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Social effects on development of food preferences

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Abstract. The purpose of this study was to answer the question as to whether the food preferences of the young are dependent on the social influences or not. The experiments were conducted on female cats bearing electrodes implanted in the mid-lateral hypothalamus, and their weanling kittens. Each mother was given a self-stimulation test; the mothers which learned to press a lever for the hypothalamic stimulation reward were chosen for the experiment. Each mother, always 4 h food deprived before the session, was given a choice of meat pellets and banana slices. Eating bananas was rewarded by the hypothalamic stimulation whereas eating meat pellets was not; as a result, the mother concentrated only on eating bananas while ignoring meat pellets. In the following sessions one or two weanling kittens were always accompanying the mother during the session.lt was found that 15 out of 18 weanling kittens used in this experiment joined the mothers in eating bananas. After separation from the mothers these kittens continued to choose bananas and ignore meat pellets when tested in the absence of the mother. Control kittens of the same age, which were never trained with the mother, refused to eat bananas. Similar results were obtained with other mother-kittens groups in which mashed potatoes or plain jellied agar were given instead of bananas. These results suggested that the food preferences of the weanling kittens were influenced by the mother's choice of food, even in the case when this food was unusual for the species.

Key words: food preferences, brain stimulation reward, imitation

INTRODUCTION

When studying neurobehavioral problems, we often ask whether a certain behavior is inborn or acquired. One such behavior is that related to food preferences. As commonly known, carnivorous animals feed on flesh, whereas herbivora and most rodents feed on plants. This support a view that basic food preferences are inborn. However, several observations suggest that social influences may play an important role in food selection. These influences are usually observed within the animal groups of the same species.

In experiments of Turner (1964), 1-day-old chicks were offered a mixture of orange and green grains; nearby, beyond a wirenetting, a model of a hen, cut out of cardboard, was made to perform, by means of a lever, pecking-like movements at the grain of one color. When the model had repeatedly pecked only at orange grains, the chicks pecked twice as much at orange than at green grains; and, vice versa, when the model pecked only at green grains, the chicks pecked significantly more at green than orange grains. The effect of the model hen on grain preference in the chicks was unquestionable.

Katz and Revesz (1921) observed that chicks that were fed in isolation until they became satiated and would no longer accept food, started to eat again as soon as they saw other birds eating. Harlow (1932), Soulairac and Soulairac (1954), and more recently Johanson and Hall (1981) reported that young rats fed in pairs or in groups ate more than those fed in isolation. Similar observations were made by James (1953) on puppies and by Tolman (1964) on chicks. In a study by Galef and Clark (1971), adult rats were offered a choice of two diets; one of them was contaminated with toxic LiCl. After the consumption of the poisoned diet and resulting sickness the rats started to avoid eating that diet. When the rat pups at early weaning age were allowed to accompany the adults at feeding time, they ate only the diet that had been consumed by the adults and they avoided the diet that had been avoided by the adults. In another study, Galef and Clark (1972) found that the presence of adult rats facilitated the development of feeding behavior in the rat pups. When the weaning pups were offered solid food for the first time, in the absence of adult rats, they did not start to eat until they reached a mean age of 25.5 days. But when the pups were offered solid food in the presence of the adults, they began to eat it much earlier, at the mean age of 19.9 days. In this case, the presence of the adult rats had a facilitatory effect on the initiation of eating solid food.

Similar influence of the mother on the initiation of eating of new food was observed in our laboratory (Wyrwicka and Long 1980, Wyrwicka 1981). In experiments on two mother cats and their 10 kittens, each litter was divided in two groups consisting of two or three kittens. The kittens of one group were placed in an experimental compartment with the mother. At the same time, the other group was placed in another, similar experimental compartment in the absence of the mother. Both compartments were located in the same room so that the behavior of both groups of kittens could be observed at the same time. The new food, a portion of canned tuna (which was never before offered to these kittens before) was placed at the center of the floor of each compartment. After entrance into the compartment, the kittens with the mother showed a brief (up to 1 min) orienting reaction (consisting on remaining motionless), then approached the mother (who already started eating tuna) and began to sniff and occasionally even lick tuna. In the following daily sessions, the orienting reaction of the kittens gradually decreased and the kittens started to eat tuna immediately after entering the compartment. In contrast, the kittens placed in the other compartment without the mother first showed a prolonged (up to 3 min) orienting reaction, then started to investigate the compartment and later, to play. Only one of the five of the kittens started to lick some tuna at the end of the first 10-min session, whereas other kittens of this group initiated eating tuna only after 5 to 8 daily sessions. This experiment clearly showed the facilitatory effect of the mother on the initiation of eating new food, similarly as in the

study by Galef and Clark (1972). A possible mechanism of this effect will be discussed later.

