Chapter 8
Behavioural, Cognitive and Neuronal Changes in the Acquisition of Tool Use

Yumiko Yamazaki and Atsushi Iriki

Abstract Tool use is observed and shared in animals with and without phylogenetic relationships. Therefore, tool use is an excellent behavioural model to explore dynamic relationships between animals' physical and cognitive abilities and their environmental conditions. In this chapter, we will focus on tool use in primates, especially Japanese macaques and common marmosets, which have not been observed to use tools in the wild but can be trained to do so through appropriate behavioural training. This approach enables us to determine the conditions that are needed for acquisition, as well as the types of cognitive and neuronal characteristics that can be observed during and after the development of tool use. Several studies of Japanese macaques have indicated that they can be trained to use tools within a few weeks, suggesting that the behavioural and cognitive components for tool use were already present before training. The acquisition of tool use is supported by structural changes in several brain regions throughout training. Furthermore, through careful, step-by-step training, the use of tools to obtain visual cues, such as an endoscope, was successfully established for the first time in macaques. Japanese macaques exhibit different characteristics in the acquisition of tool use than common marmosets as marmosets required much longer periods of time, and they worked mainly according to their own motivation to use tools. These differences were reflected in structural changes in the brain. In the discussion, we will compare the tool use behaviours of primates and other species, particularly birds, to explore the possible physical, cognitive and environmental conditions for exhibiting tool use from a comparative perspective.

Keywords Body image • Brain structural change • Common marmoset • Japanese macaque • Motor tool • Sensory tool • Tool use • VBM

Y. Yamazaki (✉)
Advanced Research Centres, Keio University,
35 Shinanomachi, Shinjuku-ku, Tokyo 160-8582, Japan

Laboratory for Symbolic Cognitive Development, RIKEN BSI,
2-1 Hirosawa, Wako-shi, Saitama 351-0198, Japan
e-mail: yumyam@brain.riken.jp

A. Iriki
Laboratory for Symbolic Cognitive Development, RIKEN BSI,
2-1 Hirosawa, Wako-shi, Saitama 351-0198, Japan

S. Watanabe et al. (eds.), *Evolution of the Brain, Cognition, and Emotion in Vertebrates*, Brain Science, DOI 10.1007/978-4-431-56559-8_8

8.1 In What do Animals Use the Tools for?

> "To use a tool is to incorporate the tool into a part of one's own body, like transferring one's thoughts from the brain to the hands. For us, the tool is the tip of our body".
> Tsunekazu Nishioka
> (Director of carpenters specializing in shrines and temples in Japan, 1988)

Numerous studies have documented tool use in animals, clearly illustrating that tool use is not limited to certain animal taxa (e.g. Beck 1980). Why only these animals, and not all animals, use tools is a puzzling question. To say that the environment drives them to use tools is too simple to be the answer because similar conditions do not cause all animals living in a specific environment to use tools (Baber 2003) nor can cognitive characteristics explain this issue because non-tool users in the wild can learn to use tools very quickly with training (Hihara et al. 2003a). Environmental adaptation and cognitive ability are necessary conditions to manifest tool use, but there might be other necessary conditions that are not sufficient.

Researches of tool use in non-human animals started with those of wild apes (e.g. Goodall 1964). Since then, many non-human tool users use tools for foraging (e.g. Malaivijitnond et al. 2007; Moura and Lee 2004; Inoue-Nakamura and Matsuzawa 1997), while others use tools for grooming or hygiene (e.g. Watanabe et al. 2007; Pansini and de Ruiter 2011; Deecke 2012; Hart et al. 2001) and for displays (McGrew 2013). Humans also use tools for other purposes (e.g. playing, writing, sewing, making tools and killing). Beck (1980) selected four functions of tool use by animals. First, animals use tools, such as rakes, to their reach. Second, animals use tools, such as stone tools and hammers, to amplify mechanical forces. Third, animals use tools to augment agonistic displays, for example, dropping branches. Fourth, animals use tools, such as sponges, to allow for more effective control of fluids.

Asano (1994) proposed three "classes" of tools that function in each of the following components of behaviour: antecedent stimuli, behaviour and consequences. The first is the "expansion of discriminative stimulus", which facilitates the acquisition and maintenance of the control of stimuli gained by the tools, for example, telescopes and clocks. The second class is "expansion of response topography", which expands the natural effects of motor organs, such as hammers and cars. The third class is the "expansion of reinforcing stimulus" and includes, for example, painkillers and money, which strengthen the effects of consequences.

According to this categorization, the rich variety of examples raised by Beck (1980) primarily fall into the second class of tools, i.e. "expansion of response topography". Thus, the questions arises, do non-human animals also use tools for expansion of discriminative and reinforcing stimuli? Are the functions of tool use essentially different between non-human animals and humans or are they just differences in volume and variations that share an original purpose? In this chapter, we attempt to search for some of the possible factors that enable animals to use tools by focusing on several examples of artificially acquired tool use in two primate species, namely, Japanese macaques and common marmosets. We would like to compare these species because of interesting ecological and physiological features. As we described below, both species are non-tool users in the wild, so they are suitable models for studying learning abilities of novel behaviour like tool use. Additionally, as primate species, they are much different in terms of hand dexterity, which is deeply related to the presence (macaques) and absence (marmosets) of cortico-motoneuronal system (Lemon 2008). This clear feature enables us to see how tool use is learned with different physiological backgrounds.

8.2 Tool-Use Learning in Japanese Macaques

8.2.1 Learning to Use Tools

Recent findings suggest that wild macaques can use tools, as exemplified by stone tool use in Thailand (Malaivijitnond et al. 2007; Gumert and Malaivijitnond 2013) and frothing with human hair by semi-captive macaques in the temples of Thailand (Watanabe et al. 2007) and frothing with their own hair by Japanese macaques in Arashiyama (Leca et al. 2010). In these cases, these animals use tools both to amplify mechanical forces and to extend the user's reach in a narrow space (Beck 1980).

