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Perspectives on object manipulation and action grammar for percussive actions in primates

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The skill of object manipulation is a common feature of primates including humans, although there are species-typical patterns of manipulation. Object manipulation can be used as a comparative scale of cognitive development, focusing on its complexity. Nut cracking in chimpanzees has the highest hierarchical complexity of tool use reported in non-human primates. An analysis of the patterns of object manipulation in naive chimpanzees after nut-cracking demonstrations revealed the cause of difficulties in learning nut-cracking behaviour. Various types of behaviours exhibited within a nut-cracking context can be examined in terms of the application of problem-solving strategies, focusing on their basis in causal understanding or insightful intentionality. Captive chimpanzees also exhibit complex forms of combinatory manipulation, which is the precursor of tool use. A new notation system of object manipulation was invented to assess grammatical rules in manipulative actions. The notation system of action grammar enabled direct comparisons to be made between primates including humans in a variety of object-manipulation tasks, including percussive-tool use.

1. Introduction

Tool-using behaviour is based on the skill of object manipulation. Primates are characterized by their ability to grasp and manipulate objects by using hand(s) in various ways [1–3]. Thus, the extent of object manipulation can be used as a unitary scale of cognitive development in primates including humans [4–6]. Although an avian species, New Caledonian crows show high levels of cognition in tool use and manufacture [7,8]. However, they differ from primates in terms of tool-use variety in modes and functions [9] as well as their dexterity in manual manipulation. More specifically, a forceful percussive action using a manually grasped object is characteristic of primates.

Primates exhibit a wide range of object-manipulation skills. Torigoe [10] tested 74 species of primates and revealed some species-/taxonomic-typical manipulative patterns. He identifies 506 patterns of manipulation of a nylon rope and a wooden cube by focusing on actions, body parts used and relations to other objects. The primates were divided into three categories based on richness of repertoire. When focusing on percussive action, only the third group of Cebus monkeys and great apes with the richest repertoire of manipulations performed this action (described as a 'strike' in the original study).

Object manipulation can also be categorized in terms of its complexity. Hayashi *et al*. [11] provide a schematic figure of object-manipulation categories. During the course of development, infant chimpanzees begin by manipulating single objects using a single action and later show more advanced manipulation using multiple actions simultaneously on multiple objects. Infant chimpanzees start to show combinatory manipulation that can be defined as manipulation of an object to relate to his/her own body, other individuals, substrate or other detached objects. Combinatory manipulation can lead to the emergence of tool-using behaviour when the combination made through manipulation is appropriate and meaningful. Object manipulation can be also linked to object play or communicative use of objects.

Matsuzawa [12] has developed the 'tree structure analysis' to highlight the hierarchical complexity of tool use. He focuses on the object involved in the tool-using behaviour and the combinations among them. According to the definition of the tree structure analysis, most of the tool use reported in wild chimpanzees falls into 'Level 1' category, where one object is combined with the target (e.g. fishing for termites by using a twig as a tool). Nut-cracking behaviour was categorized as 'Level 2', where two objects are appropriately combined with the target (e.g. a nut is placed on an anvil stone and the nut is hit with a hammer stone). The most complex type of tool use reported in wild chimpanzees is the use of a wedge stone to stabilize an anvil stone, and this is categorized as 'Level 3' tool use.

The pattern and complexity of object manipulation reflects the level of cognitive as well as manual control development. Thus, some tasks in the non-verbal developmental scale for human children use object manipulation to assess levels of cognitive development. These tasks, such as stacking blocks and nesting cups, have been applied to test cognitive development in chimpanzees [6]. They have mainly been used to assess internal developmental factors involved in object manipulation within an individual. Object manipulation also reflects social factors, with some task modifications being suitable not only to detect individual developmental change, but also the influence of other individuals. Numerous studies have tested imitative ability in chimpanzees using object-manipulation or tool-using tasks ([13,14], see reviews in [15,16]). These studies have identified different levels of social learning that influence the acquisition of skilled manipulation. Although evidence for true 'imitation' is questioned in chimpanzees (e.g. [17] arguing for and [18] against), they are known to be able to learn new manipulative skills through 'emulation' where observers learn the results of actions rather than the details of behaviour [19,20]. In general, chimpanzees need long-term exposure before acquiring tool-using behaviour.