A question had been raised as to whether the effect of the mother on feeding in the young is independent of the kind of food offered. The following experiments were designed to answer this question.

METHODS

Several experimental series were conducted on female cats and their weanling kittens. Two to four female cats and four to 18 their kittens were usually used in each series.

Test foods

As the experimental subjects were cats which usually eat meat, food other than meat was chosen to get an objective answer to the above asked question. The test food for the first experimental series was bananas. In the following series with other mother-kittens groups, the test foods were mashed potatoes (peeled and cooked in water without salt or any other additions) and jellied agar prepared by dissolving powdered, odorless and flavorless commercial agar in boiling water (6 g of agar to 1,000 ml of water) with an addition of nonnutritive green color for visibility. The cooked foods were cooled before the session. All these foods, unusual to the cats, were first tested for acceptance by all mothers before each experimental series. It was found that none of these foods was accepted by the mothers; bananas especially evoked a clearly aversive reaction, such as turning the head away from the plate with banana slices and moving away.

Experimental procedures

In order to induce the mothers to eat unusual foods, it was necessary to apply a special technique based on the self-stimulation method (Wyrwicka 1974). First, several female cats in the early period of pregnancy were chosen. In each of these cats, under pentobarbital anesthesia, one or two monopolar electrodes were implanted in the mid-lateral hypothalamus (A11:0, L3.0, H-4.0) and a reference screw electrode was placed in the skull over the frontal sinus.

One month after delivery, each mother was taken to the experimental compartment equipped with a lever connected to an electric stimulator, for a self-stimulation test. The mothers who learned to press lever for 0.3 s hypothalamic stimulation (2-3 V, 100 Hz, 1 ms dur/imp.) were chosen for the experiment. The lever was removed from the compartment, and instead, meat pellets on one plate, and banana slices on another, identical plate, were placed on the floor, at the center of the compartment. Each nother was always 4 h food-deprived before session. After entering the experimental compartment, the mother usually started to eat meat pellets but occasionally, during brief intervals in eating pellets, she approached the plate with banana slices and sniffed them. In such moments, the previously effective hypothalamic stimulation was given. As a result, in a few minutes, the mother started to ignore meat pellets and concentrated only on sniffing, touching, then licking, and finally eating banana slices. Each such action was immediately rewarded with the hypothalamic stimulation.

After a few daily sessions with using this procedure, the mother started to eat bananas as soon as she entered the experimental compartment. Eating bananas was usually continuous, with several brief intervals. The stimulation was given approximately every 2 seconds, but only during eating bananas, and never during, or immediately after, eating or approaching meat pellets. Usually, the mother received 200-300 episodes of stimulation during a 10-min session.

After several sessions, when the mother's behavior stabilized, one or two of her 4-9 week old kittens, 4 h food deprived, were introduced into the experimental compartment together with the mother and their behavior was independently observed by two persons. The amount of consumption was measured by weighing the plate with food before and after the session and calculating the difference. The consumption of food by the kittens was estimated by subtracting the average consumption

of the mother per session (which was determined before the sessions with the kittens).

The same procedure was used in other experimental series in which a different unusual foods were used. Each series was conducted on a different group of mothers and their kittens. Each mother and her kittens were used with only one kind of unusual food. However, some mothers were used in two or three series with the same test food but with different litter each time.

The sessions with the mother were conducted twice a week until the kittens reached three months of age. Then the kittens were separated from the mother and two sessions per week with kittens alone continued. The kittens were 4 h food deprived prior to each session as before in the series with the mother. One or two kittens were placed in the experimental compartment and, as before, meat pellets on one plate and banana slices on another plate were offered.