Although reports of tool use by Japanese macaques are not abundant, these animals can be trained to use tools without difficulty. By training Japanese macaques to use rake-shaped tools, we were able to determine how they learned to use rakes and to identify the neurological processes that occur during training (e.g. Iriki et al. 1996; Hihara et al. 2006). In experimental situations, the monkeys sit in chairs and are passed a rake. The experimenters control the locations of the reinforcers (food items) on the table, beginning with a position that is slightly beyond their reach. After several hundreds of trials, the monkeys gradually learn to grasp and operate the shaft of the rake and finally become skilful in retrieving the food items from anywhere on the table. This training usually takes less than 2 weeks (e.g. Hihara et al. 2003a; Quallo et al. 2009; Yamazaki et al. 2009); thus, rake use might be a relatively easy task for Japanese macaques to acquire, although there are no reports of raking or tool use to reach food items in wild populations.

8.2.2 Changes in Neural Activity Due to the Acquisition of Tool Use

Because tool use behaviour is completely novel for Japanese macaques, the acquisition of such behaviour must involve changes in neural activity and/or the rewiring of neural connectivity. If neural activity is indeed changed, there must be neural groups that are in charge of the coding of the rake itself or the rake's movement. By recording neural activity in the somatosensory region, Iriki et al. (1996) found "bimodal" neurons that code both tactile and visual stimulation of the hand. These "bimodal" neurons, located in the intraparietal sulcus (IPS), are activated when the monkey's hand is touched by the experimenter's hand or is pointed at with something such as a laser marker. When the monkeys learned to use the rake to retrieve food from the table, the visual receptive fields of the bimodal neurons expanded to the whole rake area, including both the rake shaft and their original hands. Another type of neurons in the same intraparietal region responded to the movement of the shoulder joint and to the visual marker corresponding to the point on the table that the hand could reach. When the monkey uses the tool, this type of neuron expands its response area to include areas that are accessible with the rake. These neurons change their original receptive fields only when they are actively engaged in the raking task. The receptive fields are unchanged when the animals hold the rake passively. Thus, rake-use training reprogrammed the body image of the monkey to incorporate the rake as a body part (Maravita and Iriki 2004).

8.2.3 Changes in Brain Structure Due to Tool Use

The changes in behaviour and neural activity in tool-trained Japanese macaques are supported at the genetic, axonal and structural levels of the brain. Increased expression of brain-derived neurotrophic factor and its receptor *trk*B (Ishibashi et al. 2002) was observed in the same region in which the bimodal neurons were recorded (Iriki et al. 1996). Tracer labelling has revealed novel projections from the temporo-parietal junction and the ventrolateral-prefrontal areas to the intraparietal in tool-trained monkeys (Hihara et al. 2006). These findings strongly suggest that rake-use training induces the reorganization of brain structures.

Using voxel-based morphometry (VBM), Quallo et al. (2009) compared the volumes of brain structures before, during and after rake-use training in Japanese macaques. Two out of three subjects exhibited increases in grey matter volume of more than 10% in the secondary somatosensory area (SII), intraparietal sulcus (IPS) and superior temporal sulcus (STS), as wells as increased white matter volume in the cerebellar cortex. However, the volumes of these regions were the highest at the midpoint of the training period and decreased to their original levels at the end of the training. Nevertheless, tool-use performance scores remained steady for more than 10 days after the end of the training, suggesting that these changes in brain volume are distinct from whatever changes underlie the maintenance of tool use. Thus, these brain regions increased in volume only when the monkeys were acquiring the novel behaviour through intensive training to retrieve food items through over 20,000 trials (Quallo et al. 2009).

8.2.4 Acquisition of Sensory Tools Via Motor Tools

Japanese macaques were fully competent at using rakes after 2 weeks of training. After training, they were so skilful that they were able to retrieve food items from anywhere on the table. The monkeys also demonstrated the spontaneous use of a tool to retrieve another long tool when the food item was located beyond the reach of the original rake (Hihara et al. 2003a). These abilities were supported by neurological plasticity, including newly connected projections (Hihara et al. 2006), gene expression (Ishibashi et al. 2002) and structural changes in specific regions (Quallo et al. 2009).

Referring again to the definition of tools according to their function (Asano 1994), the tool-use behaviours acquired by Japanese macaques fall under the "expansion of the response topography": The monkeys expand the accessible area of their original motor organs, e.g. their arms and hands, by using rakes. This type of "motor tool" comprises the majority of examples of tool use by non-human animals (Beck 1980). The above studies clearly indicate that Japanese macaques are potentially capable of using this type of motor tool when properly trained.

Asano (1994) also proposed the use of tools to expand discriminative stimuli. These types of tool can be considered "sensory tools" because they serve as substitutes for sensory organs (e.g. the eyes and ears), for example, binoculars and stethoscopes. Mirrors are among the most popular and classical examples of tools that can be used to acquire visual stimuli that cannot otherwise be obtained. Some studies have reported that captive animals can use mirrors to acquire discriminative cues about their own bodies (Prior et al. 2008; de Veer et al. 2003; Plotnik et al. 2006), but such examples of sensory tool use are rare in the wild. This fact suggests that some animals are competent in the use of sensory tools but that this ability does not emerge in the wild. Gaps likely exist in the levels of necessity and motivation between motor and sensory tool use, thus raising the question: Is it possible to bridge these gaps, i.e., is it possible to create sensory tools based on motor tools?

