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ORIGINAL ARTICLE

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How does stone-tool use emerge? Introduction of stones and nuts to naïve chimpanzees in captivity

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Abstract Nut-cracking behavior has been reported in several communities in West Africa but not in East and Central Africa. Furthermore, even within nut-cracking communities, there are individuals who do not acquire the skill. The present study aimed to clarify the cognitive capability required for nut-cracking behavior and the process through which the the nut-cracking behavior emerges. To examine emergence, we provided three naïve adult chimpanzees with a single opportunity to observe human models. A human tester demonstrated nut-cracking behavior using a pair of stones and then supplied stones and nuts to the chimpanzee subjects. Two out of three chimpanzees proceeded to hit a nut on an anvil stone using a hammer stone, one of whom succeeded in cracking open the nuts during the first test session. The third chimpanzee failed to crack open nuts. We used four variables (object, location, body part used, and action) to describe stone/nut manipulation in order to analyze further the patterns of object manipulation exhibited by the subjects. The analysis revealed that there were three main difficulties associated with nut-cracking behavior. (1) The chimpanzee who failed at the task never showed hitting action. (2) The chimpanzee who failed at the task manipulated nuts but rarely stones. (3) The combination of three objects was not commonly observed in the three chimpanzees. We also discuss our results with reference to the effect of enculturation in captivity and the social context of learning in the wild.

Keywords Nut cracking · Tool use · Chimpanzee · Object manipulation

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Introduction

Wild chimpanzees at Bossou, Guinea, West Africa are known to use a pair of stones as hammer and anvil to crack open oil-palm nuts (*Elaeis guineensis*; Sugiyama and Koman 1979). Nut-cracking behavior has also been reported in other communities in West Africa (Hannah and McGrew 1987; Kortlandt and Holzhaus 1987; Boesch et al. 1994). However, no evidence of nut-cracking behavior has been found at research sites in East and Central Africa even though stones and nuts are available (Goodall 1986; Nishida 1990; McGrew et al. 1997). This regional difference in the pattern of distribution of nut-cracking behavior is thought to provide evidence of culture in chimpanzees (McGrew 1992; Whiten et al. 1999; Yamakoshi 2001).

Besides the distinctive pattern of regional distribution, another interesting feature of nut cracking concerns the complexity of the behavior itself. Object–object combination, defined as the manipulation of detached objects in relation to other detached objects, has been suggested in previous studies to be a precursor of tool-using behavior (Torigoe 1985; Visalberghi 1988; Takeshita 2001; Hayashi and Matsuzawa 2003). Object–object combination is not a common behavior in primate species. Great apes and capuchin monkeys are the only species that frequently exhibit object–object combination, while other primates such as lemurs and macaques do not perform this behavior (Torigoe 1985; Fragaszy and Adams-Curtis 1991).

Matsuzawa (1996) devised a “tree-structure analysis” for describing the manipulation of multiple objects observed in tool use by chimpanzees. According to this analysis, most examples of tool use by chimpanzees can be categorized as “level 1” tool use, because they involve only a single relationship between detached objects, in which a tool is related to a target, such as a twig to termites during termite-fishing. In contrast, nut-cracking behavior is categorized as “level 2” tool use, because there are two kinds of relationships among the detached objects involved: (1) a nut is placed on an anvil stone, and (2) the nut is hit by a hammer stone. Thus, the skill requires the combination of three detached objects (an anvil stone, a hammer stone, and a target nut) in a specific order. In that sense, nut-cracking behavior using a pair of stones is likely to be one of the most complex types of tool use ever found in the wild. In fact, the age at which individuals in the wild acquire the skill is higher in "level 2" than in "level 1" tool use (Matsuzawa et al. 2001). Several previous studies have also focused on the hierarchical structure of object–object combination in human children and in non-human primates as an indicator of cognitive capability (Greenfield et al. 1972; Johnson-Pynn et al. 1999; Westergaard 1999).

A complementary approach to the above is the study of the developmental processes involved in acquiring the complex nut-cracking behavior. Infant chimpanzees in the Bossou community start to crack open oil-palm nuts at 3.5–6 years of age (Matsuzawa 1994; Matsuzawa et al. 2001). Inoue-Nakamura and Matsuzawa (1997) analyzed the developmental process in the acquisition of nut-cracking behavior at Bossou in detail. This study showed that the stone–nut manipulation evolves from a single action on a single object (only stone or only nut) to multiple actions on multiple objects (several stones, several nuts, or both stones and nuts). All basic actions necessary for nut-cracking behavior are already observed in 2.5-year-old infants. However, these infants fail to combine the actions appropriately before they reach the age of 3.5 years or older. Boesch and Boesch (1984) and Boesch and Boesch-Achermann (2000) reported the development of nut-cracking behavior in the chimpanzees of Tai forest, Côte d'Ivoire. No chimpanzee younger than 5 years old succeeded in opening a coula nut (*Coula edulis*), although their attempts were performed using the right materials and behavior. Infants in the Tai community between 5 and 6 years of age succeeded in opening coula nuts, but much perseverance and practice was required.

Infant chimpanzees in the wild have prolonged exposure to nut-cracking behavior performed by adults. They carefully observe the adults' behavior and gradually acquire the nut-cracking skill. Such long-term observation from birth seems to play an important role in infants' acquisition of the nut-cracking skill ("education by master-apprenticeship," Matsuzawa et al. 2001; "bonding- and identification-based observational learning, BIOL," de Waal 2001). However, some exceptions have been reported by Matsuzawa (1994): three chimpanzees, one juvenile and two adults, failed to show nut-cracking behavior during more than a decade's observation at Bossou.