Control experiments

For control, nine kittens of naive mothers from three litters of various age (two kittens were 13 week old, three were 18 week old, and four were 21 week old) which had never before eaten bananas or seen their mother to eat that food, were tested for eating bananas. The banana slices were offered to them in their home compartment just before their usual daily feeding time. The observations were conducted once a week in 10 min session, for three weeks.

RESULTS

The behavior of kittens accompanying the mother was similar in all experimental series with unusual foods (bananas, mashed potatoes, jellied agar). After entering the experimental compartment for the first time they showed an orienting reaction consisting in assuming freezing posture for up to one minute. Then they started to investigate the area for 2-3 min and later to play with various small objects such as a screw, a smalll opening in the wall, etc. They did not seem to pay attention to the mother eating unusual food; they also ignored meat pellets which were always present in the compartment. In further sessions, however, the kittens behavior changed. The results obtained in experiments with each unusual food will be described separately for each food.

Bananas

After several sessions with the mother, 15 of the 18 tested kitten started to approach the mother more often and, finally, they began to lick and then actually eat banana slices. Only three kittens of this group refused to eat bananas; however, they did not eat meat pellets either and spent most time playing. It was observed that most kittens which accepted bananas, initially attempted to eat exactly from the same spot on the plate where their mother had been eating. Later they ate from another spot on the plate and, in further sessions, they even ate bananas from another plate located close to the mother's plate, or from the floor when a banana slice accidentally fell from the plate. In further sessions, the kittens usually started to eat banana slices with the mother as soon as they entered the experimental compartment, and continued eating during the first 2-3 min (Fig.l). Then they began to play, occasionally returning to eat bananas for some seconds before returning to play.

After weaning, the kittens were taken, singly or in pairs, for sessions without the mother. It was observed that all kittens (except one) which previously ate bananas with the mother, continued to behave as before, i.e., they approached the banana plate almost immediately after entering the experimental compartrnent and started to eat. They usually ate continuously for about 2-3 min, then walked away to play, returning from time to time to eat banana slices again for several seconds. They ignored meat pellets. A summary of the results of these experiments is shown in Fig.2.

The amount of consumption differed from kitten to kitten. It was, however, observed that kittens whose mother ate only small amount of bananas, ate less bananas than the kittens whose mother ate

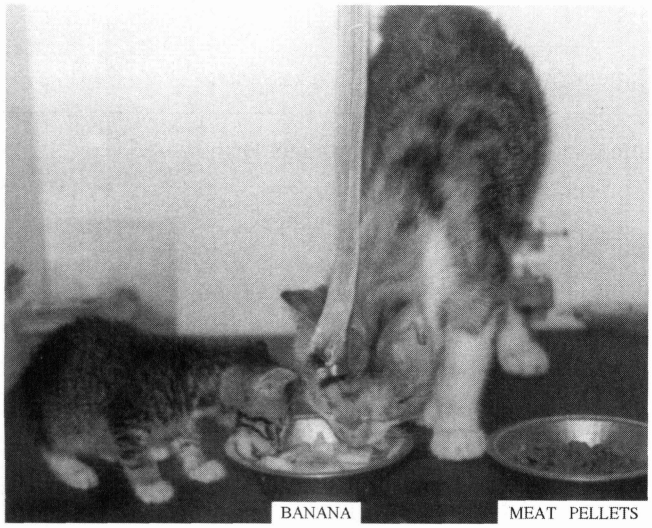

Fig.1. A picture showing a kitten eating bananas with the mother. Through the cable attached to her head, the mother obtains the rewarding electrical stimulation in the hypothalamus for eating bananas. A container with meat pellets is shown to the right of the banana container.