We addressed this question by training naïve Japanese macaques to use a special rake that functions like an endoscope (Yamazaki et al. 2009). The final goal of the training was to show that monkeys can use tools to acquire visual information to guide their behaviours under conditions in which neither their hands nor the tool is seen directly, much like the way a doctor uses an endoscope to search for lesions in the stomach. To this end, a special training protocol was invented to transfer motor tool use to sensory tool use (Fig. 8.1). First, the monkeys were trained to use the standard rake to retrieve food on the table as shown in previous studies (e.g. Iriki et al. 1996). After the appropriate motor function was acquired, the training protocol then focused on separating the visual information obtained from the monkeys' eyes to that obtained from a secondary object. To obtain visual information about a food item that was hidden behind a bump on the table, we employed a tool similar to a dental mirror to capture the image of the food item behind the bump. At this point, the rake has both sensory and motor functions. Next, several types of mirrors, including standing mirrors, manual mirrors, remotely controlled mirrors and a TV monitor, were introduced to separate the sensory and motor functions. Finally, the bump was removed from the table, which was instead covered with an opaque screen to prevent the monkeys from directly seeing anything on the table. The tool used in this training step was a "camera rake": the shaft of the rake contained a small camera capable of capturing the image in front of the transparent rake tip. The monkeys were asked to retrieve the food item under the screen by looking at a monitor on which a video image from the camera rake was displayed. During the initial use of the camera rake,

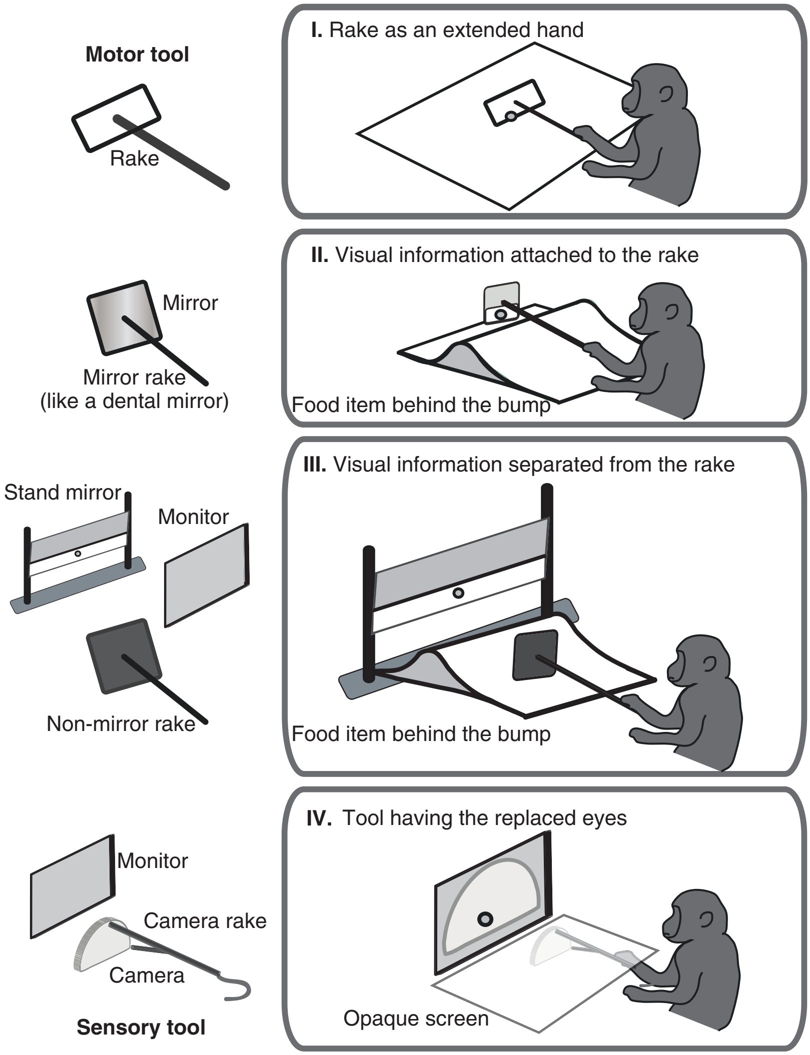

Fig. 8.1 Sensory tool training protocol for Japanese macaques. The four training phases differed in terms of the materials used. I. Rake training: the animals acquire the motor tool, and at this point, the tool is thought to become an extension of the hands. II. Mirror rake training: the subject is trained to use the rake to find and subsequently retrieve the food item behind the bump. III. Mirror and monitor use: the animals use mirrors and monitors to acquire visual information and use the rake for motor purposes. In this phase, the sensory and motor functions are separated. IV. Camera rake training: the monkey is required to search for the food item under the opaque screen by moving the camera rake and looking at the monitor that displays the image from the camera rake. The camera rake is considered a sensory tool because the animals use the rake as a substitute for their eyes. Modified from Yamazaki et al. (2009)

the monkeys made many vertical movements of the rake as though they were randomly and blindly pushing and pulling the rake. However, the monkeys eventually became capable of searching with the rake using a minimum number of circular movements to scan the entire area under the screen, as indicated by the tracking data. Thus, the monkeys successfully mastered sensory tool use to acquire a visual image that was otherwise not accessible with their eyes but that was accessible through the rake, enabling them to access a food item located beyond their reach.

Over the course of training with the sensory tool, we employed a systematic and small-step method to shape the monkeys' behaviour. The sensory tool training protocols involved two major challenges. The first was the dental mirror that was initially used to provide the monkeys with indirect visual information. The second was the camera rake, which required the monkeys to integrate information from their own movement of the rake with the visual information provided by the tip of the camera rake. Thus, these two training steps obviously required the monkeys to employ novel cognitive abilities that would not otherwise be called upon in the wild.

Humans reportedly started using mirrors approximately 8000 years ago (Enoch 2006), making mirrors the first sensory tool in human history. At a certain point, mirrors are developed into a tool to see what could not otherwise be seen. Although we do not know how early humans came to use mirrors for multiple purposes, the successful acquisition by Japanese macaques of the use of sensory tools through the use of motor tools highlights a potential route for the evolution of sensory tools in human history.

8.3 Tool-Use Learning in Common Marmosets

8.3.1 Learning to Use Tools

Given that laboratory macaques can be trained to use tools within 2 weeks and that non-laboratory macaques use several tools, a set of abilities for tool use, including both neural and cognitive abilities, is likely to be already present in these monkeys. Thus, we have several examples of tool use by old-world monkeys. Among new-world monkeys, capuchins are well known as stone tool users; however, tool use is not common among new world monkeys. Are non-tool-using new-world monkeys able to use tools if they are properly trained, similar to Japanese macaques? We addressed this question using common marmosets (*Callithrix jacchus*) as subjects.