Two questions arise from our overview of the various aspects of nut-cracking behavior. (1) Why do some individuals fail to acquire the skill even though they are members of a nut-cracking community? (2) Why do chimpanzees of a particular community perform nut cracking while those in a different community do not? These questions are in turn related to a larger question: why and how did stone-tool use emerge? Kortlandt (1986) suggested the possibility that the chimpanzees at Bossou had learned the skill through observing nut-cracking behavior by humans. However, such notions remain speculation, as the emergence of stone-tool use in a wild chimpanzee community has never been documented. The question should be modified as follows: how can nut cracking emerge through observation?

In the present study, we provided three adult chimpanzees living in a captive group with an opportunity to crack nuts. They had no prior experience with nut cracking or seeing the stone-tool use being performed. Several studies have reported nut-cracking behavior in captive chimpanzees (Sumita et al. 1985; Hannah and McGrew 1987). Visalberghi (1987) looked at emergence of nut cracking by examining the kinds of combinations between nuts and tools in captive capuchin monkeys, although the monkeys did not use anvil stones to support nuts. However, precise micro-analysis of stone/nut manipulation as an indicator of cognitive capability has not been attempted in any previous study. The present study aimed to explore cognitive capabilities necessary for the emergence of nut-cracking behavior by analyzing stone/nut manipulation in detail. The introduction of nuts and stones to naïve chimpanzees may provide clarification of what can and cannot be accomplished by the chimpanzees. We examined the subjects' behavioral repertoire during stone/nut manipulation and focused on the combination of detached objects. These variables may reflect the cognitive processes involved in the emergence of nut cracking.

Methods

Subjects

The subjects of the present study were three young adult female chimpanzees, Ai, Chloe, and Pan, living in a captive group at the Primate Research Institute of Kyoto University (Table 1). They have performed various kinds of cognitive tasks but had no prior experience manipulating nuts with stones (Matsuzawa 2003). The outdoor compound was enriched with 15-m-high climbing frames and about 500 planted trees of approximately 60 species (Ochiai and Matsuzawa 1997). The first nut-cracking test session was conducted on 25

Table 1 Chimpanzee subjects participating in the present study

Name	Date of birth	Age (years)[a]	Born	Human reared
Ai	Oct 1976[b]	21	Wild	From 1 year of age
Chloe	13 Dec 1980	16	Paris Zoo	From birth
Pan	7 Dec 1983	13	Kyoto University	From birth

[a]At time of first test session
[b]Estimated

October 1997. Each chimpanzee subject participated in a single test session in this first phase. The follow-up training sessions began around 4 years later, on 7 November 2001 for Ai and Pan, and on 16 March 2002 for Chloe. At the time of the first test session, the subjects were living in a group of 11 chimpanzees. In the year 2000, all three subjects gave birth to offspring. The follow-up training sessions were thus conducted with these same subjects in the presence of their infants. However, the present study focused on the performance only of the mothers throughout both phases.

Materials

In the first test session, we provided seven natural stones that had been used by wild chimpanzees at Bossou. The shape, size, and weight (range approximately 0.4–2.0 kg) of the stones varied. They were typical in shape and weight of stones used as both hammer and anvil in the chimpanzees' natural habitat (Sakura and Matsuzawa 1991). We used macadamia nuts (*Macadamia integrifolia*) instead of the oil-palm nuts cracked at Bossou due to ease of availability. The kernel of the macadamia nut is edible, and its round shell is hard enough to resist the chimpanzees' bite. We provided a small wooden platform ("chair") to the chimpanzees on which they were to remain seated once inside the large experimental booth.

In the follow-up training sessions, several stones not used in the wild ("non-natural" stones) were added to the natural stones used in the first test session (Fig. 1). The non-natural anvil stones (13–30 kg) had artificially made depressions on their upper surface into which nuts could be placed, preventing them from rolling off. In addition to the stones and nuts, we also provided five kinds of plants (leaves or branches) to the subjects during the training sessions. The purpose of this was to examine the occurrence of inappropriate behaviors in the context of using stones for cracking.

