by Inoue-Nakamura and Matsuzawa (1997) and Hayashi et al. (2005). Nuts and stones, including those fixed to the ground to be used as anvils, were coded as objects. Note that the stones fixed to the ground were not "detached" objects, but we still coded them as objects in the analysis. Using these terms for actions along with the objects and body parts used, the chimpanzee behavior was coded in the following manner: "a chimpanzee put (action) a nut (object) with its hand (body part) on an anvil stone (object)".

A behavioral bout was defined as a sequence of behavior during which a subject engaged in the same type of behavior in terms of actions, object(s) involved, and body part used. When a subject changed an action, object, or body part, it was coded as a new behavioral bout. We made two exceptions for the actions 'touch' and 'pick.' Touch was fundamental to all other actions, so it would be redundant to count a touch as a separate bout. Moreover, the subjects sometimes placed their hands or feet on nuts or stones on the ground, but it was difficult to determine whether they intended to do this; perhaps a nut or stone happened to be under the hand or foot of the subject coincidentally. Pick was also fundamental to many other manipulations. Therefore, touch and pick were not considered elements forming a behavioral bout. If touch or pick was followed by another type of action, the sequence was coded as a behavioral bout in terms of the latter action. If touch was not followed by another type of action, i.e., if a subject touched a nut and then abandoned it, this sequence was not counted as a behavioral bout. If a subject touched a nut, picked it up, and abandoned it, it was coded as 'hold.' Note that the consecutive use of the same action for the same target object using the same body part was considered one bout. This applied especially when a subject engaged in hitting action. In this case, the number of hitting actions (the number of times the subject hit the target) in a behavioral bout was counted.

The manipulations were divided into four categories according to the number of objects combined in a behavioral bout: manipulation of a single object, manipulation of two objects, manipulation of the correct set of three objects (a nut, anvil, and hammer), and manipulation of an incorrect set of three or more objects. The manipulation of a single object included behavior in which a chimpanzee manipulated only one object (a nut, anvil, or hammer) such as hitting an anvil with its hand. Manipulation of two objects included behaviors in which a chimpanzee manipulated two objects in a way that connected the two objects, such as putting a hammer stone on an anvil stone. Manipulation of the correct set of three objects included behavior in which a chimpanzee manipulated a nut, anvil stone, and hammer stone in a way that connected these three objects, such as the correct sequence of nut-cracking behavior, or putting a nut on a stone hammer on an anvil stone. Manipulation of an incorrect set of three or more objects included behavior in which a chimpanzee manipulated three or more objects other than the correct set of three objects in any way connecting these objects, such as putting a hammer stone on another stone that was put on an anvil stone (an anvil and two hammer stones). The frequency of each category of manipulation in a session was calculated by dividing the number of behavioral bouts that fell in a certain category of manipulation by the total number of behavioral bouts observed in a session.

When a naïve chimpanzee oriented its face toward a skilled individual performing nut cracking within 2 m of it, this behavior was scored as 'observation,' and its duration and the skilled individual were recorded. One bout of observation started when a naïve chimpanzee oriented its face toward a skilled individual and ended when the naïve chimpanzees faced in another direction for more than 3 s or began to manipulate objects itself. In other words, if the time gap between the two sequences of observation was 3 s or less and there was no manipulation during this gap, these sequences were scored as one bout of observation. To investigate the immediate influence of a subject observing a model that performed nut cracking successfully, 20 behavioral bouts before and after the observation of a model, and ten behavioral bouts before and after the observation, were compared.

To analyze another aspect of the interaction between the chimpanzees, threat and aggressive behaviors were noted. When an individual directed a threat or any type of aggressive behaviors toward another chimpanzee and the latter individual moved away from the former, this event was scored as 'exclusion.'

Results

Pre-test

Table 1 shows the frequency of the subjects' behaviors during the pre-test sessions according to the category of manipulation. Mizuki showed a higher frequency of behaviors, including combined manipulations of two or more objects. She performed (1) one bout of hitting a nut with another nut in the first session and another bout of the same behavior in the seventh session, (2) she hit an anvil stone with her hand once in the fourth session, (3) she hit a nut on

Table 1 Frequency of each type of object manipulation observed during the pre-test sessions

Target of manipulation	Individuals			
	Zamba	Tsubaki	Mizuki	Misaki
Manipulation of a single nut	164	30	168	113
Manipulation of a single stone	11	45	168	55
Manipulation of two objects	2	2	159	0
Manipulation of an incorrect set of three or more objects	0	0	20	0
Manipulation of correct set of three objects	0	0	2	0
Total	177	77	517	168

the floor with a hammer stone once in the sixth session, (4) twice she hit a nut that had been put on an anvil stone with a hammer stone in the sixth session, and (5) she hit a nut that had been put on an anvil stone with another nut once in the seventh session. However, none of these behaviors successfully cracked a nut open. These were all of the occasions on which she used a hitting action during the pre-test. The other three individuals performed manipulations less frequently, and they rarely engaged in combined manipulations of two objects.