Common marmosets have served as a "biomedical supermodel" following the successful generation of transgenic animals (Sasaki et al. 2009). The recent development of genetic manipulation techniques has enabled us to identify the genetic background of diseases and effective drugs, which is not possible in rodent models (Sasaki 2015). Thus, through the use of common marmosets, it will be possible in the future to identify genetic, neural and evolutionary factors related to tool use.

The first step in this direction was to establish a protocol for tool-use training in common marmosets, as there are no reports of these monkeys using any types of tools (Yamazaki et al. 2011). The training protocols differed between macaques and marmosets. Whereas macaques can use a precise grip to grasp the shaft of a rake without difficulty, this is not always the case with marmosets. Thus, a handle was added to the end of the shaft to make it easy for the marmosets to move the rake. Moreover, the training protocol for common marmosets consisted of small training steps that were not always necessary for the Japanese macaques (Hihara et al. 2003a; Quallo et al. 2009). Furthermore, whereas Japanese macaques must be hungry before the training session, this is not always the case with the marmosets. The training protocol was divided into four stages that included several small steps (Fig. 8.2). In the earlier stages (Stages 1 and 2), the marmosets only pulled the rake to the side. However, in the later stages (Stages 3 and 4), they were required to push and then pull the rake, and this process required a completely different motor control than that required in the earlier stages. After approximately 10,000 trials, which required nearly a year in total, the marmosets acquired tool use; i.e. they were able to retrieve the food item even when it was located behind the tool tip (Stage 4, step 3 in Fig. 8.2).

8.3.2 Changes in Brain Structure Through Tool-Use Learning

Among the differences between these two species, the clearest difference was the time required to master tool use. Whereas the Japanese macaques took approximately 2 weeks to become fully capable of retrieving the food item on the table using the rake, it took more than a year for the common marmosets to achieve a similar level of skill (Yamazaki et al. 2011). In addition, when they became capable of using the rake, the Japanese macaques tended to exhibit consistent hand use regardless of the food location. However, the common marmosets exhibited bilateral hand use even after mastering the majority of the task. The marmosets chose to use either hand depending on the position of the food item on the table. They consistently preferred adduction when retrieving the food item; i.e. when the food item was on the left side of the tool shaft, they used the right hand and vice versa. This fact reasonably corresponds to the anatomical difference in the cortico-spinal projection neurons between old- and new-world monkeys, with the exception of capuchins (Lemon 2008).

The acquisition of tool use by common marmosets is different from that of Japanese macaques; thus, are the brain regions employed for tool-use behaviour also different? When VBM was conducted to track changes in brain structures before, during and after tool-use training in common marmosets (Yamazaki et al. 2016), some of the regions of structural change were the same as those observed in the Japanese macaques, but some quite unique regions were observed in only the common marmosets. In the grey matter, volume changes in the nucleus accumbens

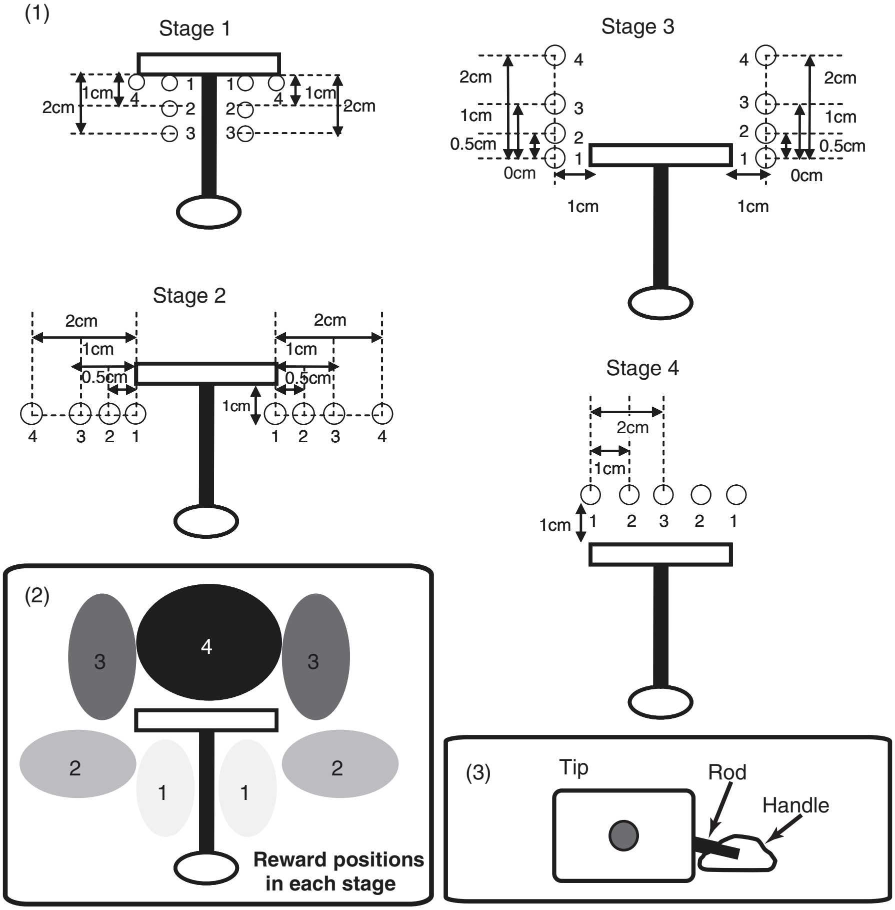

Fig. 8.2 Tool-use training of common marmosets. (1) Top view of the detailed positions of the rake (with a rectangular tip and a *black shaft*) and the food item (the small circles around the rake) in the four training phases (Stages 1–4). (2) Top view of the spatial relationships between the rake and the food item. The numbers inside each ellipse correspond to the training phases. (3) Illustration of the rake used by the common marmosets. A handle is located at the end of the shaft. Modified from Yamazaki et al. (2011)

(Acb, Fig. 8.3a) and third visual area (V3, Fig. 8.3b) were observed only during the training period. Although the increase in the Acb was prominent in the later phase of the training, the increase in V3 was consistently observed throughout training. In the white matter, the volumes of the anterior trunk of the corpus callosum (CC), the middle and inferior cerebellar peduncles (MCP and ICP) and the superior temporal sulcus (STS) increased. Interestingly, with the exception of the MCP, these white matter increases were greater in the early phase of training than in the later phase.