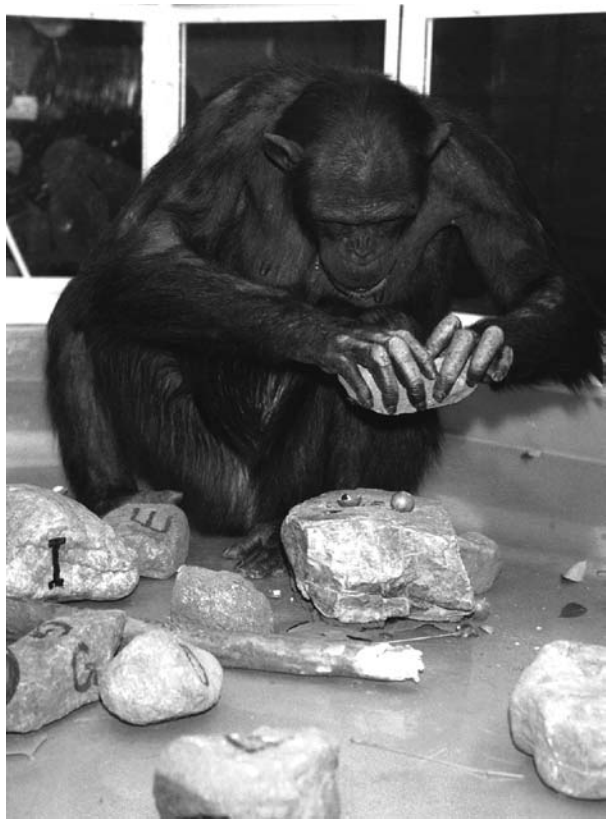

Fig. 1 A chimpanzee, Pan, hitting a nut on an anvil stone using a hammer stone

Experimental setting

In the first test session, a human tester (TM) faced a chimpanzee in a large playroom (about 36 m^2). The human tester first laid out stones in front of the subject. Then, he cracked open a nut using hammer and anvil stones and handed the kernel to the subject. This means that the chimpanzees had a single-observation opportunity to observe a nut be cracked open by a pair of stones and to see that an edible part is in it. Afterwards, the tester handed the subject several nuts one at a time and verbally and gesturally encouraged the subject to crack them open. If the subject failed to show the nut-cracking behavior and ceased any attempts, the human tester repeated his modeling of nut cracking and allowed the subject to take the kernel. The session lasted for an average of about 20 min. All events during the session were recorded by video cameras outside the booth.

In the follow-up training sessions conducted approximately 4 years later, a pair of mother–infant chimpanzees entered a room (generally measuring about 7 m^2). The stones, plants, and nuts had been placed inside the room in advance, and the tester (TM) positioned himself near the stones. The tester sat quietly without showing any modeling behavior for the first 5 min. If the subject combined stone and nut and tried to crack the latter open, we continued the observation without any demonstration or molding behavior. If the subject did not show any behaviors that may lead to nut cracking in the first 5 min, then the human tester provided active teaching in three ways: (1) demonstrating nut cracking, (2) verbally and gesturally encouraging the subject to manipulate nuts and/or stones, and (3) molding the subject's hands to crack open nuts. The session ended when 30 min had elapsed or when the subject had cracked open 30 nuts. The subjects' infants were free to access any objects around them and to interact with their mothers. The training sessions were conducted at intervals of at least 1 week. Throughout the study, the human tester modeled the nut-cracking behavior or controlled the subjects' behavior in a face-to-face situation. All sessions were video-recorded from outside, through the transparent-acrylic wall of the booth.

Analysis

We analyzed the manipulation of stones and nuts performed by the three subjects during the first test session. We described object manipulation focusing on four variables: object, location, body part used, and action (see details in Table 2). Although we mainly followed Inoue-Nakamura and Matsuzawa (1997) in classifying the actions, we established several new categories to describe more precisely the type of object manipulation observed. We also added behaviors that had not been reported in wild chimpanzees.

We described the flow of behaviors as sequences of manipulation patterns. Each manipulation pattern was defined in terms of the above-mentioned four variables. We also needed to count the frequency of each manipulation pattern. For that purpose, we introduced the term ‘‘bout’’ for further analysis. A bout was defined as a behavior involving the same four variables. When one of the four variables changed, including changes in subcategory, a bout ended and the next bout began. For example, if the subjects put a nut on stone A with the right hand and then hit the nut with stone B using the right hand, we coded the first manipulation pattern as ‘‘ put a nut on a stone with one hand’’ and the second manipulation pattern as ‘‘ hit a nut on a stone with another stone held in one hand’’ (the underlined words and phrases correspond to the four variables). As the number of possible combinations among subcategories was enormous (as indicated by Table 2), we classified manipulation patterns by focusing on the categories of the four variables rather than subcategories. The overall variety in the manipulatory behaviors exhibited was indicated by the total number of manipulation patterns observed. The frequency of a particular manipulation pattern was indicated by the number of bouts in which the pattern was exhibited.

For the training sessions, we focused only on the number of nuts cracked open by the subjects during their first ten sessions. We recorded the total number of nuts cracked open by the subjects in each session in order to trace the individuals' performance as the sessions progressed.

Results

We first present a summary of the three subjects' performance during the initial test session, followed by a report of our precise analysis of object manipulation, focusing on overall features, hitting actions, stone manipulation, and combinations among objects. We also highlight certain behaviors that are not covered in the above analysis. Finally, we report a summary of performance during the follow-up training sessions.

Summary of performance during the first test session

The length of the test session was 13 min for Ai, 18 min for Chloe and 26 min for Pan. Although the chimpanzees had had no prior experience observing or performing stone-tool use for cracking nuts, two of the three subjects, Chloe and Pan, succeeded in placing a nut on an anvil stone and hitting it with a hammer stone after a single opportunity observing human models. Moreover, one chimpanzee, Pan, successfully cracked open nuts during her first test session, 14 and 16 min after first touching the objects. The one remaining chimpanzee, Ai, did not succeed in cracking any nuts in the first test session. Further detailed analysis of the subjects' stone/nut manipulation follows, including clarification of the differences in apparent failure/success among the three subjects.