Stacking-block tasks have been applied to assess physical understanding in the context of combinatory manipulation [21,22]. Stacking-block tasks enable a direct comparison to be made between captive chimpanzees and human children in an identical test setting. Subjects received a set of four blocks (two cubic blocks and two blocks of a different shape) to be stacked up into a tower. To efficiently stack up the differently shaped blocks, the subjects were required to consider the shape and orientation of the blocks. In other words, subjects needed to selectively use appropriate orientation for stacking and to ensure that the top surface would support the next block. Both juvenile chimpanzees and human children of around 3 years of age were found to be capable of learning an efficient stacking strategy through their manipulation of blocks. Nut cracking is a rare example of behaviour that resembles stacking behaviour, as the nut should be appropriately placed on a surface that can support it while it is being hit by a hammer stone. Thus, a precise analysis of nut-cracking behaviour is essential to investigate the physical understanding of wild chimpanzees and to compare it with captive chimpanzees and/or humans.

Taken together, the detailed and sequential microanalysis of nut-cracking behaviour from object-manipulation perspectives enables us to reveal the underlying cognitive development of an individual, as well as the social influence of other individuals. Because nut-cracking behaviour is a demanding task for a chimpanzees to acquire, it allows the assessment of the longitudinal pattern of development in a problem-solving situation that has ecological validity and occurs in a natural setting. This approach also enables a direct comparison of captive with wild chimpanzees, as well as with humans.


Figure 1. A pair of captive chimpanzees: mother and offspring manipulating stones and nuts in a follow-up training session, in a nut-cracking situation originally reported in Hayashi *et al*. [23] (photo by Akihiro Hirata of Mainichi Newspaper). (Online version in colour.)

2. Introduction of nut-cracking behaviour to naive chimpanzees in captivity

Hayashi *et al.* [23] report on captive chimpanzees' object manipulation after first exposure to nut-cracking behaviour demonstrated by a human experimenter. One in three chimpanzee subjects succeeded in cracking open macadamia nuts with a pair of stone tools. One chimpanzee did not crack open nuts but did demonstrate hitting actions with a stone. One remaining chimpanzee failed to crack open nuts or demonstrate hitting actions. An analysis of the patterns of their stone/nut manipulation suggests three factors that may explain chimpanzees' difficulty in acquiring nut-cracking behaviour. First, the chimpanzee that failed concentrated on manipulating a nut, the target, and rarely diverted her attention to manipulating a stone, the tool. Second, in all three subjects, a forceful hitting action with a hammer stone was not frequently observed. Third, although a variety of combinations of two items were observed, a combination of three items was infrequent.

Approximately 4 years after the first exposure to the nut-cracking behaviour, the same three individuals accompanied by their offspring participated in follow-up training sessions of nut cracking in a similar setting (figure 1). As shown in figure 2, two chimpanzees succeeded in cracking nuts in the follow-up training sessions. One of the chimpanzees