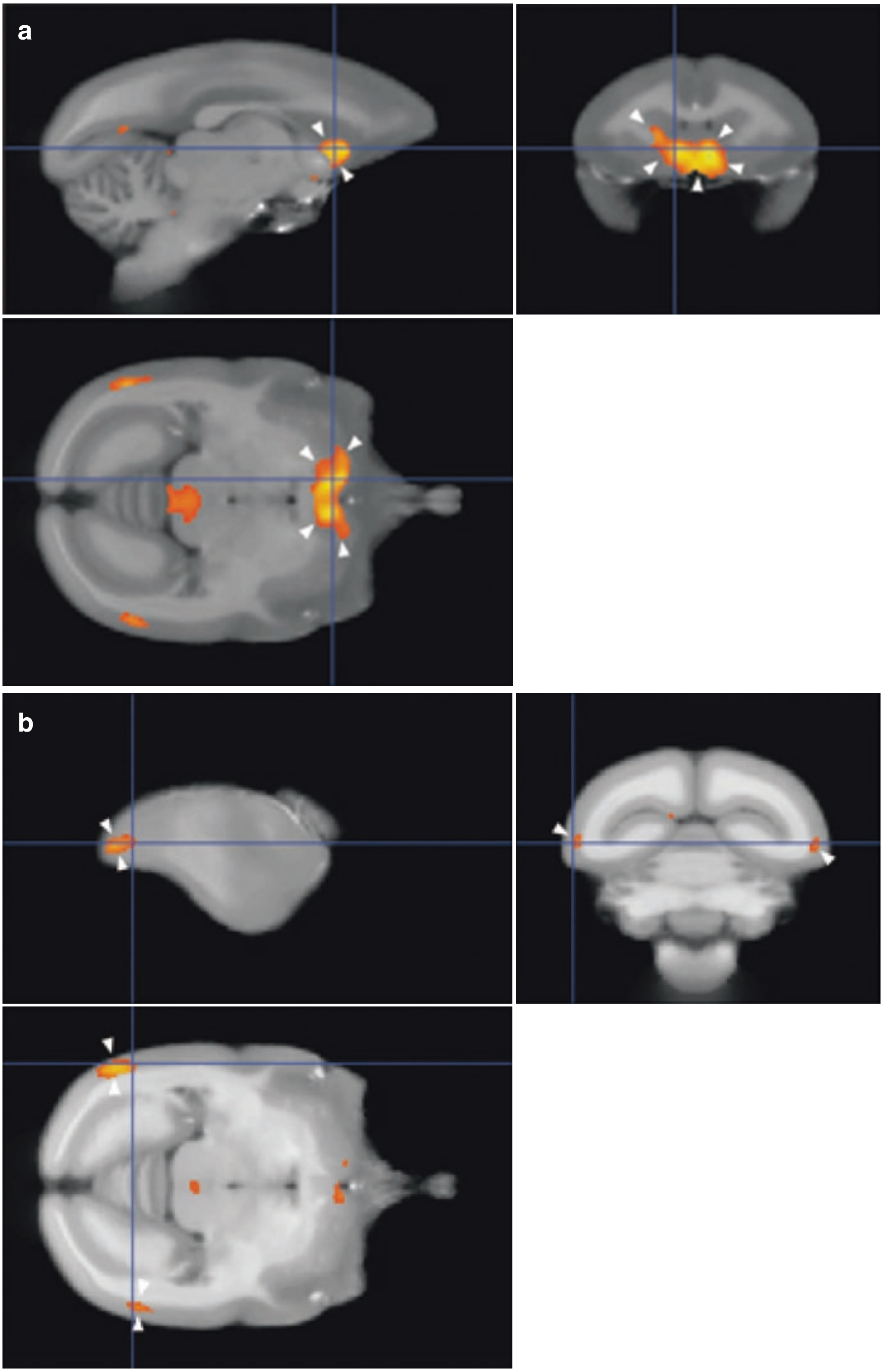

Fig. 8.3 Gray matter increases in (a) bilateral Acb and (b) bilateral lateral extrastriate cortex (V2/V3) observed only during the tool use training periods. Areas with significant increase are pointed by small triangles. Modified from Yamazaki et al. (2016)

8.3.3 How Does Tool-Use Learning Differ Between Marmosets and Macaques?

In addition to the behavioural processes of the acquisition of tool use, the differences in the altered grey and white matter regions of the brain were quite substantial when we compared Japanese macaques and common marmosets. None of the altered grey matter regions in the common marmosets (Acb and V3) corresponded to those of the macaques (STS, IPS and SII). The changes in the CC of the common marmosets were not observed in the macaques. Additionally, after the training was halted, the volumes of the changed regions decreased in the Japanese macaques, whereas these volumes were maintained in the common marmosets, although tool-use performance was maintained in both species.

What characteristics produced these differences in the two species? Overall, the difference in the length of the training period was quite prominent; approximately 2 weeks were required by the macaques, compared with 1 year for the marmosets. Not only length of the training period but also the density of training trials per day was quite different. Whereas the macaques completed several hundreds to thousands of trials per day, the marmosets completed only 30–40 trials, and sometimes they refused to work at all. This difference was the result of the food access not being limited in the case of the marmosets. In other words, the marmosets completed the task not because they were hungry but because they might have been interested in the task and the additional food resource (sweets). In contrast, it was quite difficult to make the Japanese macaques participate when they were full. Difference in hand morphology should also have contributed to the difference in learning speed. While Japanese macaques have opposable thumb and use precision grip when grasping the tool shaft, marmosets have digits with claws acting in union (Ankel-Simons 2007) and had difficulty in handling the tool shaft so that we provided a handle at the end of the shaft. The marmosets sometimes tried hard even to pick up a small piece of food by their hands when they succeeded to retrieve it.