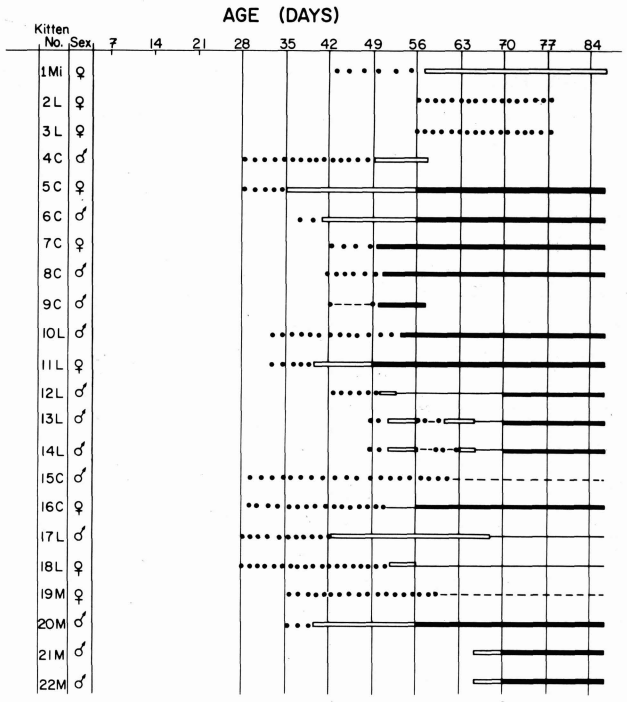

Fig.2. A summary of observations on kittens accompanying the mother during the sessions with unusual foods (bananas or mashed potatoes). Dotted line, the period during which the kitten accompanied the mother during the session but was not eating. Double solid line, the period during which the kitten ate unusual food (UF) with the mother. Solid line, the period when the kitten was eating UF while tested alone; thin solid line, consumption of UF below 2 g; thick solid line, consumption over 2 g during the 10-min session. Broken line, the period when the kitten was alone during the session while not eating UF. The unusual food was bananas for kittens Nos. 1Mi - 18L, and mashed potatoes for kittens Nos. 19M-22M.

much of this unusual food (Table I). These differences in consumption of bananas were present only during the early postweaning period, and were no longer observed when the kittens were tested at six months of age. As seen in Table I, both the original "low eaters" and "high eaters" ate even more bananas than before, with no significant differences in consumption.

Control sessions

As described in the Methods section, nine kittens of three litters (of other, naive mothers) which never ate bananas with the mothers or saw them eating bananas, were offered slices of bananas in their home compartments just before their usual daily feeding time. It was found that none of these kittens accepted bananas during the 10-min observation session, although they showed some interest in banana slices at the end of the session. When the bananas were left in the compartment overnight, they were found untouched the next morning. The same was observed when the test was repeated a week later. However, when the test was repeated for the third time, another week later, the kittens seemed more interested in banana slices but still refused to eat them during the session. In contrast, the kittens of the same age which had been trained before with the mother in eating bananas, and then tested for eating them in their home compartments, ate bananas already during the first test session, after a brief orienting reaction lasting for several seconds. (This orienting reaction could be caused by presentation of bananas in a different environment than that of the experimental compartment).

Mashed potatoes

Experiments with potatoes were conducted on only one mother and her four kittens. The kittens were introduced to the session with the mother in

TABLE I

Amount of consumption of banana by two mothers and their kittens (Means for five 10–min sessions)

Mother alone		Kittens alone (after training with mother)			
No.	g*	No.	Weeks of age		
			9 – 16	17 – 23	25 – 27**
C	3.4±0.4	5C	1.2±0.5	no data	no data
		6C	3.3±1.0	no data	no data
		7C	2.8±0.5	10.5±1.6***	10.5
		8C	2.6±0.9	14.0***$	35.0$
		9C	1.7±0.6	no data	no data
L	39.0±3.4	10L	18.0±1.5	36.1±7.4	35.0$
		11L	11.5±2.5	13.6±4.8	19.2
		12L	6.5±1.4	6.0±2.7	17.5
		13L	3.1±0.7	2.1±1.0	10.5
		14L	3.9±0.8	5.4±1.3	0.0

*Mean consumption of bananas in grams per session ±SE; **Single 24-hour test in the home compartment; *** Mean for five 24-hour tests in the home compartment; $All amount of banana given to the kitten was consumed.

pairs. Mashed potatoes and meat pellets were offered on separate identical plates. The mother who already was trained to eat potatoes for hypothalamic stimulation before, immediately started to eat them. The first pair of 5-week-old kittens showed first an orienting reaction and then started to investigate the compartment. After four sessions one of these kittens started to eat potatoes with the mother, and then consumed this food during each following session, ignoring meat pellets. The other kitten ignored both meat pellets and potatoes, and never ate potatoes during the experimental period, although it was once seen playing with a small piece of potato, pushing it with paw. This kitten was several times seen suckling on the mother when she was eating potatoes. Perhaps immaturity could be responsible for such behavior.