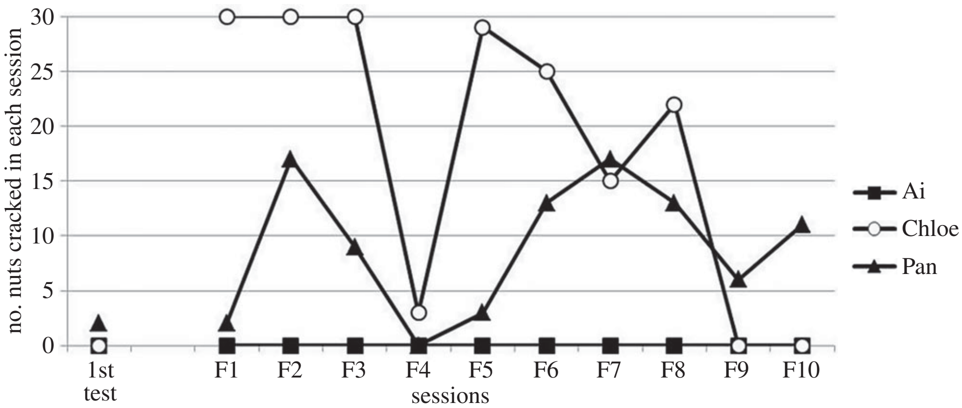


Figure 2. The number of nuts cracked open by the subjects in each session, including the first test session and the 10 sessions at the beginning of the follow-up training session that was originally reported in Hayashi *et al.* [23]. A chimpanzee, Pan, succeeded in cracking nuts from the first test session. Although a chimpanzee, Chloe, failed in the first test session, she succeeded in the first follow-up session conducted after a hiatus of approximately 4 years.

had not succeeded in the first test session with human demonstration, but succeeded in cracking open nuts during the first follow-up session without any human assistance. The opportunity to perform nut-cracking behaviour had not been provided during the 4-year hiatus, thus revealing that the chimpanzees retained the procedural memory without receiving any direct reward for a substantially long time. The two successful subjects continued to crack open nuts, although they sometimes lost motivation, partly because of interference from their offspring.

Hirata *et al.* [24] report on the acquisition process of nut-cracking behaviour in a group setting. A dominant male was trained to crack open nuts by a human experimenter. The trained chimpanzee then served as a conspecific model in a group setting. The other four chimpanzees gradually acquired the nut-cracking skill through long-term observation of conspecific models and individual practising. The total number of object-manipulation bouts observed in each individual before their first success in nut cracking ranged from 2958 to 5604, occurring within between 8 and 15 sessions of 30-min length. The process of acquisition was broken down into several steps, including the emergence of a three-object combination and hitting action. The hitting action with a tool emerged only later in the acquisition process.

3. Development of nut-cracking in the wild chimpanzees of Bossou, Guinea

Nut-cracking behaviour has been reported in a limited number of communities in West Africa [25,26]. Even among neighbouring communities, there are differences in the presence/absence of nut-cracking evidence, the species of nuts cracked in each community and the precise pattern of cracking action (such as using one or both hands for cracking) [26,27]. To tackle these enigmatic patterns of nut-cracking distribution, field experiments have been conducted in Bossou, Guinea, West Africa, since 1987. As Matsuzawa and Biro point out in their book [28], numerous studies have been conducted using detailed and experimentally controlled observations of nut-cracking behaviour in Bossou.

In the Bossou community, chimpanzee infants first succeed to crack open oil palm nuts from around 3.5 to 7 years old. Inoue-Nakamura & Matsuzawa [29] analysed precisely the manipulation of stones and nuts in infant chimpanzees before their first success. Chimpanzee infants show all of the fundamental actions necessary to perform nut cracking at the age of 2.5 years. However, they fail to combine fundamental actions in an appropriate sequence until they reach 3.5 years or more. The hitting action is performed in various combinations, such as hitting a nut on stone by hand, or hitting a nut on stone with a nut.

A comparison of chimpanzees and capuchins illuminates a marked difference in the pattern of development in the two nut-cracking species in terms of two types of behaviour. Chimpanzee infants of 1.5 years readily place nuts on an anvil stone and demonstrate the hitting action, but they rarely hit a nut with a hammer stone until they reach around 3.5 years. In the case of capuchin monkeys [30], they first demonstrate the hitting action before beginning to place nuts on an anvil stone. Thus, the order of acquisition of the two fundamental actions of placing and hitting with a hammer stone is completely reversed in chimpanzees and capuchins. This may indicate that capuchins have intrinsic tendencies to engage in hitting actions. By contrast, chimpanzees acquire hitting/percussive actions in line with other types of object manipulation during the course of cognitive development.

