

The Effect of Reciprocal Cross-Fostering of Pups in Two Species of Mice *Mus musculus* and *Mus spicilegus*: An Altered Response to Con- and Heterospecific Odors

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Received June 9, 2016

Abstract—The effect of pup cross-fostering by the house mouse *Mus musculus* and the mound-building mouse *M. spicilegus* on the odor preferences of sexually mature individuals has been studied for the first time. House and mound-building mice reared by females of a closely related species did not prefer any of the odors, in contrast to intact individuals of these species. Some individuals reared by females of a closely related species preferred the odor of foster species to conspecific odor. Early olfactory experience has been shown to alter the response of house mice and mound-building mice to odors of their own species and foster species.

DOI: 10.1134/S106235901802005X

INTRODUCTION

The effect of exposure to odors at an early age (early olfactory experience) on the formation of preferences for different odorants and con- and heterospecific olfactory signals in adult individuals is one of the aspects of research on chemical communication in mammals (Maras and Petrulis, 2008a, 2008b). A number of studies have demonstrated the formation of reactions to species-specific odors at an early age in several mammalian species. The reactions were formed due to imprinting or other forms of learning (adaptation, conditioned reflex formation, or associative learning). These phenomena affected various forms of behavior and responses to con- and heterospecific individual odors later in life (D'Udine and Alleva, 1983; Maras and Petrulis, 2008a, 2008b; Kotenkova et al., 2017). The majority of experimental studies of the influence of early olfactory experiences on subsequent responses to odors has been performed in rodents. Animals of some species reared by heterospecific parents showed altered responses to the odor of conspecifics later in life, whereas no changes observed in some other species, and the results of experiments performed in the same species were often discordant if different methods or modifications of the same methods were used.

Importantly, the results of experiments with cross-fostered rodent pups depended on a range of factors, such as species-specific and sex-specific differences in the responses to con- and heterospecific odors that could be determined by competitive relationships of the species in the wild and the species-specific features

of male and female interactions. The phylogenetic relationships of the species are also important, as they can (to some extent) define similarities or differences in features and composition of signaling substances (pheromones) between the species from of which pups were taken, and the species individuals of which fostered pups. The capacity for olfactory signal imprinting, which depends on the reaction norm in a certain species, also plays a significant role (Maras and Petrulis, 2008a, 2008b; Kotenkova et al., 2017).

The methods used are also of considerable importance. Modifications of the two-choice method are often used in experiments on assessment of odor reactions. The advantages, drawbacks, and limits of applicability for this method, interpretation of the results obtained, and certain challenges associated with studying the reaction of mammals to olfactory signals have been discussed in a number of earlier studies (Johnston, 1981; Kotenkova, 1988; Doty, 2003; Surov and Maltsev, 2016).

The controversy over the results obtained with various modifications of the method could also have been due to the experiment being performed on familiar or unfamiliar territory, that is, in the animal's home cage or on a neutral territory. The setup for odor presentation (tubes, Petri dishes, a stream of air with odor, and others) is also important. The modification must be selected experimentally for each rodent species, and the behavioral and ecological features of the species must be taken into account. The validity of this procedure for the assessment of the animals' capacity for odor recognition and characterization of attractive

and repulsive properties and the informative value of odors is supported by the consistency of results obtained by this method and those obtained using physiological and immunohistochemical methods. For instance, experiments in species of the house mouse of the supraspecies complex *Mus musculus* s. l. showed that an increase in the testosterone levels in the blood plasma of males of house and mound-building mice only occurred upon exposure to conspecific female odor, but not to the odor of a female from a closely related species (Sokolov et al., 1988). Moreover, the preference for conspecific odor over the odor of closely related species in these taxa showed a distinct correlation with the differences in neuron activation in response to these odors, both at the level of the receptor epithelium of the vomeronasal organ (VNO) and in the accessory olfactory bulb (AOB) (Voznesenskaya et al., 2010). These structures belong to the accessory olfactory system that mediates the perception of signaling substances (pheromones) in house mice (Kotenkova, 2014). Neuron activation in VNO receptors of males of house and mound-building mice was observed upon exposure to conspecific estrous female odor, whereas the odor of estrous females from a closely related species did not evoke a similar reaction (Voznesenskaya et al., 2010).

Data from studies that addressed the effect of early olfactory experience on the subsequent response to conspecific odor in house mice are controversial. Detailed analysis of these data is given in the Results and Discussion section (Quadagno and Banks, 1970; Kirchhof-Glazier, 1979; Sokolov and Kotenkova, 1987; Wuensch, 1992).

