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4 Changes in the Repertoire of Tool-using Behaviour in Japanese Monkeys

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Behavioural plasticity is one of the most important features in animals that enable us to adapt to new environments and technologies. In humans, the use of educational systems and cultural inheritance can intentionally shape new behaviours, allowing us to construct new repertoires. Such recurrent development enhances the innovation of technologies.

Such behavioural plasticity has been witnessed in a framework of tool-use training in Japanese macaques: they were able to acquire tool-using behaviour through intensive training (Iriki et al., 1996; Ishibashi et al., 2000), even though they showed no inclination to use tools either in the wild or in captivity. In addition to using a rake-shaped tool, they spontaneously used rakes of different lengths combinatorially (Hihara et al., 2003), and emitted differential calls according to different conditions in tool-using situations (Hihara et al., 2003). These studies indicated that, by systematically manipulating the conditions, macaques could show tool-using behaviour, which was followed by emergent behavioural changes without any additional training.

In addition to the behavioural change, several neural changes in the tool-trained monkeys were observed, such as changes in the receptive field of bimodal (visual-tactile) parietal neurons (Iriki et al., 1996), increase of brain-derived neurotrophic factor in the anterior bank of the intraparietal sulcus during and after the tool-use training (Ishibashi et al., 2002), and lengthening of the axons of the neurons projecting from parietal to prefrontal regions and vice versa (Hihara et al., 2006). With the same monkeys that were used in the present study, morphological changes in several brain regions were documented using voxel-based morphometry (Quallo et al., 2009). Before, during, and after the tool-use training, monkeys were scanned using MRI to compare the signals between the training stages. Significant increases in grey matter volume were observed in the right superior temporal sulcus, right secondary somatosensory area, and right intraparietal sulcus. If these biological changes in brains are related to the cognitive functions employed in given periods, there must be corresponding changes in behaviour.

Changes in the kinematics of tool-using behaviour were observed in a previous study (Ishibashi et al., 2000). The authors categorized three different learning stages. In Stage 1, the monkeys started using tools in a stereotypical manner. Then, they increased the number of successful retrievals using various actions in Stage 2. In Stage 3, smoothness and velocity of the tool tip movement were increased as the training proceeded.

In the present study, we explored the types of repertoires developed and analysed them quantitatively. We identified five behavioural categories related to tool use and applied them throughout the training period.

Method

Subjects

Three adult male Japanese monkeys (*Macaca fuscata*, F, E, and N) participated in the experiment. The weights of the individual monkeys at the beginning of the experiment were 5.6 kg (F), 5.1 kg (E), and 4.1 kg (N). The monkeys were individually housed in cages where water was freely available. During the training period, they were fed daily in their cages with monkey chow. Apples and sweet potatoes were reserved as rewards in the training sessions. The study was approved by the Animal Experiment Committee and was conducted in accordance with the RIKEN Brain Science Institute's Guidelines for Conducting Animal Experiments.

Apparatus

All training was carried out individually in an experimental room separate from the monkey housing. During the training sessions, each monkey sat on the monkey chair and could freely move his arms. The chair was fixed to the table (75 (w) ×

85 (d) × 71 (h) cm). The rake, which was used throughout the experimental period except for the initial habituation described below, was 30 cm long with a 1 cm diameter shaft and a 10 × 6 cm rectangular head which was made of aluminium and weighed 50 g. Food rewards of apples and sweet potatoes, cut into cubes of about 1 cm, were used throughout the experiment.

Before beginning the rake-use training, the monkeys were trained to use an external object, a tool (35.5 cm long) with a pink spoon-shaped tip (5 cm in diameter), to get a food reward. All training sessions were videotaped for the analysis of changes in the repertoire.

Procedure

Habituation

During the initial two-week habituation period, the subjects were transported from their home cage to the training room in a monkey chair. Monkeys were restrained at the waist and the neck but were able to move the head freely. They were trained to reach out and grasp food rewards. The habituation sessions were carried out for 60 min once a day, five days a week.

Initial tool-use training

Before training the monkeys with the rake, we introduced the habituation period, in which the tool with a spoon-shaped tip was used. The food item was placed on the tool's tip and the monkey was allowed to grab the handle. The spoon-tipped tool could be used to pick up or drag the food across the table. The purpose of this was to train the monkeys to use tools to pull food towards themselves.

