Journal of Comparative Psychology
1990, Vol. 104, No. 3, 233-237

0735-7036/90/$00.75

Social Transmission of Food Preferences in Japanese Monkeys (*Macaca fuscata*) After Mere Exposure or Aversion Training

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In Experiment 1, 3 mother–child pairs of Japanese monkeys (*Macaca fuscata*) were given simultaneous choice tests between raisins and popcorn. The mothers and offspring showed different choice patterns. Cofeeding opportunities were then alternated with individual choice tests. In Experiment 2, 2 other pairs were added. Each animal was again offered simultaneous choice tests between marshmallows and almonds. Food aversion conditioning was used to create different choice patterns for mothers and offspring. After cofeeding and choice tests, the differences in choice patterns disappeared in both experiments. The changes after contact with the other's eating pattern during cofeeding was as follows: foods consumed by either came to be eaten by both; foods consumed by both continued to be eaten by both; and foods consumed by neither continued to be ignored. The results provide evidence for social transmission of food preferences in this species.

In a series of experiments on food aversion learning in captivity and in the wild, the individual learning factors that alter feeding habits in Japanese monkeys have been examined (Hasegawa & Matsuzawa, 1981; Matsuzawa & Hasegawa, 1982, 1983; Matsuzawa, Hasegawa, Gotoh, & Wada, 1983). However, results of recent experimental studies have shown that social transmission also has an important effect on the modification of feeding preference in some species of animals. For example, social interactions among Norway rats can substantially alter the diet selection of naive rats faced with a choice between novel foods; a naive rat that encounters a recently fed conspecific (a demonstrator) 1–2 hr after that demonstrator has eaten will exhibit a marked increase in its preference for the diet eaten by its demonstrator (Galef & Wigmore, 1983; Posadas-Andrews & Roper, 1983; Strupp & Levitsky, 1984). A red-winged blackbird can also acquire either food preference or food aversion through the observation of a conspecific's eating or falling ill (Mason & Reidinger, 1981, 1982).

In primate species many field studies have also suggested that food preference can be socially transmitted (e.g., anubis baboon, Ransom & Rowell, 1972; chacma baboon and vervet monkey, Cambefort, 1981; chimpanzee, Nishida & Hiraiwa, 1982; Takasaki, 1983; gorilla, Watts, 1985; Japanese macaque, Itani, 1958; Kawai, 1965; Kawamura, 1959; Yamada, 1957; mantled howling monkey, Whitehead, 1986). For example, classical studies by Japanese primatologists (Itani, 1958; Kawamura, 1959; Yamada, 1957) have suggested that social transmission has an important effect on the modification of feeding preference in free-ranging Japanese monkeys. The primatologists also argue that mother–child interaction is a very important aspect of such social transmission. However, most of their arguments were based on episodic observations. Evidence under strictly controlled conditions is lacking. In the case of Itani's observations of the propagation of eating of a novel food (caramels), it is possible that each member of the group started eating caramels after individual trial and error learning. If they did so, the increase of caramel eaters may not be an example of social transmission but rather an accumulation of independent experiences.

Weiskrantz and Cowey (1963) conducted an imitation experiment, in which an observer monkey who previously accepted very little black-currant juice (nonconsumer) became a consumer after observing another monkey drink it readily in the cage adjacent to the observer. It must be noted, however, that even when the nonconsumer served as a demonstrator, a paired observer became a consumer after the observation period. Thus, it is not clear whether increased consumption of the juice by the observer resulted from social

This study was supported by a Grant for Cooperative Research from the Primate Research Institute of Kyoto University.

Hiroshi Imada, Kwansei Gakuin University, encouraged and helped us throughout the study. The faculties of the Department of Psychology, Primate Research Institute of Kyoto University, especially Kiyoko Murofushi, gave assistance for the study. Sheila Chase, Hunter College of City University of New York, made valuable comments. Shunji Gotoh and Masae Hasegawa helped us with the treatment of food aversion conditioning in monkeys. We thank these persons and organizations.

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transmission or simple facilitation of drinking any fluid from a specific container.

The purpose of our study was to demonstrate social transmission of food preferences in Japanese monkeys.

Experiment 1

The first experiment was designed to investigate whether or not a mother monkey and its child, by chance having different food preferences initially, would have the same food preferences after experience in a cofeeding situation, in which both were placed together in a cage and able to observe each other eat.