Group test

All four naïve chimpanzees acquired the nut-cracking behavior during the group test. Zamba, Tsubaki, Mizuki, and Misaki first succeeded in the 8th, 11th, 13th, and 15th sessions, respectively. All individuals continued to succeed after their first successes. The number of behavioral bouts observed in each chimpanzee from the first session of the group test until the first success was 3,114 bouts for Zamba, 2,958 bouts for Tsubaki, 3,184 bouts for Mizuki, and 5,604 bouts for Misaki. The process by which each of the four individuals first succeeded and the general trend for these four chimpanzees are outlined below.

Combinatory manipulations

Figure 2 shows the percentage of each category of manipulation across sessions for each chimpanzee. During the process leading up to their first successes, the manipulation of two objects was seen in all sessions, starting from the first session. The manipulation of three or more objects (both correct and incorrect sets of objects) was rarely seen in the first half of the processes, except for Tsubaki's first session and Mizuki's fifth and eighth sessions. The proportions of each of the four categories of manipulation differed across sessions in each chimpanzee (χ^2 test, Zamba: $\chi^2 = 606.15$, $df = 21$, $P < 0.001$; Tsubaki: $\chi^2 = 402.30$, $df = 30$, $P < 0.001$; Mizuki: $\chi^2 = 184.92$, $df = 36$, $P = 0.14$; Misaki: $\chi^2 = 1{,}179.68$, $df = 42$, $P < 0.001$). The proportion of manipulations of three or more objects was the highest in the last session (the session in which each of the subjects first succeeded) in all four chimpanzees.

Figure 3 shows the percentage of each item (nut/stone) handled directly in each of the three manipulation categories (manipulation of the correct set of three objects and manipulation of an incorrect set of three or more objects were lumped together). For this calculation, an analysis was made to see whether the item manipulated directly by the chimpanzees was a nut or a stone in each category of manipulation. For example, the combined manipulation that involved placing a nut on a stone is categorized as a combination of two objects, and in this example, the item handled by the subject directly is the nut. Handling a stone was more frequent in the combination of two objects than in the manipulation of a single object, and more frequent in the combination of three objects than in the combination of two objects (Page test for ordered alternatives (Siegel and Castellan 1988), $L = 56$, $P < 0.001$).

Order of combination of three or more objects

Figure 4 shows the proportion of manipulations across ten behavioral bouts according to the order of object combinations in manipulations involving three or more objects. Initially, the object combinations were often inappropriate, such as combining three stones or combining a stone and two nuts. Gradually, however, the frequency of combining a correct set of three objects increased. The proportion of manipulations of the correct set during the last ten behavioral bouts was 100% (10/10) in all four subjects, which was higher than the corresponding proportion during the first ten behavioral bouts involving three or more objects in each of the four individuals.

When the chimpanzees began to combine the correct set of three objects, the order of the combination was not always correct. They sometimes put the objects in an incorrect order, such as placing a nut on a hammer stone on an anvil stone. The frequency of combining objects in the correct order, i.e., an anvil on the bottom, a nut in the middle, and a hammer on top, increased during the last stages of the process before their first successes. When behavioral bouts that involved the manipulation of three or more objects were divided chronologically into the first and second halves, the frequency of combining objects in the correct order tended to be higher in the second half than in the first half (χ^2 test, Zamba: $\chi^2 = 1.12$, $df = 1$, $P = 0.29$; Tsubaki: $\chi^2 = 29.87$, $df = 1$, $P < 0.001$; Mizuki: $\chi^2 = 5.50$, $df = 1$, $P = 0.019$; Misaki: $\chi^2 = 53.78$, $df = 1$, $P < 0.001$).