What was the motivation for the common marmosets to participate in the task? The marmosets love eating sweetened food items, so the reinforcer (i.e. small pieces of sweetened jelly) itself obviously motivated them to complete the task. However, the attraction of a favourite food does not explain the sustained motivation for participating in the training by the common marmosets. The training protocol for the marmosets was divided into four stages, with several minor steps in each stage, and the task became increasingly difficult as they mastered the steps. Occasionally, they required many attempts before successfully retrieving the food item, particularly in the later phases of training. In these phases, the reinforcement rate per minute was lower than that in the earlier phases.

One possible factor is that the study employed only female subjects to exclude sex differences in the volumes of the brain regions. In a study involving a foraging situation (Yamamoto 2004), females exhibited faster response times than males when a familiar food was placed in an unfamiliar container, and the authors suggested that energy intake was not the main reason for the observed sex difference. Despite limited evidence that female marmosets are more motivated to forage, the results of the marmoset VBM study may be related to the original disposition of the female marmosets. If this is the case, the increased volume of the Acb in common marmosets, which was prominent in the later phases of training, is consistent with previous results reporting the activation of the Acb by tasks that require effort to obtain a reward (Salamone and Correa 2012) and when subjects perform a task skilfully (Lutz et al. 2012). Such self-driving motivation is referred to as "intrinsic motivation" in humans (Kage 1994).

The postures assumed by the subjects when engaging in tool use were also different between the two species. The macaques sat in a chair and retrieved the food items in the upright position. The marmosets were in a quadrupedal position when they used the rake to retrieve the food item from the table. Whereas the macaques maintained a constant viewpoint from the chair, the marmosets moved along the table edge and had different viewpoints depending on the positions of the food items. These visual characteristics likely affected the increase in the volume of the visual areas that were only observed in the common marmosets.

8.4 Changes in Brain Structures and Their Functions in Relation to Tool-Use Learning

The successful acquisition of tool use by Japanese macaques and common marmosets under laboratory conditions clearly indicates that tool use, in this case motor tool use, is not restricted to species that have a natural tendency to use tools in the wild. The brain structures of the two species exhibited plasticity in response to novel object use that aided the incorporation of the object into their bodies. The groups of structural changes indicate that two different processes occurred during tool-use learning.

One group of structural changes corresponded to the novel sensorimotor learning and the reconstruction of the brain network during the incorporation of tool into their own bodies. The IPS, STS, SII, CC, V3 and cerebellum belong to this group. This group is obviously important for learning new skills, and the IPS has been confirmed to be involved in sensorimotor plasticity in humans (Draganski et al. 2004). Specifically, the changes in the IPS that have been confirmed to be involved in tool-use acquisition in electrophysiological, fMRI and neuroanatomical studies (Iriki et al. 1996; Obayashi et al. 2001; Hihara et al. 2006; Ishibashi et al. 2002) are deeply related to novel skill acquisition within a relatively short time.

The other group corresponds to the motivational aspect of the sustained participation in the training. The Acb is the only structure in this group. To date, there are no reports of structural changes in the volume of the Acb due to behavioural experience. The fact that the Acb change was observed only in the marmosets and not in Japanese macaques or human subjects suggests that long-term participation in the training and the associated gradual behavioural changes are supported by Acb activation. Thus, increased activation of the Acb may be responsible for sustaining the motivation to use tools despite many failures.

The implication of the latter group of structural changes is that this type of brain change is necessary for learning to use tools that typically take years to master, regardless of whether the subjects are humans or non-human animals. As we know from examples of human tool use, e.g. pencils and chopsticks, learning is a slow process that is gradually developed and reinforced by the consequences of tool use and by the increasingly skilful use of the tool. Within this circularity, tool use is developed and refined. The evidence from common marmosets sheds light on the hidden process of how tool use is maintained, and this maintenance resulted in the further evolution of tool use.

8.5 Tool Use and Cognitive Evolution

Evidence of tool use in populations of captive primates suggests that the potential ability for tool use, particularly motor tool use, is widespread among animals. After a comprehensive review of tool use by various animals (Beck 1980), we observed many new lines of evidence in wild animals. Observations of New Caledonian crows, for example, provide surprising evidence in the sense that they not only use tools but also make tools themselves (e.g. Hunt 1996). These crows become skilful in making tools over the course of development and experience (Hunt and Gray 2004). Moreover, tool shapes are thought to evolve (Hunt 2000). Thus, the question arises as to how such evolved tool use affects the cognitive abilities of crows. Whether the cognitive ability to understand physical relations is a prerequisite for tool use or whether the emergence of tool use drove the general cognitive abilities of tool-using animals is sometimes a difficult and puzzling question. However, excellent tool use skills do not correspond to excellent performance in cognitive tasks in other physical domains (Povinelli 2000; Taylor et al. 2014; Jelbert et al. 2015).

Considering the evolution of cognition in relation to tool use, one important observation from New Caledonian crows is that they use tools for non-foraging, explorative purposes (Wimpenny et al. 2011). In these experiments, crows spontaneously brought stick tools with their beaks to explore novel objects that were potentially harmful or dangerous. The crows may use stick tools as extended versions of their beaks, as suggested by the neural activities of Japanese macaques (Iriki et al. 1996). However, the crows differentiate between the stick and their actual beak because they can avoid dangerous objects by maintaining distance between these objects and their beaks. Such multifunctional tool use has been observed in chimpanzees (McGrew 2013). Archaeological evidence suggests that prehistoric humans frequently used their manufactured tools for secondary purposes (Saito 2011). All of these species can manufacture tools. Originally, these tools were manufactured for specific purposes, but after a while, the tools came to serve a variety of purposes.

Studies of tool manufacturing suggest that tool-using species influence their environments through the use of tools and that they acquire feedback from the environment, with which they modify the tools for better use. This circular process allows both the tool and the underlying cognitive ability to evolve in a specific direction. However, during the modification of the original tool, the animals may find another purpose for the tool, and they may develop another process that can broaden the environments to be modified. At this point, tool use becomes context-free and can be associated with anything far removed from its original purpose. Because the number of animals that manufacture tools is limited (Beck 1980), tool manufacture must represent a substantial challenge for animals in general. However, when animals acquire the technology, unexpected interactions between the tool and the environment emerge and lead to additional paths for tool evolution.