Analysis of stone/nut manipulation during the first test session

The chimpanzees manipulated stones and nuts in various ways. Each manipulation pattern was defined as a combination of the four variables: object, location, body part used, and action. We identified a total of 56 manipulation patterns, of which 23 were exhibited by Ai, 29 by Chloe, and 44 by Pan. The total number of bouts observed was 147 for Ai, 271 for Chloe, and 515 for Pan. Table 3 lists all manipulation patterns and their descriptions, as well as the number of bouts recorded for each manipulation pattern for each subject. Pan's repertoire included the majority of manipulation patterns exhibited by Ai and Chloe. Among the 56 manipulation patterns, 13 (23%) were common to all three subjects. Eleven manipulation patterns (20%) were common to Pan and Chloe, three manipulation patterns (5%) to Pan and Ai, and none to Chloe and Ai. A total of 17 manipulation patterns (30%) were exhibited solely by Pan, 5 manipulation patterns (9%) by Chloe, and 7 manipulation patterns (13%) by Ai.

As Table 3 shows, the single chimpanzee who failed (Ai) did not show any kind of hitting action on any object. The total number of bouts that included a hitting action was 0 for Ai, 48 for Chloe, and 42 for Pan. Nut-cracking behavior cannot be accomplished without hitting action.

Next, we looked more closely at the object that was being manipulated by the subjects, in other words, whether the ‘‘object’’ variable was a stone or a nut. Focusing on the ‘‘object’’ category in Table 3, Table 4 lists the number of bouts and the number of manipulation patterns for stones and nuts in the three subjects. This clearly shows that almost all of the manipulation exhibited by Ai, who failed to crack nuts, was performed

Table 2 List of the four variables used to describe manipulation patterns

Variable	Definition	Category	Subcategory	Definition	Number of categories	Number of subcategories
Object	Manipulated object	Stone	$n=7$		3	10
		Nut	Nut, shell			
		Nut on stone				
Location	Target of the manipulated object	Stone	$n=7$		6	13
		Two stones		Pile of two stones		
		Nut	Nut, shell			
		Not on stone				
		Chair				
		No location		No combination made among objects		
Body part used	Body part used for manipulation	One hand	Right, left		4	6
		Both hands				
		Mouth				
		One foot	Right, left			
Action[a]	Action used for manipulation	Touch		Touch an object with hands and/or feet	22	22
		Kiss		Bring an object into contact with lips (kiss), tongue (lick), and nose (sniff) without holding it		
		Hold		Hold a stone (includes transportation). The stone must be lifted up		
		Press		Press an object against the ground or another object; distinguished from touch by the jerky movement of the object		
		Hit		Hit an object against/on the ground or a stone with the hands, irrespective of whether or not another object is being held by the subject		
		Put		Put an object on another object		
		Turn		Turn over an object		
		Point		Point to a stone with the index finger		
		Drop		Drop a stone that is placed on another stone		
		Pick		Pick up a nut, a kernel, or a piece of kernel stuck inside a broken shell with the fingers		
		Mouth		Place a nut in the mouth; distinguished from Bite or Eat by the lack of use of teeth		
		Bite		Bite a nut using the teeth. Simultaneous contact with a hand is required		
		Eat		Eat a kernel using the teeth. Simultaneous contact with a hand is not required		
		Peel		Peel off the shell of a nut, including picking out the kernel stuck inside		
		Support		Support a nut on the stone with a hand so as to prevent it from rolling off		
		Replace		Replace a nut on the stone with a hand		

Table 2 (Continued)

Variable	Definition	Category	Subcategory	Definition	Number of categories	Number of subcategories
		Hold + kiss*		Kiss an object while holding it		
		Transfer*		Change the hand with which an object is held		
		Release*		Place an object on the floor		
		Contact*		Bring an object into contact with another object and retrieve it; distinguished from Put by the lack of releasing		
		Try to hand over*		Attempt to give an object to the tester		
		Hand over*		Give an object to the tester		

[a]We followed Inoue-Nakamura and Matsuzawa (1997) in describing the actions. Actions marked by *asterisks* were not described in the previous study. The other actions are those from the previous study, which listed actions separately for stones and nuts and identified 21 actions for stones and 19 for nuts. We, however, listed actions jointly, so that in some cases the original definition was changed to include "an object," meaning either stone or nut. We did not use some actions that were used in the previous study because we identified the body part used instead

on the nuts themselves, while she rarely manipulated stones. In contrast, Pan, the successful subject, manipulated stones in various ways. The results of statistical analyses using χ^2 tests are shown in Table 5.

All three chimpanzees showed manipulation patterns in which they combined two or three objects together. These are listed in Table 6. "Putting a nut on a stone" is a necessary two-object combination for nut cracking. All three chimpanzees showed this combination and it appeared within 1–4 min after the subject first touched the objects (1 min in Ai, 1 min in Chloe, and 4 min in Pan). However, the subjects also showed other types of two-object combinations which are not necessary for nut cracking. For example, Chloe hit a stone with a nut and Pan hit a stone with another stone. "Hitting a nut on a stone with another stone" is the necessary combination of three objects for nut cracking. Ai and Pan showed other types of three-object combination not necessary for nut cracking, although the number of manipulation bouts for these combinations was very small.

Figure 2 shows the time course of behavioral change in the first test session for each subject. Two kinds of data are shown together: number of manipulation patterns and number of bouts recorded as appropriate manipulation patterns: hitting a nut on a stone with another stone. The number of manipulation patterns reached an asymptote level by the end of the first test session in each subject. Chloe first hit a nut on an anvil stone with a hammer stone 2 min after she first touched the objects. She then shifted to hitting a nut on the floor with a hammer stone, but returned to hitting a nut on an anvil stone with a hammer stone 9 min after the first touch. Pan first hit a nut on an anvil stone with a hammer stone 10 min after the first touch. She succeeded in cracking open nuts 14 and 16 min after the first touch. Ai did not show the manipulation pattern of hitting a nut on a stone with another stone.