Rake-use training

The monkeys were trained to use a rake to retrieve a food item placed beyond arm's reach. Initially, the rake was placed near the food so that the subject only had to pull the rake back to his side. Then, they were trained to move the rake not only vertically but also horizontally to encourage them to make a swinging movement. The distance between the food and the rake tip was gradually increased. We continued the rake-use training until the monkeys could make smooth, circular movements with the rake, without any pause or interruption within a trial. In the final phases, the monkeys were trained to retrieve food from a position beyond the rake. A trial ended when the food item was successfully retrieved with or without help from the experimenter, or when the food item dropped from the table. Daily training sessions lasted about 90 min.

Data analysis

The number of food items obtained was determined by examining the offline video recordings. Reaction time was measured from the point when the experimenter put a food item on the table and allowed the monkeys to use the rake, to the point when they started moving the rake.

We sorted the monkeys' behavioural repertoires into five categories as follows: (1) "throw rake": throwing the rake elsewhere so that they could not retrieve the food item; (2) "push food": pushing the food item with the rake, so that they could not retrieve it in the first challenge in a trial; (3) "rotate rake": rotating the shaft of the rake so as to rotate the rake tip on the table; (4) "swing rake": handling the rake shaft and swinging the rake to the food item; and (5) "sweep rake": moving the rake tip in a circular sweeping motion and locating it behind the food item, so as to pull it back.

To remove the trials with lower motivation from the analysis, we used the trials within 10 minutes with less than 20-seconds inter-trial intervals. We calculated several variables to make the following five analyses: (1) the number of food items obtained within 10 minutes by each monkey; (2) the time taken by each monkey to get one food item (total reaction times within 10 minutes divided by total number of food items obtained within 10 minutes); (3) the number of times each of the five behaviour repertoires was produced (number of trials in which any of the categories was observed divided by total number of trials); (4) average reaction times of each repertoire within 10 minutes (sum of reaction times in the trials with any of the repertoires divided by number of trials with any of the repertoires); and (5) the correlation between rate of each repertoire and average reaction times within 10 minutes. Analysis (5) was applied to the data obtained on days 12–15, when tool-using behaviour had been fully mastered.

Results

All three monkeys were successfully trained to use rake-shaped tools. Monkeys E and F used their right hand to rake and their left hand to retrieve the food reward. Monkey N used both hands to both rake and retrieve the food. Figure 1 shows the total number of food items obtained (upper panel) and average reaction time (lower panel) for each monkey in the 15 training days. All monkeys showed similar increasing and decreasing functions in the course of training.

Figure 2 shows the change in ratio of each repertoire in each monkey. Monkeys F and E showed few of the five behavioural repertoires on the first and second days, and then increased the "pushing food" behaviour from the third to fifth days.

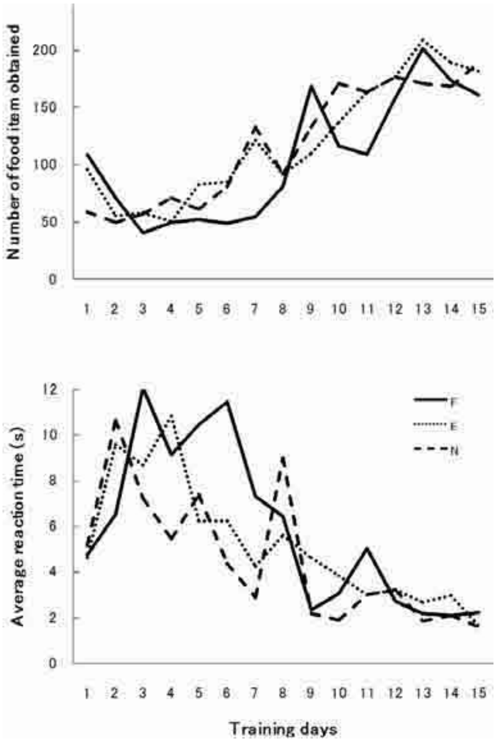

Figure 1. Total number of food items obtained (upper panel) and average reaction time(s) (lower panel) in each daily training session for each monkey (F, E, and N) in the course of tool-use training.

From the seventh or eighth day, they increased the "sweeping rake" behaviour. The "pushing food" behaviour was decreased and disappeared on the 11th or 12th day. In contrast, the "swinging rake" behaviour continued to increase from the eighth day until the end of the training.