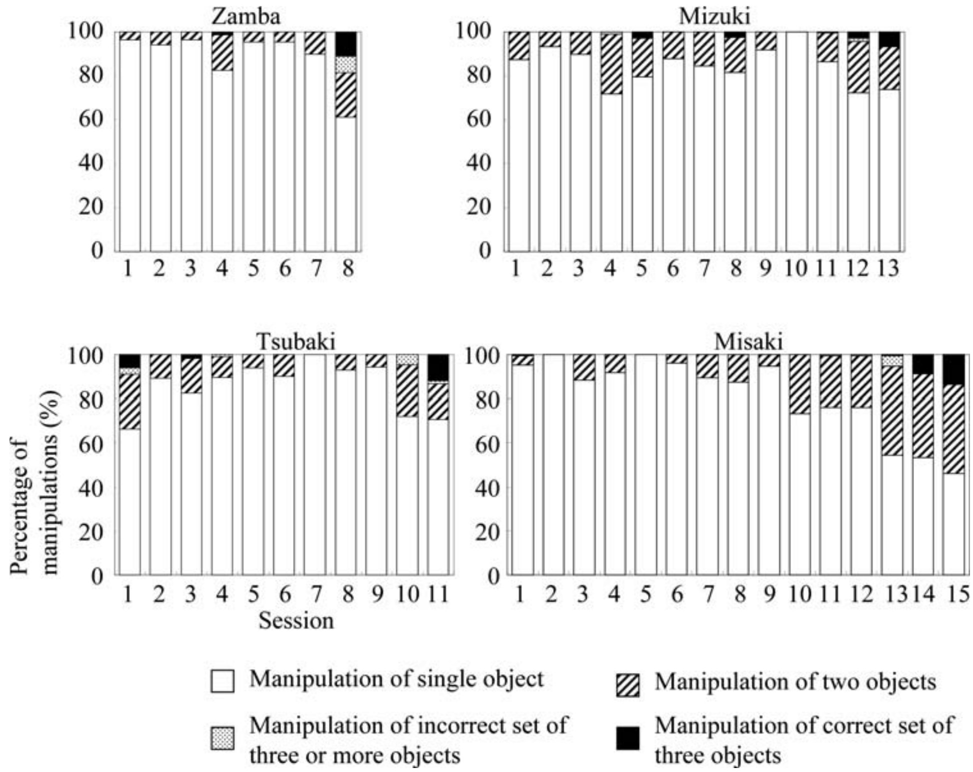

Fig. 2 Percentage of each manipulation category across sessions

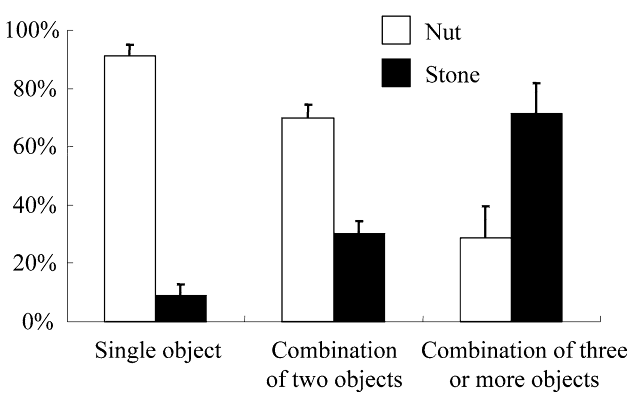

Fig. 3 Percentage of each item (nut/stone) handled directly in each of the three manipulation categories

Stepping on and hitting actions

Hitting actions were rarely seen until one or two sessions before their first successes or until the session in which they first succeeded, except for Mizuki. In addition to a hitting action, stepping on a nut can be regarded as a correct action from a functional perspective, because it puts pressure on the nut and may serve to crack open a nut, although this was not actually the case. Table 2 shows the change in the frequencies of stepping on and hitting actions across sessions. All subjects first performed stepping on before the emergence of the hitting action. To investigate the change in frequency of these actions, the entire process was divided into the first and second halves of sessions and the frequency was compared; if there was an odd number of sessions, the halfway session was further divided into the first and second halves (e.g., when there were 11 sessions, the first half of the process consisted of sessions 1–5 and the first half of the sixth session, and the second half of the process consisted of the second half of the sixth session and sessions 7–11). In all subjects, stepping on was evident in the first half of the process, but subsequently became more infrequent as the frequency of hitting increased in the second half (Zamba, Fisher's exact test, $P < 0.001$; Tsubaki, $\chi^2 = 64.69$, $df = 3$, $P < 0.001$; Mizuki, Fisher's exact test, $P = 0.037$; Misaki, Fisher's exact test, $P < 0.001$).

Method and target of hitting actions

Figure 5 shows the change in the frequency of the method or object used to hit something, that is, whether object was hit with the hands directly, with a nut, or with a stone, across ten blocks of hitting actions. Initially, the chimpanzees used their hands to hit an object. Each subject's first hitting actions were performed with empty hands, and subsequently, hitting with a hammer stone predominated. When the hitting actions were divided chronologically into the first and second halves, the frequency of hitting with the hand tended to be higher in the first half, while hitting with a hammer stone was higher in the second half (χ^2 test,