Neither the Japanese macaques nor the common marmosets exhibited tool manufacture or differential tool use during the course of the experimental sessions. However, the tool-trained monkeys spontaneously differentiated vocalizations depending on the different conditions of the experiments and exhibited sequential raking to acquire an appropriate tool to retrieve the food item (Hihara et al. 2003a, b) and showed novel tool use for getting sensory information like endoscope (Yamazaki et al. 2009). These observations represent the first step of the evolution of cognitive ability via tool use. The altered brain areas (Quallo et al. 2009) and newly connected networks (Hihara et al. 2006) support such novel behaviour and its further evolution.

However, in the case of common marmosets, such novel behaviour has not yet been observed. Rather, marmosets exhibit structural changes in brain areas that are known to be related to reward (Yamazaki et al. 2016) in addition to areas that are related to sensorimotor learning. Thus, the results suggest that sustained tool-use training had an emotional aspect, which may include the experience of pleasure (Berridge and Kringelbach 2015). The fact that sustained tool use was supported by positive emotions contributes to the primary step for the maintenance of tool use.

Schaik et al. (1999) argued that several conditions, such as extractive foraging, dexterous manipulation, intelligence related to imitation and insight, would be the keys for tool use to emerge. These conditions explain well about the absence of tool use in Japanese macaques and common marmosets in different levels. However, Japanese macaques showed emergence of novel cognitive abilities after tool use, and common marmosets showed motivational change during the extensive tool learning, which would propose another hidden sets of conditions for tool use. Such new perspectives of cognitive abilities related to tool use cannot be found without artificial training on primate species which originally do not use tool in the wild.

8.6 Conclusion

We have reviewed the artificial training projects that have been employed to teach two different types of monkeys to use tools, and these species exhibited surprising abilities that otherwise cannot be observed in wild situations. However, there are huge gaps between these monkeys and tool-manufacturing animals, such as chimpanzees and New Caledonian crows, in the sense that the former species use tools when they are shaped to do so, whereas the latter voluntarily make tools to manipulate their environment. It remains unknown why Japanese macaques seldom use tools even though they acquire rake skills easily when taught.

Why animals use tools, how do they begin using them, and how they manufacture tools are all difficult questions to address, and it is difficult to empirically reconstruct the developmental paths. However, training animals to use tools can be used to approximately reconstruct the evolution of tool use. Tracking the changes in brain structure, neural activities and networks and observing the drastic behavioural changes in the subjects will provide an effective framework to reconstruct tool-use behaviour from a comparative perspective.

Acknowledgements The authors wish to acknowledge Dr. Watanabe in Keio University for the support and advice of the studies presented here.

References

Ankel-Simons F (2007) Chapter 8 - postcranial skeleton. In: Ankel-Simons F (ed) Primate anatomy, 3rd edn. Academic, Burlington, pp 283–390

Asano T (1994) Tool using behavior and language in primates. In: Hayes S, Hayes L, Sato M et al (eds) Behavior analysis of language and cognition. Context, Reno, pp 145–148

Baber C (2003) Cognition and tool use: forms of engagement in human and animal use of tools. CRC, Florida

Beck BB (1980) Animal tool behavior. Garland, New York

Berridge KC, Kringelbach ML (2015) Pleasure systems in the brain. Neuron 86(3):646–664. doi:10.1016/j.neuron.2015.02.018

de Veer MW, Gallup GG Jr, Theall LA et al (2003) An 8-year longitudinal study of mirror self-recognition in chimpanzees (*Pan troglodytes*). Neuropsychologia 41(2):229–234. doi:S0028393202001537 [pii]

Deecke VB (2012) Tool-use in the brown bear (*Ursus arctos*). Anim Cogn 15(4):725–730. doi:10.1007/s10071-012-0475-0

Draganski B, Gaser C, Busch V et al (2004) Neuroplasticity: changes in grey matter induced by training. Nature 427(6972):311–312. doi:10.1038/427311a

Enoch JM (2006) History of mirrors dating back 8000 years. Optom Vis Sci 83(10). doi:10.1097/01.opx.0000237925.65901.c0

Goodall J (1964) Tool-using and aimed throwing in a community of free-living chimpanzees. Nature 201:1264–1266

Gumert MD, Malaivijitnond S (2013) Long-tailed macaques select mass of stone tools according to food type. Philos Trans R Soc Lond Ser B Biol Sci 368(1630):20120413. doi:10.1098/rstb.2012.0413

Hart BL, Hart LA, McCoy M et al (2001) Cognitive behaviour in Asian elephants: use and modification of branches for fly switching. Anim Behav 62:839–847. doi:10.1006/anbe.2001.1815

Hihara S, Obayashi S, Tanaka M et al (2003a) Rapid learning of sequential tool use by macaque monkeys. Physiol Behav 78(3):427–434

Hihara S, Yamada H, Iriki A et al (2003b) Spontaneous vocal differentiation of coo-calls for tools and food in Japanese monkeys. Neurosci Res 45(4):383–389. doi:S0168010203000117 [pii]

Hihara S, Notoya T, Tanaka M et al (2006) Extension of corticocortical afferents into the anterior bank of the intraparietal sulcus by tool-use training in adult monkeys. Neuropsychologia 44(13):2636–2646. doi:10.1016/j.neuropsychologia.2005.11.020

Hunt GR (1996) Manufacture and use of hook-tools by New Caledonian crows. Nature 379(6562):249–251

Hunt GR (2000) Human-like, population-level specialization in the manufacture of pandanus tools by New Caledonian crows *Corvus moneduloides*. Proc Biol Sci 267(1441):403–413. doi:10.1098/rspb.2000.1015

Hunt GR, Gray RD (2004) The crafting of hook tools by wild New Caledonian crows. Proc Biol Sci 271(Suppl 3):S88–S90. doi:10.1098/rsbl.2003.0085