Table 3 also reports certain behaviors that do not directly lead to successful nut cracking. For example, Ai pressed a nut on the floor or on a stone with one hand or with a foot. Chloe hit a stone with a nut. Both Chloe and Pan tried to crack open the nut on the floor. However, these attempts were unsuccessful as the round macadamia nut could not be positioned stably on the floor and rolled around after being hit. We also noted other unique behaviors shown in the nut-cracking situation, although they are not listed as examples of object manipulation in Table 3. All three chimpanzees tried to hand over a nut to the human tester when they failed to open it. One chimpanzee, Chloe, moved the hands of the human tester near a stone/nut (called "crane" behavior), or even hit a nut on a stone with the tester's hand.

Summary of performance during the follow-up training sessions

Figure 3 shows the cumulative number of nuts cracked by each subject during the first ten sessions of the training phase. Chloe, who had hit a nut in the first test session, succeeded in cracking open nuts in the first training session. She cracked all 30 nuts provided to her in 18 min. She began to crack open nuts by herself without any aid from a human model. Pan, who had succeeded in the first test session, cracked open only two nuts in the first training session. Both Chloe and Pan continued to crack open nuts throughout the first ten sessions of the training phase. In contrast, Ai did not succeed in cracking open any nuts. Even though the tester attempted various ways of active teaching in a

Table 3 List of manipulation patterns observed in each chimpanzee

Object	Location	Body part used	Action	Description	Number of bouts recorded		
					Ai	Chloe	Pan
Stone	–	One hand	Touch	Touch a stone with one hand	3	4	29
Stone	–	Both hands	Touch	Touch a stone with both hands	0	1	5
Stone	–	Mouth	Kiss	Kiss a stone with mouth	0	4	0
Stone	–	One hand	Hold	Hold a stone in one hand	1	25	61
Stone	–	Both hands	Hold	Hold a stone in both hands	0	0	3
Stone	–	One hand	Turn	Turn over a stone with one hand	0	2	9
Stone	–	Both hands	Turn	Turn over a stone with both hands	0	0	4
Stone	–	One hand	Point	Point to a stone with an index finger	0	0	2
Stone	–	One hand	Drop	Drop a stone from one hand	0	0	2
Stone	–	One hand	Hold + kiss	Kiss a stone while holding it in one hand	0	0	4
Stone	–	Both hands	Hold + kiss	Kiss a stone while holding it in both hands	0	1	0
Stone	–	Both hands	Transfer	Transfer a stone from one hand to the other	0	7	5
Stone	–	One hand	Release	Release a stone on the floor with one hand	0	24	59
Stone	–	Both hands	Release	Release a stone on the floor with both hands	0	0	2
Stone	–	One hand	Try to hand over	Try to hand over a stone to the tester with one hand	0	4	11
Stone	–	One hand	Hand over	Hand over a stone to the tester with one hand	0	0	1
Stone	Stone	One hand	Contact	Contact a stone to another stone with one hand	0	0	3
Stone	Stone	Both hands	Contact	Contact a stone to another stone with both hands	0	0	1
Stone	Stone	One hand	Put	Put a stone on a nother stone with one hand	1	0	4
Stone	Stone	One hand	Hit	Hit a stone with another stone held in one hand	0	0	7
Stone	Stone	Both hands	Hit	Hit a stone with another stone held in both hands	0	0	1
Stone	Nut	One hand	Hit	Hit a nut on the floor with a stone held in one hand	0	16	5
Stone	Nut	Both hands	Hit	Hit a nut on the floor with a stone held in both hands	0	0	4
Stone	Nut on stone	One hand	Hit	Hit a nut on a stone with another stone held in one hand	0	21	15
Stone	Nut on stone	Both hands	Hit	Hit a nut on a stone with another stone held in both hands	0	0	7
Nut	–	One hand	Pick	Pick up a nut with fingers	41	35	57
Nut	–	Mouth	Mouth	Mouth a nut	2	16	55
Nut	–	One hand	Touch	Touch a nut with one hand	4	7	2

Table 3 (Continued)