Monkey N showed various kinds of repertoires until the eighth day. On the ninth or tenth day, the "throwing rake" and "pushing food" repertoires disappeared and the "swinging rake" behaviour, which had decreased on the seventh day, was increased again until the end of the training.

The reaction time for performing each repertoire is depicted in the left panel and has been averaged for all training days in the right panel of Figure 3 in each monkey. Average reaction time on all training days in each monkey was 9.09 ("throw rake"), 10.64 ("push food"), 2.71 ("rotate rake"), 2.48 ("swing rake"), and 3.01 ("sweep rake"). One-way analysis of variance revealed a significant difference among the repertoires (F (4) = 4.38, p = .026), but this difference was significant

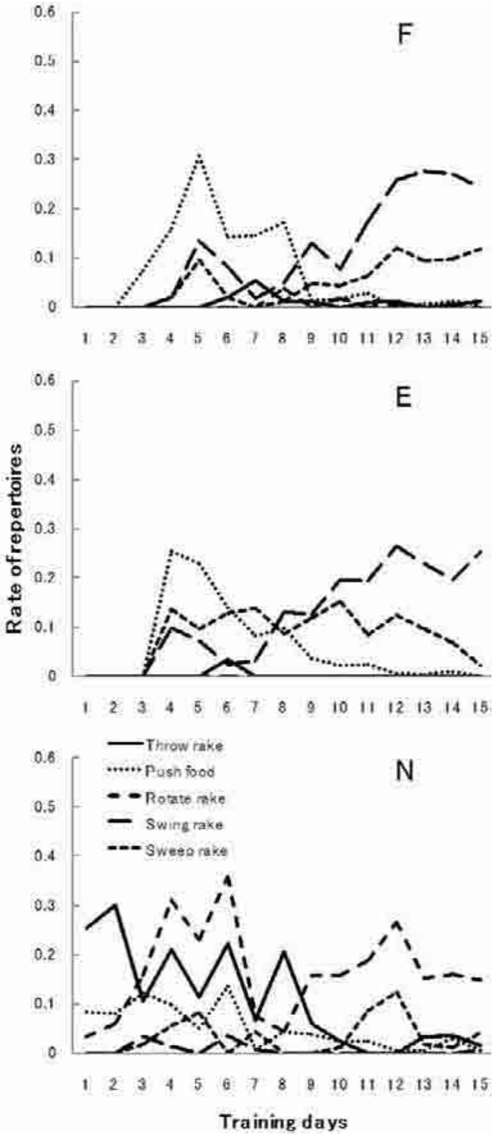

Figure 2. Rate of five repertoires performed by each monkey (F, E, and N) in the course of training sessions.