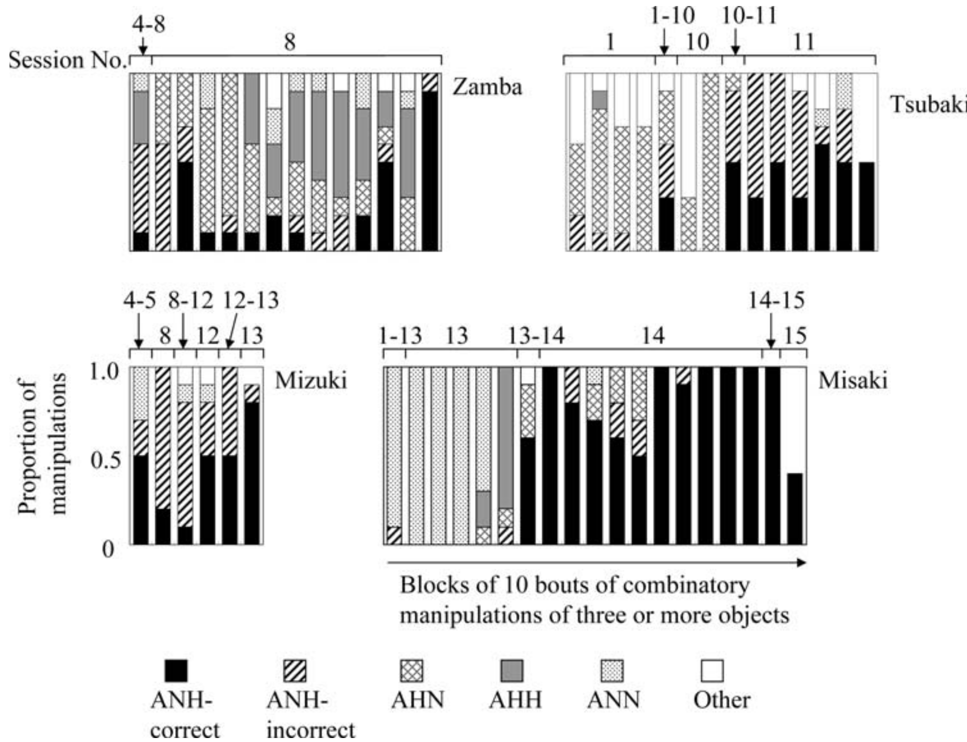

Fig. 4 Proportion of manipulations across blocks of ten behavioral bouts according to the order of object combinations in manipulations involving three or more objects. *A* anvil stone, *N* nut, and *H* hammer stone. 'XYZ' means *X* at the bottom, *Y* in the middle, and *Z* on top; e.g., "*ANH*" anvil at the bottom, a nut in the middle, and hammer on top, such as putting a hammer on a nut on an anvil. "*ANH-correct*" indicates a correct action (hitting a nut on an anvil using a hammer) and "*ANH-incorrect*" indicates other actions performed with a hammer on a nut on an anvil. The *numbers* on top of each *graph* indicate the session number in which each block of ten behavioral bouts took place

Table 2 Frequency of stepping on and hitting actions across sessions

Individual	Action	Sessions														
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Zamba	Step-on	0	2	0	0	0	0	0	0	–	–	–	–	–	–	–
	Hit	0	2	0	3	1	2	1	103	–	–	–	–	–	–	–
Tsubaki	Step-on	36	0	1	1	0	0	0	0	1	1	1	–	–	–	–
	Hit	4	0	5	3	0	0	0	0	1	7	48	–	–	–	–
Mizuki	Step-on	1	0	0	5	2	0	3	1	0	0	0	0	0	–	–
	Hit	7	0	3	20	34	11	0	19	0	0	4	29	21	–	–
Misaki	Step-on	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0
	Hit	0	0	0	0	0	0	0	2	0	0	4	5	169	283	33

Zamba: $\chi^2 = 11.18$, $df = 1$, $P < 0.01$; Tsubaki: $\chi^2 = 13.02$, $df = 1$, $P < 0.001$; Mizuki: $\chi^2 = 11.86$, $df = 1$, $P < 0.001$; Misaki: $\chi^2 = 66.91$, $df = 1$, $P < 0.001$).

Figure 6 shows the proportion of hitting actions according to the three target items across blocks of ten hitting actions (i.e., whether the chimpanzees hit a nut, hammer stone, or anvil stone). The target item of the hitting action was not always a nut, as the chimpanzees sometimes hit a hammer stone or an anvil stone.

Observation of model individuals

All four naïve individuals observed model individuals (Figs. 7, 8). A clear increase in the frequency and the duration of observation of models was confirmed during the process leading to their first successes. When we tried to compare 20 behavioral bouts before and after the subject observed a model to investigate the immediate influence of observing a model, we could not collect sufficient cases for statistical analysis because the subjects tended to observe a model intermittently, and there were often fewer than 20 behavioral bouts between two observations of a model. Using the sign test, when ten behavioral bouts were compared between before and after the subject observed a model, no significant change was detected in the mean number of objects combined in a bout ($N = 23$ excluding 10 ties, $P = 0.20$), the maximum number of objects combined during the ten behavioral bouts ($N = 16$ excluding 17 ties, $P = 0.60$), the number of hitting actions ($N = 4$ excluding 29 ties, $P = 0.69$), the number of bouts manipulating the