There is also a difference in the type of anvil used by chimpanzees and capuchin monkeys. Chimpanzees in Bossou use a pair of movable stones as hammer and anvil. Chimpanzees in the Tai forest use a wooden hammer and anvil besides stone tools [16]. Capuchin monkeys usually use rock outcrops, boulders and logs as anvils [31]. Although capuchins place nuts on specific parts (pits) of the anvil, the anvil itself is not movable. In the basic definition of tool use by Beck [32], a tool should be an 'unattached object', i.e. something detached from environmental substrate, such as a twig broken off of a tree branch. In this sense, the use of a pair of stones in chimpanzees is Level 2, but the use of outcrops in capuchins can be categorized as 'incomplete Level 2' or 'intermediate between Levels 1 and 2'.

Hirata *et al.* [24] used anvil stone embedded in the ground of an outside enclosure. The hammers were attached to the anvils with chains. In this setting, one infant first succeeded when she was 1 year and 11 months of age [33], much earlier than has been recorded in wild chimpanzees. The setting of the objects may have helped the infant to focus on the task-related objects and to facilitate the exploratory manipulation of the anvils, hammers and nuts. Moreover, the infant had ample opportunity to observe the nut-cracking behaviour of experienced adults, including the mother. Abundant experiences in manipulative exploration in a physically- and socially enriched environment may have played an important role in the early acquisition of nut-cracking behaviour in the infant. Immediately after the first success, the infant was tested further, with detached stones in an experimental room. The infant readily transferred the knowledge gained from the embedded anvils in the outside enclosure to the use of a pair of movable stones as anvil and hammer.

Even after the first success in cracking open nuts, it takes a long time for chimpanzees to fully acquire the efficient skill of cracking. Biro *et al.* [34] report the average number of blows required to crack open a nut as a function of age. Nut-cracking performance gradually reaches an asymptote between the ages of 8 and 14 years in Bossou. This means that chimpanzees require at least 5 years to reach the efficiency seen in skilled adults who usually need only a couple of blows to crack open nuts. Thus, longitudinal development can be observed through the analysis of manipulation in the complex tool-using behaviour of cracking nuts.

4. Strategies to cope with difficult manipulative tasks: perspectives of action grammar

Subjects were required to develop some sort of behavioural strategies for complex manipulative tasks, including tool use. In this sense, we had to apply not only a repertoire-based or developmental analysis, but also a sequential analysis of object manipulation to reveal their strategies in a micro-timescale. This is because, for example, an individual should perform an action to correct an error occurring when conducting a tool-using task, e.g. when a chimpanzee fails to crack open a nut after consecutive hits with a light-weight hammer, the chimpanzee should choose to use a new and more suitably weighted hammer for hitting the nut. Chimpanzees in Tai forest are also known to selectively use harder and heavier tools for hammering to crack open harder nuts [35].

Grammatical rules for object manipulation have been a focus of previous developmental studies in humans [36,37]. Further, the nesting-cup task, which requires subjects to seriate cups of different diameter into a nesting structure, has been used as the main methodology to assess the rule-bound strategies in both human and non-human primates [38,39]. These studies mainly used only three categories, focusing on the pattern of cup combinations (figure 3). The three categories are adequate for illuminating developmental trends in humans. Humans start to combine two cups with 'pairing' method (before one year old), and then start to combine three or more cups with 'pot' method (from one to two years) followed by 'subassembly' method (becomes popular from 3 years). However, the three categories failed to show clear species differences, because 'subassembly' strategy, the most advanced combinatory strategy, which involves moving seriated cups as a unit to combine with another cup or unit, was observed in all tested primate species (humans, chimpanzees and capuchins). Thus, other researchers have tried to search for other types of measure which focus on error-correction strategy in the nesting-cup task [41].

Hayashi [40] invented a notation system of action grammar for the nesting-cup task. The notation system focuses on three components of object manipulation in the form of '$n_1 \times n_2$'. The first numeral refers to 'object', indicating which object was manipulated by the subject. The second alphabetical code refers to the 'action' used to manipulate the object. The third code refers to the 'location' the object was related to through the manipulation (occurs only in combinatory manipulation). The flow of entire manipulation can be coded by using this notation system, which can then be used for the basis of further analyses of sequential and grammatical rules. Hayashi & Takeshita [42] used the notation system to compare the efficiency of cup-combination processes in chimpanzees and humans. A combination of nine cups is not an easy task for humans of around 3 years of age or for adult and juvenile chimpanzees. Subjects of both species show inefficient combination, and a 'trial-and-error' pattern was frequently observed.