Method

Subjects. Three mother–child pairs of Japanese macaque (*Macaca fuscata*), living in the Primate Research Institute of Kyoto University, Inuyama, Aichi, Japan, served as subjects. They were, mother and offspring, respectively, M1 and C1 (a male), M2 and C2 (a female), and M3 and C3 (a female). M1 and M3 were 8 years old, and M2 was 11 years old. The three infants were all 1 year old. M1 and M2 were brought to the institute at least 1 year before the study and had had 5 and 10 years experience, respectively, in the wild before their capture. M3 was born at the institute and had been separated from the troop and housed separately in a home cage for 2 years before the study. Each child was reared in a cage with its mother from birth. However, during the study all subjects were individually caged and fed twice a day, once in the morning and once in the afternoon. They had free access to water.

Apparatus. All experimental operations were done in the individual home cages (60 cm wide × 65 cm high × 65 cm deep) or in a pairing cage (250 × 65 × 65 cm). One wall (65 × 65 cm) of the pairing cage was made of transparent Plexiglas that had two holes (7 cm in diameter) through which the subject could reach a food tray.

Procedure. The experiment consisted of single-feeding and paired-feeding sessions. Single-feeding sessions were given in the home cage, which had two food trays (11 × 7 × 17 cm), one with 40 pieces of popcorn (0.16 g each) and the other 40 raisins (0.55 g each). The food trays were attached to the outside of the front lattice of the cage, and the subjects were allowed to eat the target foods for 30 min. The locations of the foods were changed each day. In order to make both popcorn and raisins available to the subjects throughout the session, the experimenter added food to each tray before it became empty. The number of each food item consumed was recorded.

Paired feeding was the same as single feeding except that it was carried out in the pairing cage. Both the mother and its child were placed in the cage and given the opportunity to eat both popcorn and raisins for 30 min.

The paired-feeding situation allowed the mother to interact with its offspring and vice versa. The single-feeding situation for each subject served to test for initial preferences and for the aftereffect of the social interaction.

First, several single-feeding sessions were administered until the amount of food consumed by each subject became stable.

Then paired-feeding sessions were introduced. Two paired-feeding sessions and two single-feeding sessions were given in alternation. This alternation of two paired-feeding and two single-feeding sessions was repeated until 10 paired-feeding sessions were given in all. Finally, single-feeding sessions were given for 10 days. Each daily session immediately followed the afternoon feeding.

Before introducing the single-feeding and paired-feeding sessions, all subjects had been habituated to the single-feeding and paired-feeding situation for about 1 month until they took laboratory chow freely from the food trays.

Results and Discussion

Figure 1 shows the food consumption for each monkey in the single-feeding sessions. As shown in the extreme left portion of Figure 1, the mothers and their offspring showed different food preferences in all three pairs. However, after the introduction of paired-feeding experiences, the choice patterns for each food by either the mother or the offspring changed. Before the introduction of paired-feeding, 2 offspring, C1 and C2, did not eat raisins. After having observed their mothers eat raisins, they started to eat raisins as well. The newly acquired food intake by the 2 offspring was maintained throughout the sessions. Neither monkey of the M2–C2 pair consumed popcorn. M3 increased its consumption of raisins after paired feeding.

The foods that either the mother or its offspring ate before the paired feeding came to be consumed by both the mother and its offspring. The foods that both members of the pair ate before continued to be consumed throughout the sessions. The foods eaten by neither continued never to be consumed. In conclusion, the food preferences moved toward agreement between the mother and its offspring. These results suggest that the food preferences were transmitted from the mother monkey to its offspring or vice versa.

Before the initiation of eating the novel food, the monkeys typically showed the following behaviors: looking at one's partner, muzzling, grabbing food from the partner's hand, and so on. These behaviors further support the assumption that the social interaction between the mother and its offspring was important in the change of food preferences.

Experiment 2

The results of Experiment 1 suggest that the food preferences may be socially transmitted. However, it can also be argued that the change of choice pattern observed in C1 and M3 occurred merely by repeated exposure to the foods, without the interaction with their partners.

Experiment 2 was designed to confirm the conclusion of Experiment 1 by showing the same change pattern of food choice as observed in C2 of Experiment 1. That is, offspring start to eat only one food, which their mothers also eat, but never eat the other food that their mothers do not eat. Disagreement in food preferences between the mother and its offspring was formed artificially by food aversion conditioning.