Object	Location	Body part used	Action	Description	Number of bouts recorded		
					Ai	Chloe	Pan
Nut	–	One hand	Bite	Bite a nut while holding t in one hand	19	14	22
Nut	–	One hand	Eat	Eat a kernel that was held up by one hand	7	5	2
Nut	–	Mouth	Eat	Eat a kernel that was directly picked up by mouth	0	1	7
Nut	–	One hand	Press	Press a nut against the ground with one hand	3	0	0
Nut	–	Foot	Press	Press a nut against the ground with one foot	5	0	0
Nut	–	Both hands	Peel	Peel off the shell of a nut using both hands	0	0	2
Nut	–	Mouth	Kiss	Kiss a nut with mouth	0	1	6
Nut	–	One hand	Replace	Replace a nut on a stone with one hand	2	0	0
Nut	–	One hand	Hold + kiss	Kiss a nut while holding it in one hand	1	0	6
Nut	–	Both hands	Transfer	Transfer a nut from one hand to the other	6	6	5
Nut	–	One hand	Release	Release a nut on the loor with one hand	4	10	14
Nut	–	Mouth	Release	Release a nut on the floor with both hands	0	0	3
Nut	–	One hand	Try to hand over	Try to hand over a nut to the tester with one hand	3	24	6
Nut	–	Mouth	Try to hand over	Try to hand over a nut to the tester with mouth	0	1	0
Nut	–	One hand	Hand over	Hand over a nut to the tester with one hand	6	9	5
Nut	–	Mouth	Hand over	Hand over a nut to the tester with mouth	0	1	0
Nut	Stone	One hand	Contact	Contact a nut to a stone with one hand	8	2	25
Nut	Stone	Mouth	Contact	Contact a nut to a stone with mouth	0	0	1
Nut	Stone	One hand	Put	Put a nut on a stone with one hand	19	17	35
Nut	Stone	Mouth	Put	Put a nut on a stone with mouth	0	0	12
Nut	Nut	One hand	Put	Put a nut on another nut (shell) with one hand	2	0	0
Nut	Chair	One hand	Put	Put a nut on a chair	3	0	0
Nut	Stone	One hand	Hit	Hit a stone with a nut held in one hand	0	10	0
Nut	Two stones	One hand	Contact	Contact a nut to a pile of two stones with one hand	2	0	1
Nut	Two stones	One hand	Put	Put a nut on a pile of two stones with one hand	2	0	0
Nut on stone	–	One hand	Press	Press a nut against a stone with one hand	3	0	0
Nut on stone	–	One hand	Support	Support a nut on a stone with a hand to prevent it from rolling	0	2	2
Nut on stone	–	One hand	Hit	Hit a nut on a stone with one hand	0	1	3

face-to-face situation, Ai never forcefully hit a nut on a stone with another stone.

Discussion

The present study demonstrates that nut cracking can emerge in chimpanzees after no more than a single opportunity to observe a model. Indeed, since no testing was performed without prior observation of a model, it remains a possibility that the emergence of nut cracking would have occurred spontaneously. The important point here is that prolonged observation was unnecessary for the two chimpanzees who were successful. However, it also became clear that nut-cracking was a difficult task in general. The following sections will dis-

Table 4 The number of bouts and the number of different patterns of stone/nut manipulation in the three chimpanzees. The figures in parentheses show the percentage of the total for each classification

Object	Ai	Chloe	Pan
Number of bouts			
Stone	5 (3)	109 (40)	244 (47)
Nut (including "Nut on stone")	142 (97)	162 (60)	271 (53)
Total	147 (100)	271 (100)	515 (100)
Number of manipulation patterns			
Stone	3 (13)	11 (38)	23 (52)
Nut (including "Nut on stone")	20 (87)	18 (62)	21 (48)
Total	23 (100)	29 (100)	44 (100)

Table 5 χ^2 Tests for stone vs. nut manipulation in each subject pair

	Ai	Chloe	Pan
Number of bouts			
Ai	–	65.14**	94.25**
Chloe	–	–	3.68NS
Pan	–	–	–
Number of manipulation patterns			
Ai	–	4.04*	9.79**
Chloe	–	–	1.44NS
Pan	–	–	–

*$P < 0.05$, **$P < 0.01$, *NS* not significant

cuss the three main difficulties underlying nut-cracking behavior, the possible reasons for one of our subjects' failure, the role of enculturation, and a plausible explanation for cultural differences in the wild.

Why is nut cracking difficult?

In this study, two of three naïve chimpanzees succeeded in cracking open nuts. The remaining one chimpanzee, Ai, failed to acquire the nut-cracking skill even after extensive sessions during the follow-up training phase. Our analysis indicated that there were three main difficulties which may underlie apparent failure: (1) the lack of hitting action, (2) the scarcity of stone manipulation, and (3) the difficulties involved in combining three objects.

Lack of hitting action Torigoe (1985) compared object manipulation among 74 species of non-human primates. The results showed that "strike" (corresponding to hitting action in the present study) was not a common action in most primate species; only the great apes and capuchin monkeys performed "strike" action in the context of object manipulation. When Toth et al. (1993) tested a male bonobo named Kanzi in a stone-flaking task, he initially also lacked the pounding action necessary for flaking. Hitting action can be divided into two types of manipulation: hitting by hand, and hitting with an object. In the latter case, the point of impact and the fine adjustment of the force used to hit may have a great effect on the result of the hitting action. If the angle of the strike is too sharp or the impact surface too small, the nut will be propelled sideways, off the anvil. If the force is insufficient, the hard shell will not crack. If the force used is too great, the nut will be smashed completely.

Scarcity of stone manipulation The goal of nut-cracking behavior is to obtain the edible kernel of a nut. The subjects initially pay attention to nuts and then must shift their attention to stones, as the tools necessary to crack open the nuts. Putting the target nut aside and shifting attention to the stones can be seen as a form of "detour" in reaching the goal in a problem-solving task.