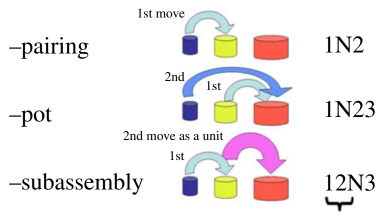


Figure 3. Three categories used in classic studies of nesting-cup task: schematic illustration of the movement of cups and corresponding codes described in the notation system of action grammar proposed by Hayashi [40]. (Online version in colour.)

A sequential analysis of nut-cracking behaviour was conducted using this notation system. As all of the stones in the Bossou field-experiment site had been identified and numbered, the number of stones was put in the two numeral positions, before and after the alphabetical code for action ($n_1 \times n_2$). An unbroken nut was given the number 0 and the kernel and shells of a broken nut were numbered 1 and 2, respectively. The action codes are listed in table 1. Using this notation system [40], the sequence of nut-cracking behaviour can be encoded sequentially. The sequential codes can then be used to analyse the transition patterns of manipulatory actions. Figure 4 shows the sequential codes and transition patterns identified in an adult female chimpanzee and a juvenile offspring who had just begun to succeed in nut cracking. The sequential codes shown in the figure were taken from a 10 min video (some parts of the video are provided as electronic supplementary material, Movie S1). The adult chimpanzee showed an efficient pattern of sequential behaviour. She first grasped the hammer and adjusted the angle of the anvil stone. Once she had it settled, she showed an efficient chain of behaviour: pick up nut, put nut on anvil, hit nut on anvil with hammer, contact hammer with anvil (until the next percussions), pick up kernel of opened nut and eat the kernel. She used her left hand for hammering and her right to adjust the anvil and manipulate the nut or kernel. Thus, she showed consistent laterality and highly sophisticated coordination of both hands. Conversely, the juvenile was less efficient: the nut sometimes fell from the anvil during percussion, and his percussion was not sufficient, leading him to hit the nut on the anvil with the hammer many times without successfully opening it. He sometimes switched the hammering hand after failures.

Chimpanzees seem to adopt different behavioural strategies to overcome difficulties in cracking open nuts (figure 5). Younger chimpanzees tend to show ineffective strategies, such as putting multiple nuts on an anvil simultaneously or switching the hammering hand. Younger chimpanzees also tend to try many behavioural strategies even if the strategy is

Table 1. The list of action codes used in the notation system of action grammar.

code[a]	action	categories used in Inoue-Nakamura & Matsuzawa [29]	description
T	touch	touch, kiss	touch object with hand/foot/mouth
CH	change horizontal angle	roll	change the angle of anvil with horizontal rotation
CV	change vertical angle	roll	change the angle of anvil with vertical rotation
CP	change position	pull, push	change the positioning of anvil by horizontal movement on the ground
G	grasp	hold, lift, pick, grasp, take, peel	grasp and lift up object with hand
H	hit	hit	hit object with/without holding another object in hand (numerals were deleted if repetitive hits were observed with the same set of objects)
P	pile	put	put object on another object and release the hand
V	reverse	turn	turn over object and reverse it upside-down
W	wipe	brush	wipe surface of object and brush away broken shells
S	support	support	support object to fix it by keeping contact with hand/foot
D	drop/disassemble	drop	drop object from hand or disassemble object from a set of combined objects
B	bite	mouth, bite	bite object in hand with mouth
E	eat	eat	eat kernel of opened nut
R	replace	replace	replace nut on stone for better positioning
U	put	put	put object on another object and retrieve it without releasing the hand
F	floor		release object in hand onto the floor
L	fall		object fell off from a set of combined objects
M	miscellaneous	step, lay, press, kick, hug, sit, fling, point, rake, scrounge	