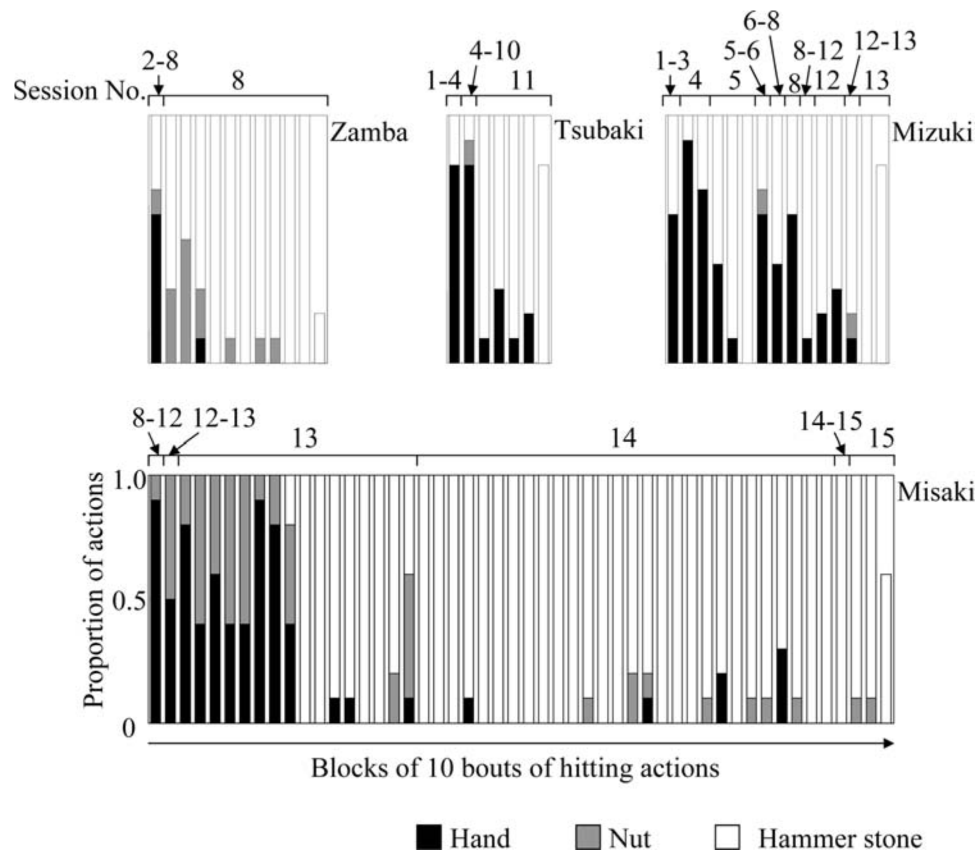

Fig. 5 Change in the method or object used to hit a target across blocks of ten hitting actions. The *numbers* on top of each *graph* indicate the session number in which each hitting action took place

correct set of three objects (the sample size was not sufficient to allow the test; there was one case in which its frequency increased after the observation of a model, two cases in which it decreased after the observation, and 30 cases in which it did not occur during ten bouts before and after observation of a model), or the correct sequence of behavior, i.e., hitting a nut on an anvil with a hammer (the sample size was not sufficient to allow the test; there was one case in which its frequency increased after the observation of a model, one case in which it decreased after the observation, and 31 cases in which it did not occur during 10 bouts before and after observation of a model).

Tolerance and observation of model individuals

Figure 8 shows the duration of observations of other chimpanzees successfully cracking nuts for each of the four naïve chimpanzees across sessions. The targets of observation differed among the naïve individuals. Zamba, who succeeded earliest, observed Loi. Tsubaki, who succeeded after Zamba, first observed Loi, and then both Loi and Zamba when Zamba succeeded. Mizuki and Misaki mainly observed Tsubaki after her success. The difference arose from the fact that the model did not allow some of the chimpanzees to approach. Table 3 shows how often each individual was excluded by certain individuals. Misaki and Mizuki were often excluded by threat and aggression: Mizuki by Zamba and Misaki by Loi. In contrast, Zamba and Tsubaki were excluded much less frequently.

All individuals began to show frequent manipulation of a correct or incorrect combination of three or more objects after their longer observations of models. In the cases of Tsubaki, Mizuki, and Misaki hitting a nut on an anvil with a hammer became evident in the session after they observed their preferred target model for the longest time.

Discussion

We investigated the process by which naïve chimpanzees acquired the use of stone tools to crack open a hard nut shell in the presence of model individual(s) in a group of five captive chimpanzees. Each of the chimpanzees tested made many relevant and irrelevant manipulations of the nuts and stones during the process leading to its first success, and we describe the behaviors of the chimpanzees before their first successes.