Method

Subjects. Two mother–child pairs, living in the Primate Research Institute of Kyoto University, were added as subjects to the 3 pairs used in Experiment 1. They were, mother and child, respectively, M4

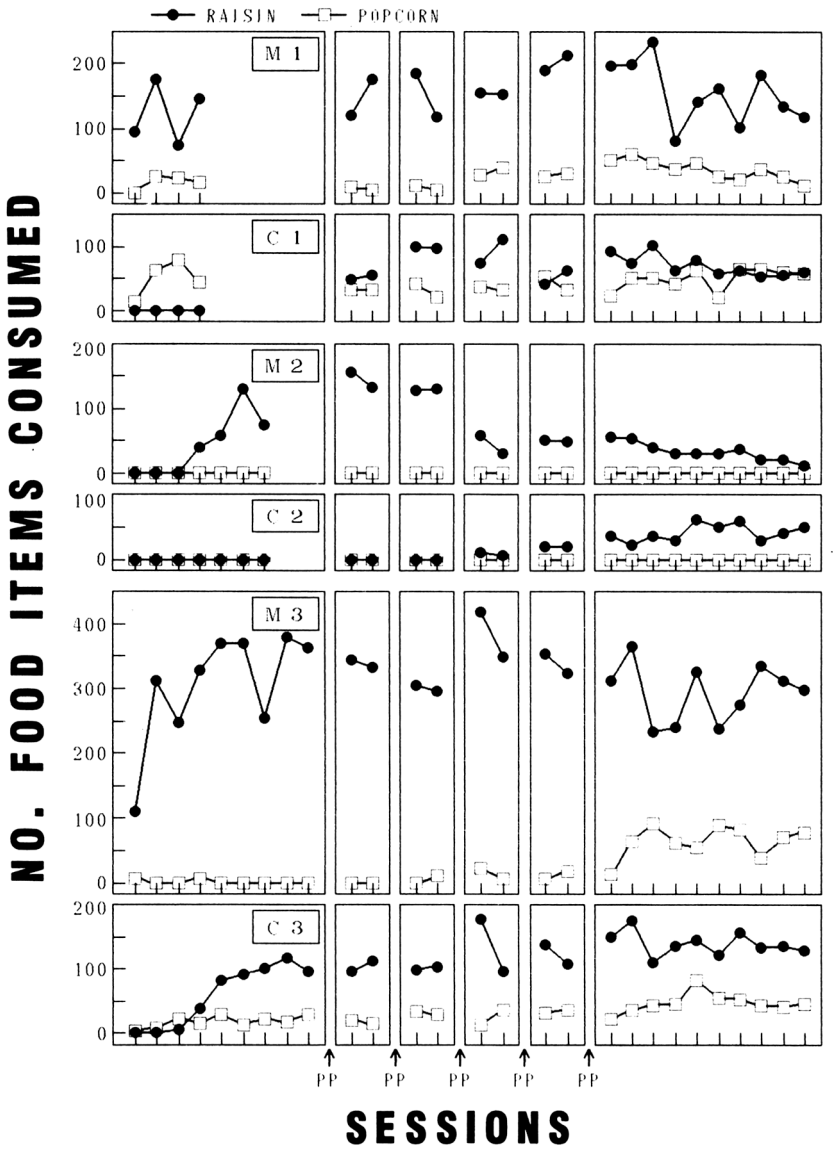

Figure 1. The food consumption for each monkey in the single-feeding sessions. (P = paired feeding).

and C4 (a female) and M5 and C5 (a female). M5 was more than 15 years old, and M5 was 10 years old. C4 was 2 years old, and C5 was 1 year old. M4 was brought to the institute 10 years and M5 1 year before the study. They had had about 10 years experience in the wild before their capture. Each child was reared in a cage with its mother from birth. Other conditions of subjects were the same as those in Experiment 1.

Apparatus. The apparatus was the same as that in Experiment 1 except that experimental operations on the two new pairs were done in individual home cages (85 × 65 × 80 cm) or in a pairing cage (70 × 75 × 70 cm) of different dimensions.

Procedure. In Experiment 2, almonds (1.16 g each) and marshmallows (0.77 g each) were used as test foods. The experiment progressed in three stages. In the first stage several sessions of single feeding were administered to all subjects.

In the second stage, food aversion conditioning was given to each subject to make the food preferences of the mother different from its offspring in each pair. Cyclophosphamide (20 mg/kg) was injected intravenously in each offspring 30 min after presentation of both marshmallows and almonds. The mothers received the same treatment 30 min after exposure of one of the two foods; M1 and M2 were exposed to marshmallows, and M4 and M5 were exposed to almonds. According to a previous study (Matsuzawa & Hasegawa, 1983), this procedure produces a long-lasting, strong aversion to novel foods. No such treatment was given to M3 because it did not eat marshmallows from the beginning. Conditioning took place once a day until all subjects showed complete aversion to target food or foods on two consecutive single-feeding sessions. As a consequence of the food aversion conditioning, the offspring ate neither food, and the mothers ate only one of the two foods. Thus the artificially established food preference provided the baseline stage for the next test stage for social transmission of food preference.

In the final stage, the same test procedures as those in Experiment 1 were introduced. The paired-feeding sessions and single-feeding

sessions each took place for 2 consecutive days with four repetitions of the sequence.