Inoue-Nakamura N, Matsuzawa T (1997) Development of stone tool use by wild chimpanzees (*Pan troglodytes*). J Comp Psychol 111(2):159–173

Iriki A, Tanaka M, Iwamura Y (1996) Coding of modified body schema during tool use by macaque postcentral neurones. Neuroreport 7(14):2325–2330

Ishibashi H, Hihara S, Takahashi M et al (2002) Tool-use learning selectively induces expression of brain-derived neurotrophic factor, its receptor trkB, and neurotrophin 3 in the intraparietal multisensory cortex of monkeys. Brain Res Cogn Brain Res 14(1):3–9

Jelbert SA, Taylor AH, Gray RD (2015) Reasoning by exclusion in New Caledonian crows (*Corvus moneduloides*) cannot be explained by avoidance of empty containers. J Comp Psychol 129(3):283–290. doi:10.1037/a0039313

Kage M (1994) A critical review of studies on intrinsic motivation. Jpn J Educ Psychol 42(3):345–359

Leca JB, Gunst N, Huffman MA (2010) The first case of dental flossing by a Japanese macaque (*Macaca fuscata*): implications for the determinants of behavioral innovation and the constraints on social transmission. Primates 51(1):13–22. doi:10.1007/s10329-009-0159-9

Lemon RN (2008) Descending pathways in motor control. Annu Rev Neurosci 31:195–218. doi:10.1146/annurev.neuro.31.060407.125547

Lutz K, Pedroni A, Nadig K et al (2012) The rewarding value of good motor performance in the context of monetary incentives. Neuropsychologia 50(8):1739–1747. doi:10.1016/j.neuropsychologia.2012.03.030

Malaivijitnond S, Lekprayoon C, Tandavanittj N et al (2007) Stone-tool usage by Thai long-tailed macaques (*Macaca fascicularis*). Am J Primatol 69(2):227–233. doi:10.1002/ajp.20342

Maravita A, Iriki A (2004) Tools for the body (schema). Trends Cogn Sci 8(2):79–86. doi:S1364661303003450 [pii]

McGrew WC (2013) Is primate tool use special? Chimpanzee and New Caledonian crow compared. Philos Trans R Soc Lond Ser B Biol Sci 368(1630):20120422. doi:10.1098/rstb.2012.0422

Moura AC, Lee PC (2004) Capuchin stone tool use in Caatinga dry forest. Science 306(5703):1909. doi:10.1126/science.1102558

Nishioka T (1988). Ki ni Manabe (in Japanese, 木に学べ). Shogakkan (小学館), Tokyo

Obayashi S, Suhara T, Kawabe K et al (2001) Functional brain mapping of monkey tool use. NeuroImage 14(4):853–861. doi:10.1006/nimg.2001.0878

Pansini R, de Ruiter JR (2011) Observation of tool use and modification for apparent hygiene purposes in a mandrill. Behav Process 88(1):53–55. doi:10.1016/j.beproc.2011.06.003

Plotnik JM, de Waal FB, Reiss D (2006) Self-recognition in an Asian elephant. Proc Natl Acad Sci U S A 103(45):17053–17057. doi:10.1073/pnas.0608062103

Povinelli D (2000) Folk Physics for apes: The chimpanzee's theory of how the world works. Oxford University Press, Oxford

Prior H, Schwarz A, Gunturkun O (2008) Mirror-induced behavior in the magpie (Pica pica): evidence of self-recognition. PLoS Biol 6(8):e202. doi:10.1371/journal.pbio.0060202

Quallo MM, Price CJ, Ueno K et al (2009) Gray and white matter changes associated with tool-use learning in macaque monkeys. Proc Natl Acad Sci U S A 106(43):18379–18384. doi:10.1073/pnas.0909751106

Saito M (2011) The Archaeology of diversion. Bull Nagoya Univ Arts 32:143–154

Salamone JD, Correa M (2012) The mysterious motivational functions of mesolimbic dopamine. Neuron 76(3):470–485. doi:10.1016/j.neuron.2012.10.021

Sasaki E (2015) Prospects for genetically modified non-human primate models, including the common marmoset. Neurosci Res 93:110–115. doi:10.1016/j.neures.2015.01.011

Sasaki E, Suemizu H, Shimada A et al (2009) Generation of transgenic non-human primates with germline transmission. Nature 459(7246):523–527. doi:10.1038/nature08090

Taylor AH, Cheke LG, Waismeyer A et al (2014) Of babies and birds: complex tool behaviours are not sufficient for the evolution of the ability to create a novel causal intervention. Proc Biol Sci 281(1787). doi:10.1098/rspb.2014.0837 van Schaik CP, Deaner RO, Merrill MY (1999) The conditions for tool use in primates: implications for the evolution of material culture. J Hum Evol 36(6):719–741. doi:10.1006/jhev.1999.0304

Watanabe K, Urasopon N, Malaivijitnond S (2007) Long-tailed macaques use human hair as dental floss. Am J Primatol 69(8):940–944. doi:10.1002/ajp.20403

Wimpenny JH, Weir AA, Kacelnik A (2011) New Caledonian crows use tools for non-foraging activities. Anim Cogn 14(3):459–464. doi:10.1007/s10071-010-0366-1

Yamamoto ME, Domeniconi C, Box H (2004) Sex differences in common Marmosets (Callithrix jacchus) in response to an unfamiliar food task. Primates 45(4):249–254. doi:10.1007/s10329-004-0088-6

Yamazaki Y, Namba H, Iriki A (2009) Acquisition of an externalized eye by Japanese monkeys. Exp Brain Res 194(1):131–142. doi:10.1007/s00221-008-1677-1

Yamazaki Y, Echigo C, Saiki M et al (2011) Tool-use learning by common marmosets (*Callithrix jacchus*). Exp Brain Res 213(1):63–71. doi:10.1007/s00221-011-2778-9

Yamazaki Y, Hikishima K, Saiki M et al (2016) Neural changes in the primate brain correlated with the evolution of complex motor skills. Scientific Reports 6:31084