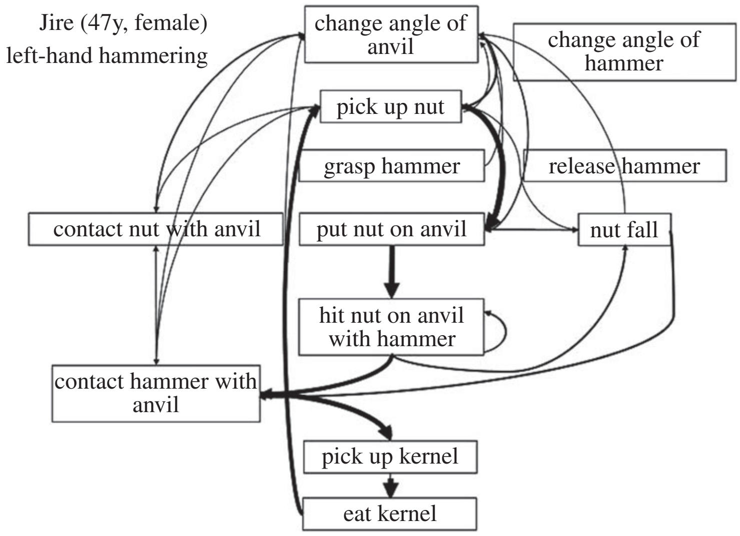
[a]A capital letter indicates that the action was performed by the right hand and a lower case letter that the action was performed by the left hand.

not directly related with the error to be solved. For example, when a nut falls from the anvil, a young chimpanzee may respond to this error by changing hammer stone. Adult chimpanzees develop some behavioural-adjusting strategies that are effective to solve the specific error that they are facing, such as changing to a heavier hammer after consecutive hit errors with a lighter hammer or changing the angle of an anvil by rotating or pushing it after a nut falls from the anvil. However, we should be careful when considering the underlying mechanisms of these behavioural strategies. Adult chimpanzees may acquire such strategies through cumulative experiences of nut cracking. In other words, adults may alternatively use error-correction strategies that previously proved to be successful, such as adjusting the anvil by rotation, changing the hammer or hitting with more power, without appropriate physical understanding as indicated in the second row in figure 5.

Electronic supplementary material, Movie S2, shows an example of metatool formation in an old adult female. Her behaviour can be coded as follows, using the above-mentioned notation system of action grammar:

> 135G/0 g/0p74/135H0-74/H/H/H/H/135F/39t/39G/39P0-74/39D/39G/39H0-74/H/39cp/39H0-74/H/H/H/H/H/39P135/135G/135H0-74/H/H/H/H/H/H/H/H/H/H/0d0-74/74ch/74p39/135U74-39/0p74-39/135H0-74-39/H/H/H/H/135H1-74-39/H/H/1 g/1E.

From a sequential analysis based on this notation system, inferences can be made about physical/causal understanding in chimpanzees. The chimpanzee did not succeed in cracking open the nut because the nut was placed in a shallow depression of the anvil (stone-74) which meant that the hammer blows did not put force on the nut. After consecutive unsuccessful hits, she adopted several behavioural strategies. First she changed hammer from stone-135 to stone-39, and then switched back to stone-135 again. From an action-grammar perspective, she detected the error and applied a behavioural-adjusting strategy of changing hammer that was already in her behavioural repertoire. However, the behaviour of changing the hammer could be judged not to be based on accurate physical causal-understanding, because the real cause of the failure was the missed hit caused by a physical barrier of the shallow depression on the anvil's surface. She then shifted to her second alternative strategy and adjusted the anvil by rotating it horizontally. This resulted in the positioning of the anvil stone-74 onto the discarded hammer of stone-39. Thus, stone-39 worked as a wedge stone for anvil stone-74, and this combination of stones can be classified as Level 3 tool use. However, this may raise scepticism about the application of that classification in this particular sequence of behaviour, because the wedge stone was not actively inserted beneath the anvil stone to stabilize it. Thus, the chimpanzee did not use the wedge intentionally but rather used (*a*) 1391g/39G/39F/401CH/0G/401CH/1391U401/0U401/401CH/0P401/1391h0-401/1391U401/1G/1E/401CH/0G/0U401/401CH/0P401/1391h0-401/1L/1391u401/0G/0P401/1391h0-401/1391u401/1G/1E/0G/0P401/0L/401CH/0G/0P401/1391h0-401/1L/1391u401/1G/1E10G/0P401/0L/0G/0P401/1391h0-401/1391u401/1G/1E/0G/0P401/1391h0-401/ 1391u401/1G/1E/0G/0P401/1391h0-401/1391u401/1G/1E/0G/0P401/1391h0-401/h/1391u401/1G/1E/0G/0P401/1391h0-401/1391u401/1G/1E/0G/0P401/1391h0-401/h/ 1391u401/1L/1G/1E/