Difficulties in combining three objects Nut-cracking behavior comprises the only instance where three detached objects have to be combined hierarchically (known as "level 2" tool use, Matsuzawa 1996). However, most examples of tool use reported in wild chimpanzees are based on the combination of two detached objects ("level 1" tool use). The three subjects in the present study showed appropriate combinations of two objects necessary for nut cracking (putting a nut on a stone) within 1–4 min after they first contacted the objects. However, the subjects also produced a considerable number of other inappropriate combinations of two

Table 6 Object–object combinations exhibited by the three chimpanzees. Asterisks indicate behaviors that are necessary for nut cracking

Number of objects involved	Description	Object	Location	Action	Number of bouts		
					Ai	Chloe	Pan
Two	Put a nut on a stone*	Nut	Stone	Put	19	17	47
	Contact a nut to a stone	Nut	Stone	Contact	8	2	26
	Hit a stone with a nut	Nut	Stone	Hit	0	10	0
	Hit a nut on the floor with a stone	Stone	Nut	Hit	0	16	9
	Put a stone on another stone	Stone	Stone	Put	1	0	4
	Contact a stone to another stone	Stone	Stone	Contact	0	0	4
	Hit a stone with another stone	Stone	Stone	Hit	0	0	8
Three	Hit a nut on a stone with another stone*	Stone	Nut on stone	Hit	0	21	22
	Contact a nut to a pile of two stones	Nut	Pile of two stones	Contact	2	0	1
	Put a nut on a pile of two stones	Nut	Pile of two stones	Put	2	0	0

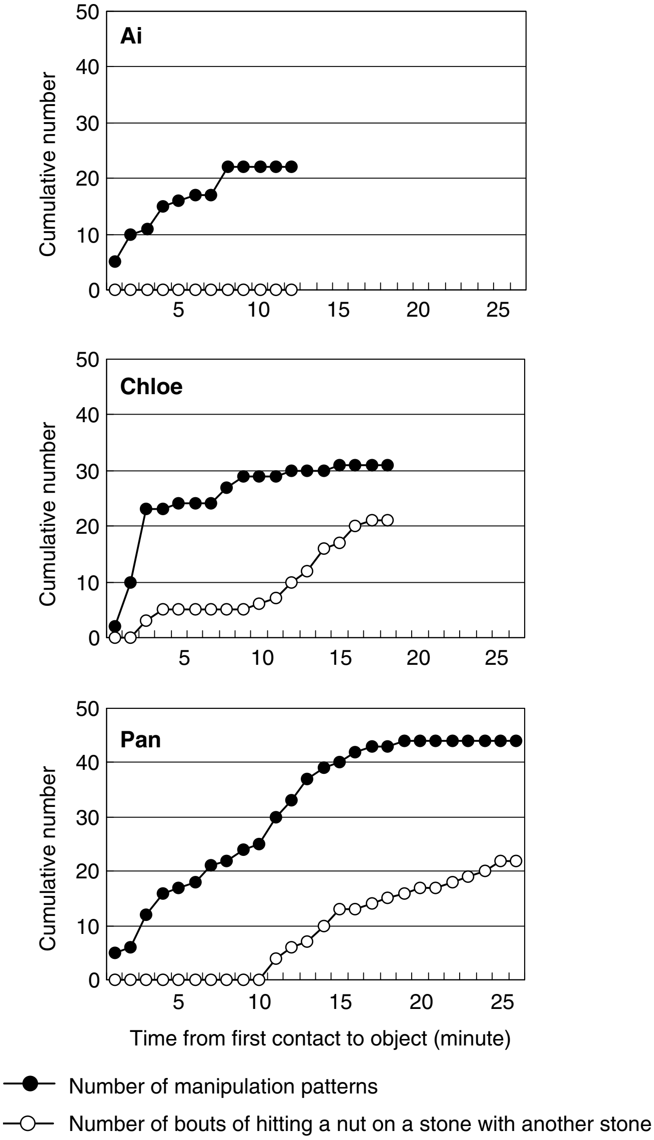

Fig. 2 The time course of behavioral change during the first test session for each subject. Two kinds of data are shown together. *Solid symbols* represent the cumulative number of manipulation patterns shown by the subjects. *Open symbols* represent the cumulative number of bouts of hitting action using a hammer stone shown by the subjects

objects. This means that the subjects attempted to solve the problem by combining two objects, a frequent behavioral pattern in chimpanzees.

Let us return to the first question raised in the Introduction: why do some individuals fail to acquire the skill even though they are members of a nut-cracking community? An individual has to conquer all three main difficulties to acquire the tool-using skill. The reason for the failure could be a subtle deficit such as physical disability or malfunctioning, or the individual may have missed a ''critical period'' of learning (Matsuzawa 1994). Even a normal individual may not acquire the skill if he/she fails to conquer just one of the three difficulties.

Ai's failure

We would like to expand our discussion by considering in more detail the case of our subject, Ai, who failed to crack open nuts in the present study. Interestingly, Ai has demonstrated remarkable abilities in a variety of cognitive tasks (Matsuzawa 2003). For example, she has learned to use visual symbols to express how she perceived the outside world (Matsuzawa 1985a, b). She has also learned to label sets of 0–9 items using the corresponding Arabic numerals (Biro and Matsuzawa 2001), and she can memorize up to five numerals at a time (Kawai and Matsuzawa 2000). However, she failed to acquire nut-cracking behavior in the current study. Thus, the acquisition of nut-cracking behavior may not be correlated with other kinds of cognitive ability in the adult chimpanzee.

Ai's failure at nut cracking derived mainly from two sources: the lack of manipulation of stones and the lack of hitting action. Ai ate the kernel of macadamia nuts cracked open by the human tester even though she did not use stone tools by herself. Thus, her failure was not due to a lack of motivation. In addition, Ai succeeded in a honey-fishing task simulating termite-fishing inside an experimental booth (Hirata and Celli 2003). Thus, she possesses the eye–hand coordination necessary for using tools.