The experiments with two other kittens of the same litter started when they were nine weeks old. They were no longer nursed by the mother but they still lived with her in the same home compartment. When introduced into the experimental compartment, these kittens showed only a brief orienting reaction and then approached the mother. In a while, they started to eat potatoes with her. They did not pay attention to meat pellets. After several sessions with the mother, these kittens were daily taken for session alone (in the absence of the mother), during further two weeks. Both kittens continuously ate potatoes during the first 4-5 min of the session. One of these kittens ate greedily and sometimes vomited after a few minutes of continuous eating; usually, this kitten consumed the vomited potatoes and returned to eat more. After a period of eating the kittens walked away from the potato plate to play, returning only from time to time to eat potatoes again for a while. On an average, they consumed about 10 g potatoes per kitten during a 10 min session.

After following 15 daily sessions with these kittens, a test for food preference between tuna (the food known as preferable for the cats) and plain mashed potatoes was performed.The kittens were already familiar with tuna because they were occasionally offered tuna in their home compartment. During the test, a portion of tuna was offered on one plate and a portion of mashed potatoes on another, identical plate. The kittens (which, as usual, were 4 h

food deprived before the session) first rushed to the potatoes and ate them vigorously. Some 10 s later, they turned to eat tuna, and after another 10 s they returned to eat potatoes. They alternated between eating potatoes and tuna several times, while playing during brief intervals in eating.

No further observations were made on this group of kittens.

A brief summary of kittens behavior during the experimental series with these kittens is shown at the bottom of Fig.2 (kittens Nos. 19M to 22M).

Jellied agar

Experiments with jellied agar were conducted on six mothers and their 16 kittens. The kittens introduced singly or in pairs into the experimental compartment with the mother, first showed the usual orienting reaction and then investigated the environment and played. After a few sessions, they joined their mother in consuming jellied agar. The measuring of agar consumption was quite difficult because during eating much of the jelly was spilled around the plate on the floor. It was only estimated that the mean consumption was 2-3 g per kitten, whereas the mean consumption by the mother was about 10 g during a 10 min session.

In order to check whether the taste of unusual food facilitates or inhibits the effect of the mother on the kittens' consumption of agar, some flavors were added to plain agar such as 0.001% quinine solution, 1% saccharin solution, and chicken broth. Agar with each flavor was offered in separate series of sessions. It was found that an addition of 0.001% quinine solution to the agar resulted in a decrease in consumption in both the mother and the kittens, whereas an addition of broth resulted in an increase in consumption. An addition of 1% saccharin solution to plain agar did not change the consumption in the mother but slightly diminished the consumption in the kittens.

The kittens were then tested for acceptance of the both plain and flavored agar in the absence of the mother. It appeared that again their consumption of agar with broth was the highest, and that with quinine was the lowest. However, the consumption of agar with quinine was, unexpectedly, higher in the absence of the mother than in her presence. Possibly, in this case, the mother's behavior (unnoticeable to the experimenter) could exert an inhibitory effect on consumption by the kittens.

More experimental data on this topic can be found in an earlier publication (Wyrwicka 1981).

DISCUSSION

The above described studies showed that the influence of the mother on food preferences of her weanling kittens was independent of the kind of food, and that young kittens would supposedly choose any food being consumed by the mother, even when this food (bananas, potatoes, or jellied agar) was clearly unusual for their species. This fact provided an objective evidence that food preferences may not be so much inborn as acquired through social influences early after birth.

It seems that the simplest explanation of the above described facts is to regard them as a result of imitation. The process of imitation (or, more strictly, imitative behavior) can be defined as the act of an individual's copying certain motor behavior performed by another individual. A variety of studies on imitation showed that it occurs quite often in life and is observed from the earliest moments after birth (reviews by Davis 1973, Galef 1976, Melzoff and Moore 1977, Wyrwicka 1978).