Results and Discussion

In the paired-feeding sessions, all of the mothers avoided the food to which they had a conditioned aversion but ate the other food. The food consumption for each offspring in each session is shown in Figure 2. As the paired feeding was repeated, all the offspring again started to eat the target food that their mother ate in the paired-feeding sessions, almonds for C1, C2, and C3, and marshmallows for C4 and C5. However, they did not eat the control food, which their mother never ate in the paired-feeding sessions, during the tests made after eight repetitions of paired-feeding sessions. The attenuation of aversion in offspring occurred only for the target food, not for the control food.

The mothers' eating behavior played an important role in the extinction of aversions to the target food but not to the control food for the offspring.

General Discussion

The food preferences of all 5 mother–child pairs became more alike after paired-feeding, although the pair members showed discrepant feeding preference initially. This change was shown when the discrepancy occurred by chance (Experiment 1) and when it was produced artificially (Experiment 2).

The change of food preference demonstrated here cannot be explained in terms of the independent feeding experiences of each animal. The change was induced by social transmission of food preferences during paired feeding. This change is

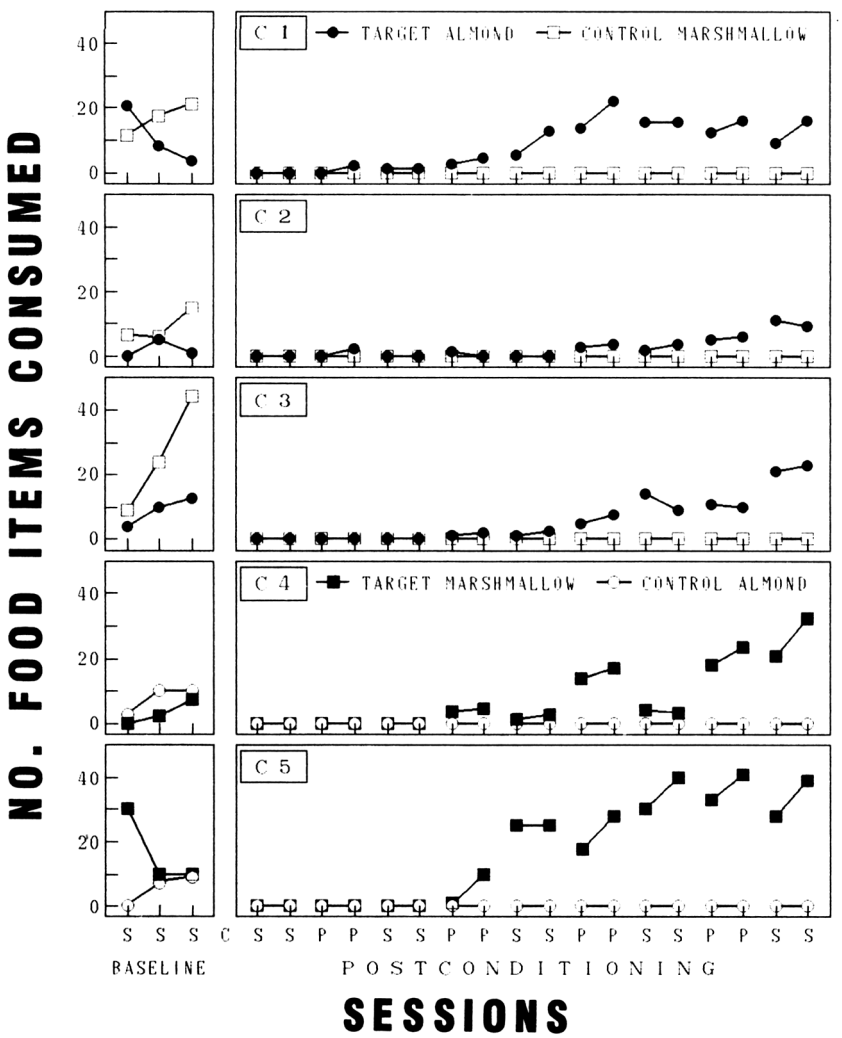

Figure 2. The food consumption for each offspring in each session. (S = single feeding; P = paired feeding; C = conditioning.)

based on the following rule: (a) the foods consumed by either the mother or the offspring came to be eaten by both; (b) the foods consumed by both continued to be eaten; and (c) the foods consumed by neither continued never to be eaten.

The ability to learn socially what may be eaten has great advantages in the wild. Through social transmission monkeys can learn to eat novel and safe foods and expand their food repertoires. Our study shows that the food preferences of one monkey can be socially transmitted to another.

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Received August 23, 1989
Revision received November 15, 1989
Accepted November 16, 1989 ■