(*b*) N04CV/N04CV/N04CH/0g/0pN04/130G/130H0-N04/H/H/H/H/H/H/H/H/H/H/H/H/130F/130G/130H0-N04/H/0L/130F/0g/0pN04/0L/1G/1E/0G/0PN04/130ch/130v/130g/130h0-N04/h/h/h/h/0L/130f/130v/0G/0PN04/130g/130h0-N04/0L/130f/130v/0G/0P04/130g/130h0-N04/h/h/h/h/h/0L/130f/130ch/0g/0pN04/130g/130h0-N04/0L/130f/0G/0PN04/0L/0G/0PN04/0L/0G/0PN04/130g/130hN04/130h0-N04/h/1L/130f/1G/1E/130CH/130t/0g/0pN04/130g/130h0-N04/h/h/130f/1G/1E/

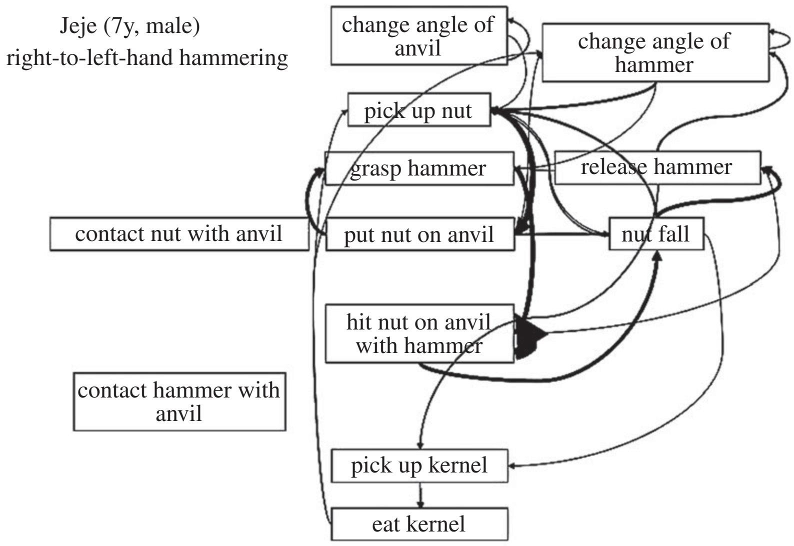


Figure 4. The sequential codes and transition patterns in (*a*) an adult female chimpanzee and (*b*) a juvenile offspring. The thickness of arrows indicates the frequency of shifting patterns. The numerals indicated the number of each manipulated stone (such as 39, 130, 1391, 401 and N04), intact nut (0), kernel of opened nut (1), shells of opened nut (2). The action codes are listed in table 1.

two different behavioural strategies in sequence to cope with the repetitive hit errors. Even if the resulted combination of the stones is identical, a closer look into the sequence of behaviours using an action-grammar perspective may thus reveal the existence/absence of accurate physical causal-understanding and/or insightful intentionality in an individual.

5. General discussion

The study of nut-cracking behaviour was ideal for assessing cognitive development in chimpanzees, both in the wild and captivity. Precise analyses focusing on the pattern of object manipulation and its grammatical/sequential order provided useful information about the underlying cognitive development and physical understanding exhibited in complex tool-use behaviour. The general findings gained from developmental studies suggest that the difficulty of nut-cracking acquisition may not exist in each action itself. Instead, the difficulty exists in formulating an appropriate combination of actions and objects in an appropriate sequence [43].