The fact that imitative behavior is observed in the first hours of life in human neonates (Melzoff and Moore 1977) suggests that imitation is an inborn process. The neural mechanism of this process may be understood as follows (Fig. 3). Visual and other stimuli from the demonstrator's gesture activate their representation of this gesture in the infant's brain motor system through inborn sensorimotor connections. The existence of such connections was demonstrated by electrophysiological research of Woolsey (1958), lesion studies by Stepien and Stepien (1959) and Dobrzecka et al. (1965) as well as by histological horseradish perox-

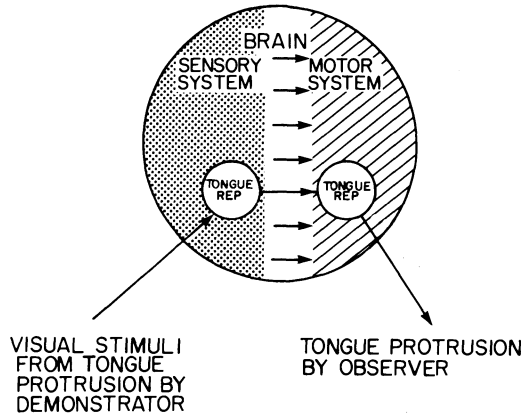

Fig.3. A simplified model of the unconditional reflex arc for imitation of tongue protrusion. Visual stimuli from the tongue protrusion of a demonstrator produce activation in the tongue representation (Tongue Rep) in the brain sensory system in the observer. This activates, through sensorimotor connections (arrows), the tongue representation in the brain motor system, resulting in the tongue protrusion by the observer.

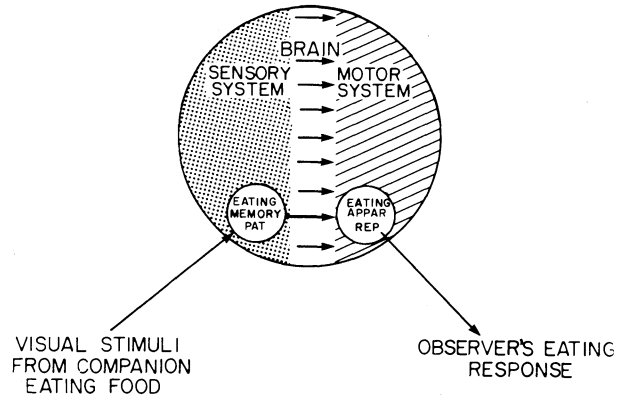

Fig. 4. A simplified model of the unconditional reflex arc for imitation in eating behavior. Visual stimuli from the companion's eating food activate a memory pattern of associations related to previous eating experiences (Eating memory pat) in the brain sensory system of the satiated observer; this activates, through sensorimotor connections (arrows), the representation of the eating apparatus (Eating appar rep) in the brain motor system of the observer, resulting in the resumption of eating.

idase labeling technique by Miller and Vogt (1984). The activation in the representation of the demonstrator's gesture in the infant's brain motor system leads to the infant's reaction which is similar to that performed by the demonstrator. This process has the characteristics of an unconditional reflex and should be regarded as such.

However, there exist various forms of imitative behavior, from simple ones, such as those occurring in neonates, to more complex forms, such as those observed in food intake. In feeding behavior, not a single stimulus but a complex of stimuli related to previous feeding experiences is involved in the act of imitation. Visual stimuli from the mother's (or another companion's) eating food activate a memory pattern of association related to former acts of eating in the brain sensory system of the non-hungry observer (Fig. 4). This activates, through the sensorimotor connections, the representation of the eating apparatus in the brain motor system of the observer, leading to eating. The same model may be used for explanation of the imitation of mother by kittens in food intake.

A question may be asked as to why imitation does not always occur. In our experiments, about 20% of kittens did not imitate the mother in eating unusual foods. Also the experiments showed that adding quinine to the jellied agar resulted in a decrease in consumption, whereas adding broth to agar led to an increase in consumption. These changes in imitative behavior could be caused by certain sensory factors, such as a strong orienting or investigatory reaction, taste of the food, oversatiation, and others. The problem of inhibition of imitation is still open for research.

The experiments described in this article were conducted under artificial conditions in order to obtain objective evidence concerning the development of food preferences. Such conditions do not exist in nature. In nature the mother usually eats the food which for generations secured the survival of the species. By imitating the mother (or other adults of the colony), the animals of the same species continue to choose the same general kind of food.

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