First, the naïve chimpanzees were observed spontaneously manipulating nuts and stones in a free-play situation before they had observed any models. At this time, the nuts were also novel for them. Mizuki performed the correct sequence of nut-cracking behavior (i.e., putting a nut on a

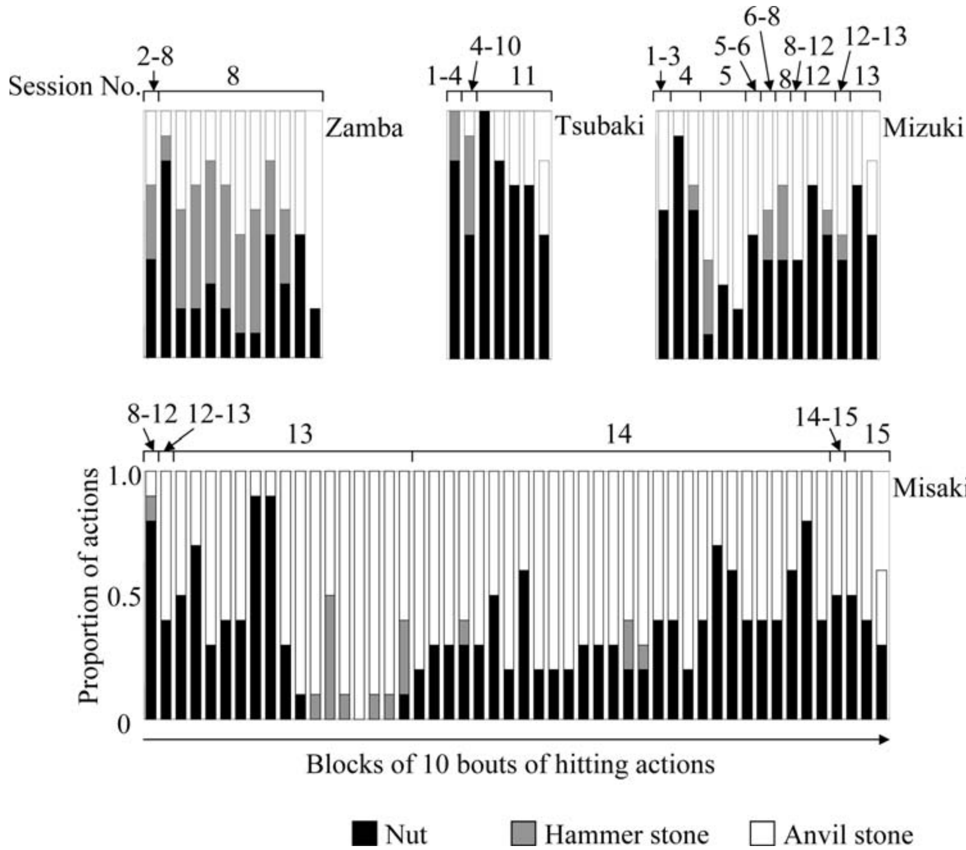

Fig. 6 Change in the target of hitting actions across blocks of ten hitting actions. The *numbers* on top of each graph indicate the session number in which each block of ten hitting actions took place

Fig. 7 Zamba and Tsubaki observing Loi in the first session of the group test

stone and hitting the nut with another stone) during this pre-test period, but it never led to success. This is evidence that the chimpanzees were capable of innovative tool use for nut cracking, which is thought to have occurred at some time in West Africa, as wild chimpanzees in this region have a culture of tool use for nut cracking (Whiten et al. 2001). However, the fact that Mizuki did not succeed in cracking open a nut after using the correct sequence of behaviors and that the behavior ceased in later sessions of the free-play situation indicates that it is still a difficult task for the chimpanzees and rarely leads to accidental success. The other three chimpanzees in this study did not show any behavior close to the correct sequence of nut cracking. This is also consistent with the case of wild chimpanzees, as individuals in East Africa do not perform nut-cracking behavior despite the availability of target nuts and stone tools in their environment (McGrew et al. 1997); it is not a behavior that chimpanzees can achieve easily on their own.

Nut-cracking behavior requires relating three objects, i.e., a nut, hammer, and anvil, in an appropriate combination. During the process leading to the four chimpanzees' first successes, combinatory manipulations of three or more objects were rarely seen initially and began to increase one or two sessions before their first success, while combinatory manipulations of two objects were seen from the first session. A hitting action was rarely seen initially in any subject. As Hayashi et al. (2005) indicated combinatory manipulations of three objects and hitting actions make nut-cracking behavior difficult for chimpanzees. This contrasts the behavior of capuchin monkeys, whose acquisition of nut cracking seems to be supported by their natural tendency to pound objects (Visalberghi 1987), although a future study should probe their understanding of this tool use. Conversely, the chimpanzees' acquisition of this tool use is not supported as strongly by such a natural tendency