Sequential analyses of actions involved in nut-cracking behaviour revealed the behavioural strategies adopted by

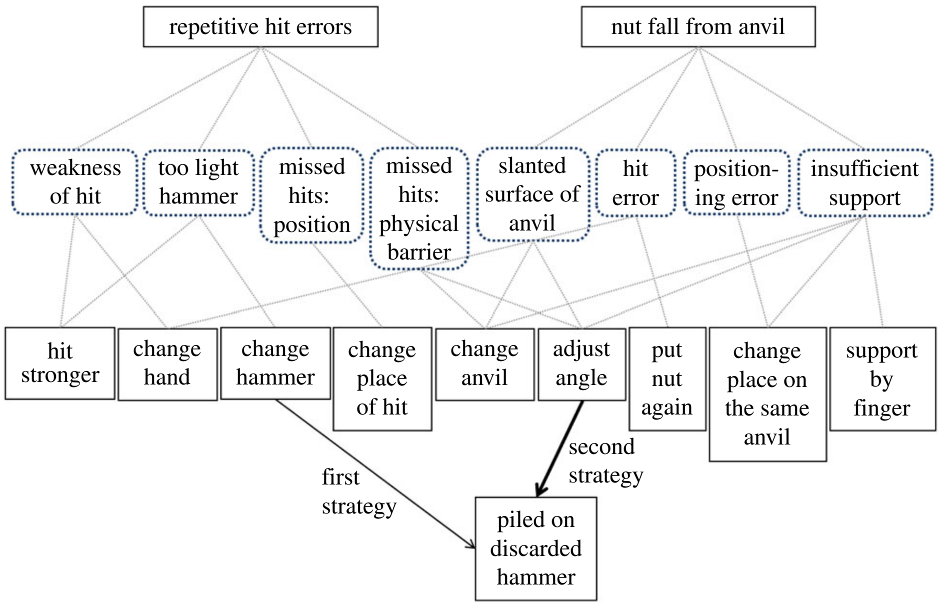


Figure 5. Schematic flow of behavioural strategies in the context of nut cracking. Rectangles show observable events and behavioural strategies taken by chimpanzees. Oval-dotted rectangles are not observable cause of the events. The cause and observable events/strategies are interconnected based on the theoretical assumption and probability. The top row shows two major errors occurs in nut-cracking sequence. The second row shows the possible causes of the errors (note that these causes are not obvious and recognizable for chimpanzees). The third row shows the actual behavioural strategies observed after the errors. The fourth row shows the result of behavioural strategies taken by the old female chimpanzee during her metatool formation (discarded hammer worked as a wedge stone). (Online verison in colour.)

wild chimpanzees when they face to errors in its execution. Efficient coping strategies to deal with errors appeared later in their lives, which suggests that these may be gradually acquired after long-term interaction with the objects and the achievement of an efficient level of skill [16,44]. Future studies are needed in order to accumulate more observational and developmental data, as not so many cases of wedge-stone use have been reported in chimpanzees, and the actual process of making wedges has not been reported elsewhere. The sequential and grammatical analyses focusing on error-correction strategy will be useful in helping to answer the question of the existence of causal understanding and insightful intentionality (such as active insertion of a wedge stone as occurs in humans) during the complex tool use observed in chimpanzees.

The most complex tool use ever reported in non-human primates is the use of the wedge stone as a metatool. Although we need to accumulate more knowledge of the actual making process, the chimpanzee can be seen to be advanced among non-human primates in terms of the complexity of tool use. Humans have exaggerated tool complexity and even make tools to make other tools. Humans may have learned tool use through imitation of skilled individuals with the help of active teaching. However, complex and sophisticated tool use in humans may also require some sort of individual learning of fine control or adjustment, as is the case in chimpanzees. In particular, tool making with percussive actions can be highly complex, and its acquisition needs individual learning for fine control of manual action [45]. Both cultural/social and physical/individual perspectives are essential to understanding the evolution of percussive actions in human lineage.

Ethics. The captive study of chimpanzees complied with the Guidelines for Care and Use of Nonhuman Primates (v. 3) laid down by PRI and with the national laws in Japan.

Competing interests. I have no competing interests.

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