Finally, we wish to highlight a behavior that Ai exhibited during the first test session. Ai showed pressing action on the nut with her hand or foot, and put a nut on a stone and pressed it with her knuckle instead of hitting it with another stone. These behavioral patterns have also been observed in the wild, in infant chimpanzees who have not yet acquired stone-tool use (Inoue-Nakamura and Matsuzawa 1997). Matsuzawa (1994) also reported that a juvenile chimpanzee at Bossou who failed to use stone tools would occasionally hit a nut on an anvil stone with her wrist. In sum, the behavior of Ai was comparable to that of infant and juvenile chimpanzees who do not have the skill to crack open nuts.

The effect of enculturation

The subjects of the present study lived in a captive environment and were highly ''enculturated'' (Tomasello et al. 1993). All of them were raised by humans either from birth or from the age of 1 year. They had had abundant experience interacting with humans and had participated in various kinds of cognitive experiments in face-to-face situations, including those focusing on imitation of gestures and object manipulation (Myowa-Yamakoshi and Matsuzawa 1999, 2000; Kojima 2003). These factors may have had an effect on the chimpanzees' performance in the nut-cracking situation. The chimpanzees carefully observed the tester's manipulation and attempted to crack open the nuts by themselves.

All three chimpanzees exhibited behaviors that could not occur in the wild. They ''gave'' nuts to the tester

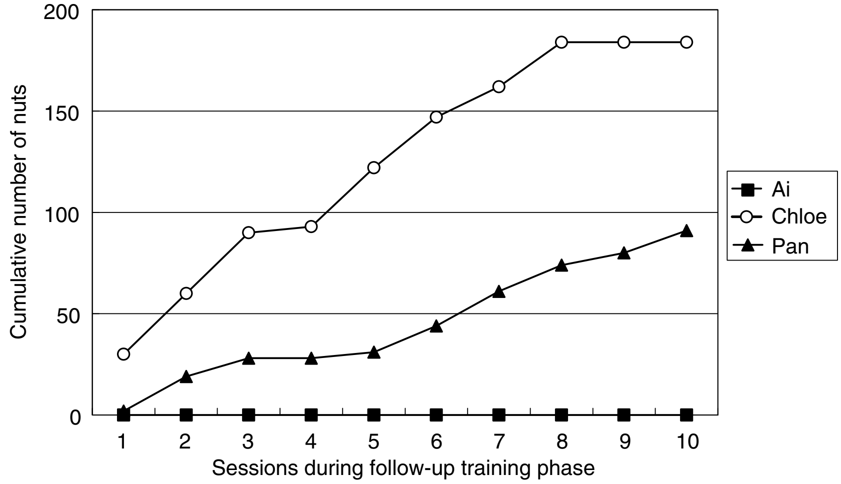

Fig. 3 Cumulative number of nuts cracked by each subject during ten sessions during the second phase

after failing to crack them open. Some authors have reported that apes in captivity attempted to have the tester solve a problem that was beyond their capabilities, in what is referred to as "social tool use" (Bard 1990; Gomez 1990). One of our chimpanzees, Chloe, showed an interesting behavior in terms of comparison with human studies. Chloe took the hands of the tester and moved them near the stone or the nut ("crane" behavior). She even took the tester's hand and hit a nut on a stone with it. Such behavior that uses an adult's hands as tools is often reported in autistic children (Frith 1989).

A plausible explanation for cultural differences

Let us return to the second question: why do chimpanzees of particular communities perform nut cracking while those in a different community do not? First, let us consider the social learning situation in the wild. Adult nut-crackers in the wild rarely perform active teaching. There have been only two possible cases reported (Boesch 1991), although observation of nut-cracking behavior has been conducted for many years (Boesch and Boesch-Achermann 2000; Matsuzawa et al. 2001; Biro et al. 2003). Instead, the infants carefully observe the behavior of adults, and the adults, in turn, are tolerant of the infants' behavior. The reason why the majority of individuals in nut-cracking communities succeed in acquiring the behavior may be derived from a form of social learning described as "education by master-apprenticeship" (Matsuzawa et al. 2001) or "BIOL" (de Waal 2001). Long-term exposure to the adults' behavior from just after birth may facilitate infants' acquisition of the complex skill.

The natural environment that wild chimpanzees inhabit provides various food resources. The foods can be categorized into two types (Yamakoshi 2001). One includes "easy-to-get" foods, such as fruits, that are not physically protected. The other includes "hard-to-get" foods, such as nuts or termites inside a mound, that are protected; the individual must use tools to obtain them. Even if an individual succeeds in acquiring nut-cracking behavior, he can also choose other "easy-to-get" foods as opposed to employing the complex tool use. The problem is one of "cost–benefit". If the availability of "easy-to-get" foods decreases, individuals may choose to use complex tools.

In contrast, consider an infant chimpanzee living in a community whose members are habitual nut-crackers. The mother is likely to use the stone tools and spend considerable time cracking nuts. The infant who is attached to the mother for a long time has no opportunity to look for other "easy-to-get" foods. This limitation on the infant's behavior as well as the increased opportunity to observe nut cracking at close distance may facilitate the infant's acquisition of the most complex type of tool use in the wild.

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