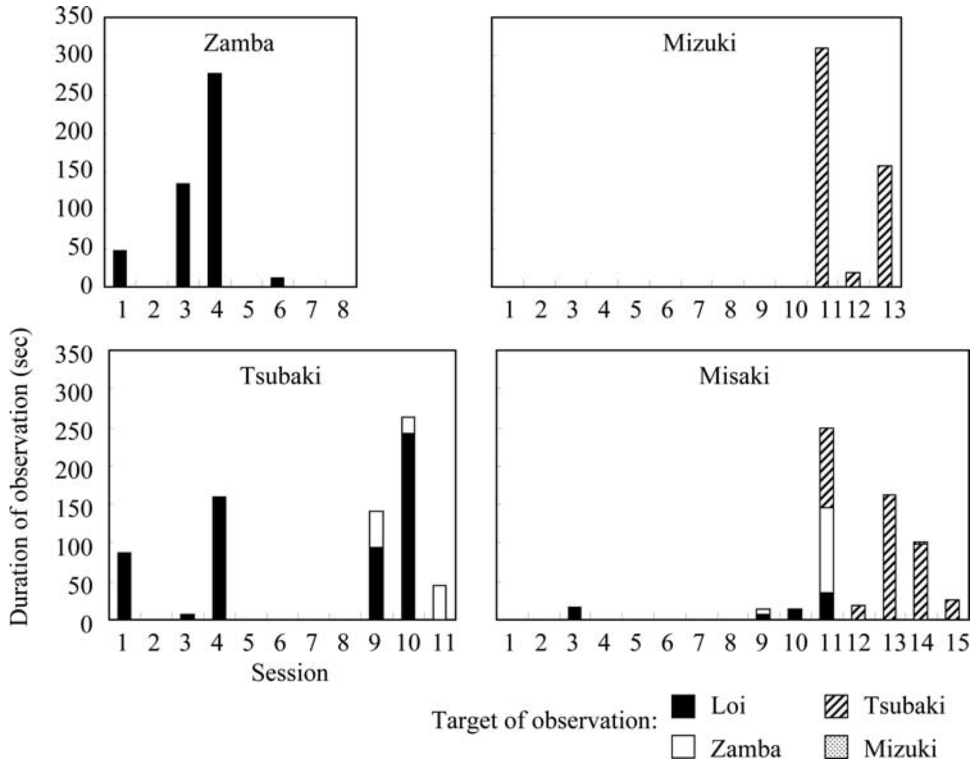

Fig. 8 Observation of model(s) according to the target of observations across sessions

Table 3 Frequency of exclusion in each chimpanzee dyad

Escapee	Chaser				
	Loi	Zamba	Tsubaki	Mizuki	Misaki
Loi	–	0	0	0	0
Zamba	9	–	0	0	0
Tsubaki	12	3	–	0	0
Mizuki	15	23	6	–	0
Misaki	37	17	4	7	–

to pound an object, but places more weight on their systematic understanding of this tool use before their first success, as discussed below.

We were able to track the entire history of the acquisition of tool use for nut cracking by naïve chimpanzees. The process could be broken down into several steps. First, we focused on combinatory manipulations. When we looked at the item directly manipulated by the chimpanzees in each manipulation category, manipulating a stone was more frequent in the manipulation of two objects than in the manipulation of a single object, and more frequent in the manipulation of three objects than in the manipulation of two objects. Therefore, attention to stones is one of the key factors in acquiring nut cracking, as suggested by Hayashi et al. (2005).

When the chimpanzees began to combine three objects, the combinations of objects were often inappropriate initially, such as combining three stones or combining a stone and two nuts. Gradually, however, the frequency of combining the correct set of three objects increased. When the chimpanzees began to combine a correct set of three objects, the order of the combination was not always correct. They sometimes put the objects in an incorrect order, such as placing a hammer stone on an anvil stone and placing a nut on a hammer stone. The frequency of combining objects in the correct order, i.e., the anvil at the bottom, a nut in the middle, and a hammer on top, increased during the last stages of the process. Note that these behavioral changes took place before their first success. In summary, a gradual change from incorrect object combinations to the correct combination was observed in all subjects before their first successes.

Apart from the correct combination of objects, another key factor in acquiring nut-cracking skills is the action of hitting as a means to apply sufficient pressure to a nut shell to break it. At first, the chimpanzees sometimes tried to crack open nuts in a different way, by stepping on them. Stepping on a nut can be regarded as a correct action from a functional perspective, because it puts pressure on the nut. In all subjects, stepping on was first observed before the emergence of the hitting action. This behavior was observed relatively more frequently than the hitting behavior in the first half of the process, but subsequently became more infrequent as the frequency of hitting increased. Their behavioral change shows that the chimpanzees initially recognized the goal, but not the action required to achieve the goal, even after they observed a model.

Initially, the chimpanzees used their hands to hit an object. Each subject's first hitting actions were performed with empty hands, and this continues to predominate in the initial stage. Hitting with a hammer stone came to predominate later on. Therefore, the chimpanzees recognized the action (hitting) at some point during the process, but not how to use a tool (using a stone hammer to hit the target item). The target item of the hitting action was not always a nut; the goal of nut cracking is to open nuts, but the chimpanzees sometimes disregarded the nuts and performed only the hitting action using a target other than a nut, such as hitting an empty anvil stone or hitting a hammer stone on an anvil stone. These examples show that the key action for this tool use—hitting—is not tightly linked to the final goal of this tool use for some time during the acquisition process.