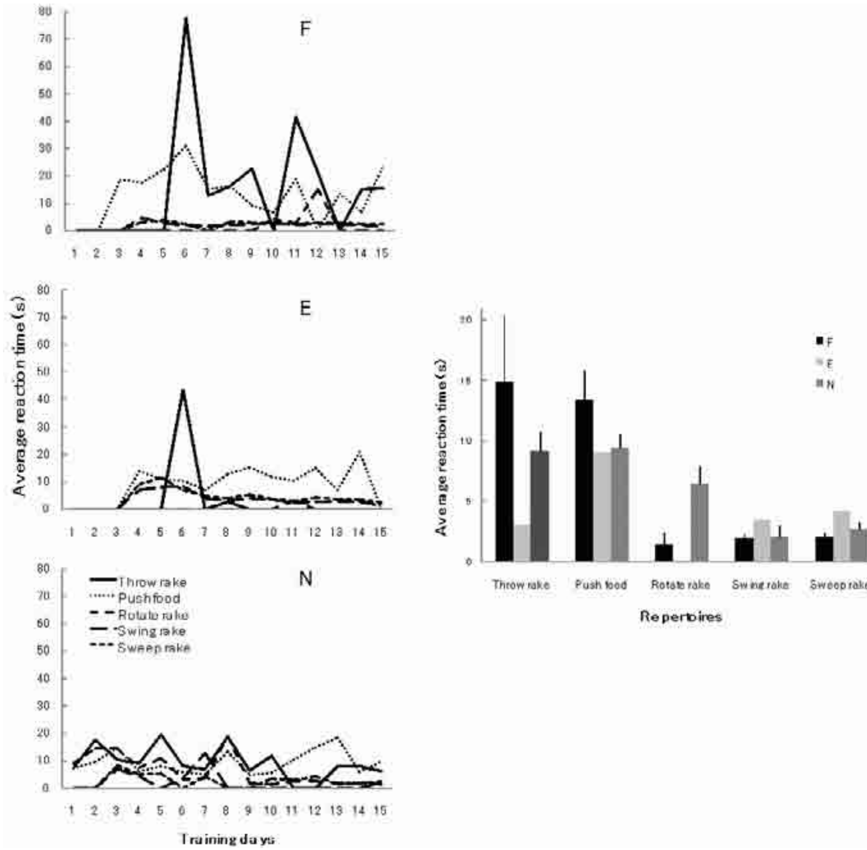

Figure 3. Time course of the reaction time(s) to perform each repertoire (left panel), and averaged (with standard error of means) for all training days in each monkey (F, E, and N).

only between “push food” and “swing rake” ($t = 4.72$, $p = .04$).

Analysis of the relation between the rate of repertoires and reaction times on all training days is depicted in Figure 4. The results show that the more the rate increased, the longer the average reaction times became.

Discussion

During 15 days of rake-use training, three monkeys smoothly acquired the ability to wield the rake (see Figure 1), as has been repeatedly described earlier (Ishibashi et al., 2000; Hihara et al., 2003; Yamazaki et al., 2009). The decrease in reaction

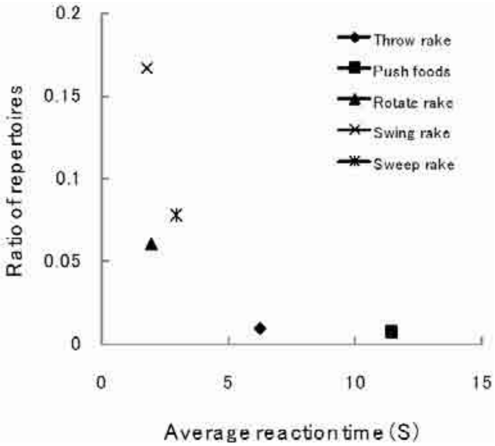

Figure 4. Correlation between average reaction time(s) and ratio of five repertoires in the monkeys in 15 training days.

time suggests a cognitive change in the subjects, in which they recognized the rake as an external object to be manipulated and later integrated it as if it were one of their body parts.

There were individual differences in appearance and disappearance of the repertoires in the course of training (see Figure 2), though the monkeys had pretty much the same procedures for mastering the tool use. Monkeys F and E showed similar behaviours, with high rates of "push food" in the earlier phase and "swing rake" and "sweep rake" in the later phase of the training. Monkey N showed a high rate of "throw rake" in the early phase, rather than "push food", but, similarly to the other two monkeys, he developed "swing rake" repertoires in the later phase of the training. In general, there was a clear tendency for the monkeys to change repertoires, starting with non-efficient repertoires (i.e., "throw rake" and "push rake"), before developing skilful repertoires (i.e., "swing rake" and "sweep rake") (see Figure 3).

The correlation between reaction time and rate of repertoires (Figure 4) indicated that, in the acquisition phase of tool-using behaviour, effective repertoires had shorter reaction times than non-effective repertoires. In this phase, mastery of the tool-using behaviour meant that the monkeys required less time to select effective behavioural repertoires wherever the food items were located, which is also reflected in the average reaction times depicted in Figure 3 (right panel).

In comparison with the results obtained by Quallo et al. (2009), there seemed to be a good correspondence between changes in grey matter volume and behavioural repertoires. That is, we observed a reversal in the rate of non-effective and effective repertoires around days 8–10, which corresponded to the detection of significant volume changes in the right superior temporal sulcus, secondary somatosensory area, and intraparietal sulcus (Figure 3 and S3 in Quallo et al., 2009). Thus, changes in repertoires in the direction of effective tool use would have been supported by changes of a neural basis that contributed to the reorganization of the connections among these regions to include the tool as part of their body (Iriki et al., 1996). Further study is needed to clarify the interaction between performance and neural changes that produce completely new behaviours, such as tool use, from experience.

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