In our study, the anvil stones were fixed to the ground to prevent the chimpanzees from carrying them to unobservable areas. In this sense, the situation is different from wild chimpanzees in Bossou, Guinea, where the chimpanzees use loose stones as anvils (Sugiyama and Koman 1979; Matsuzawa 1994; Biro et al. 2006). Rather, the situation is similar to the case of the Taï Forest on the Ivory Coast, where chimpanzees occasionally use a tree root or rock as an anvil to crack nuts (Boesch and Boesch-Achermann 2000), or the case of capuchin monkeys, which use rocks as anvils (Fragaszy et al. 2004). However, we do not believe that our results would have differed markedly when we had used loose stone as anvils, as the chimpanzees in our study readily used loose stone as anvils in another situation after their first success (Foucart et al. 2005; Bril et al. 2009).

To repeat the points described above, this study showed how chimpanzees acquire tool use for nut cracking. This process can be broken down into several steps. The first is the emergence of a behavior to apply pressure to a nut (involving an incorrect action: stepping on). The second is the emergence of the use of a combination of three objects. The third is the emergence of the hitting action. The fourth is using a tool for hitting, rather than hitting with an empty hand. The last is hitting a nut. The chronological order followed to achieve these steps might differ across individuals, but the point is that the chimpanzees grasped these different aspects at different stages before their first success. In other words, they recognized these different components separately and practiced them one after another; gradually, they united these factors in their behavior, leading to their first success. Note that we analyzed the chimpanzees' behavior before their first successes. Therefore, their behavioral changes were never linked to a food reward. In this sense, the success was not brought about by random trial and error, but arose from their systematic understanding of this tool use.

These behavioral changes before the success might be comparable to that of the wild infant chimpanzees observed by Inoue-Nakamura and Matsuzawa (1997); the chimpanzees in our study, which were all older than 4 years (mean = 6 years and 5 month, SD = 1 year and 4 months) might have gone through the process more quickly than wild infant chimpanzees between birth and 3.5 years of age. However, there is no detailed description of how infant chimpanzees combine objects and how they begin to hit a target in the context of nut cracking. There may be differences between infants and older individuals in terms of their acquisition of nut cracking. In addition, comparisons to capuchin monkeys will help to understand the evolution of cognition underlying tool use in general and the stone tool use that characterized the hominid lineage in particular.

Another implication of this study is the effect of observing a model. It is difficult to prove the effect of observing a model in our study because we lack control data on how the chimpanzees would have behaved if they had not observed a model. However, we can make some inferences about social influences on learning. First, the chimpanzees in our study performed less-advanced manipulations in the pretest situation before observing a model, and they showed continuous progress in the presence of a model. However, it is also true that they did not show evidence of immediate true imitation (Whiten and Ham 1992). Their behavior did not clearly improve immediately after observing successful nut cracking by a peer. Studies have shown that chimpanzees are capable of imitation, but it is still difficult for them (e.g., Myowa-Yamakoshi and Matsuzawa 1999). Our study is in line with these previous studies.

Nevertheless, there may be influences of observing a model when a longer time span was considered. This could be inferred from the order of acquisition and their relationship with the individual who had already acquired the skill. The dominance hierarchy affected who could approach whom. Zamba could observe Loi, the model chimpanzee who was taught by humans how to crack open nuts using stone tools, while the two younger females, Mizuki and Misaki, were never able to approach Loi to observe him. Therefore, Zamba was able to observe Loi cracking nuts for the longest time out of the four naïve chimpanzees, and he was the first of the four to acquire nut-cracking behavior. When Zamba finally cracked a nut on the eighth day, the oldest female, Tsubaki, was able to observe him. Probably stimulated by this, she also began to observe Loi. She was able to crack nuts on the 11th day. After Tsubaki was able to crack nuts on the 11th day, the two younger females, Mizuki and Misaki, were able to observe her. Mizuki first succeeded on the 13th day, and Misaki succeeded on the 15th day.

The observation of group members seemed to have a gradual, long-term influence on the acquisition of nut cracking by naïve chimpanzees. In natural settings where both humans and non-human animals learn complex skills, they will engage in both observation of a model behavior and exploration by themselves. This study simulated such a natural setting, in which the chimpanzees could freely choose whether they observed a model or explored by themselves. Our results illustrated the step-by-step learning of several components of nut cracking, and this might be practiced through intermittent observation of a model and direct handling of related objects between observations. Observation of a model might have a penetrative effect over a few days, during which time the subjects also engaged in their own trials and errors. Many studies of social learning have tried to elucidate the subjects' behavior immediately after observing a model. Our study points out the necessity of considering the effect of social learning from a long-term perspective.

Matsuzawa et al. (2001) applied the term "education by master-apprenticeship" to describe the process of learning skills in chimpanzee communities (see also Matsuzawa 2009). According to this description, a chimpanzee "master" skilled in a certain type of tool use does not actively teach the chimpanzee "apprentice," who is naïve in the use of this tool, but acquires the skill through long-term repetitive observation of the master, who is supported by high levels of tolerance on the master's part. Their claim is true for our case.

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