Many still-unsolved problems are related to the influence of early olfactory experience on the selection of the odor of a potential mate in rodents, that is, on the formation of precopulation isolation mechanisms. Our earlier analysis of published studies and our own data showed that mate in many rodent species was based on odor and performed at a stage that preceded copulative behavior (Kotenkova, 2014). It is not completely clear whether animal reactions to species-specific odors are innate or formed due to imprinting and/or other forms of learning. There are other, yet-unanswered questions, for instance, whether metabolites of foster species can acquire a signaling value or if the modification of reactions to heterospecific odors is entirely mediated by classical conditioning; what are the compounds that modify behavioral reactions under the influence of early olfactory experience; and what are the neuronal mechanisms that underlie changes in the reaction to species-specific odors? It is necessary to select model species before performing experiments intended to solve these problems.

The species of mice *Mus musculus* and *M. spicilegus* that we selected for testing take significantly more time to investigate conspecific urine odor than heterospecific urine odor (including the odor from closely

related species) upon two-choice test, regardless of the sex of the odor donors (Kotenkova et al., 1989; Sokolov et al., 1990; Kotenkova and Naidenko, 1999). Estrous female odor evoked the activation of vomeronasal organ receptors and neuronal activation in the accessory olfactory bulb of males of house and mound-building mice only if the female was conspecific, whereas estrous female odor from a closely related species did not evoke this response (Voznesenskaya et al., 2010). We could not find similar data for other closely related species among the publications available to us. Our studies revealed strong directionality of olfactory preferences for conspecific odors in mice; therefore, modification of such preferences by early olfactory experience was amenable to experimental detection, both at the behavioral level and at the level of activation of specific brain regions.

The aim of the present work was to study the asymmetry of behavioral responses to con- and heterospecific urine odor in cross-fostered individuals of house and mound-building mice, that is, the effect of early olfactory experience on the formation of odor preference.

MATERIALS AND METHODS

The group of cross-fostered house mice used in the study included eight males and four females from three litters, and the group of cross-fostered mound-building mice included eight males and eight females from four litters. The group of male control house mice fostered by conspecifics included seven animals reared by their own mother and six animals fostered by conspecific females other than their biological mothers. Cross-fostered house mice were involved in six series of experiments (69 trials in total), and mound-building mice were involved in five series of experiments (73 trials in total) (Tables 1, 2). Two series of experiments (22 trials) were performed with control males from four litters. Pups were transferred between nursing females of a closely related sympatric species at 1–8 days of age; that is, house mouse pups were transferred to nursing mound-building mouse females and mound-building mouse pups were transferred to house mouse females (Fig. 1). Males were isolated from the females for 2–3 days before the pups were born. Litters were swapped regardless of the pup number and sex, but each of the litters swapped included both males and females.

Males reared by their biological mothers were used in one series of control experiments, and the other control group included males transferred to other nursing house mouse females at 5–6 days of age. All males were removed from the foster mothers' own litters, but the female pups remained with their biological mothers. The pups were left with the females until four weeks of age, and all house mice and mound-building mice used in the experiments were housed in the same room. Animals were housed individually

Table 1. Time of investigation of conspecific and foster species (mound-building mouse) urine odor by the house mouse *Mus musculus*

Series	Recipients (number, sex)	Age of pup transfer to mound-building mouse female, days	Odor sources	Odor investigation time (average, min–max), s	Number of experiments *		P
					with longer investigation	total	
1	3♂♂ 1♀	3	♀ MBM ♀ HM	19.6, 1.5–9.4 23.8, 2.1–110	5 9	14	NS
2	4♂♂ 3♀♀	3	♂ MBM ♂ HM	18.9, 5.1–39.9 15.6, 3.5–45.4	5 4	9	NS
3	4♂♂	6	♀ MBM ♀ HM	4.9, 3.5–33 2.8, 2.5–44.1	11 0	15	<0.05
4	4♂♂	6	♂ MBM ♂ HM	3.6, 3–20.1 2.8, 2.5–35	4 1	7	NS
5	4♂♂	6	♂ MBM ♀ HM	5.1, 3.1–44.5 3.3, 2.6–21.5	7 1	8	NS
6	4♂♂	6	♂ HM ♀ MBM	2.6, 2.1–15.5 4.3, 3.5–18.6	1 8	16	<0.05

HM, house mice; MBM, mound-building mice, anestrus females; NS, differences not significant; P, significance level; in Tables 1–3. * Odor investigation time was similar in the rest of the experiments; in Tables 1 and 2.

Table 2. Time of investigation of conspecific and foster species (house mouse) urine odor by mound-building mice *Mus spicilegus*

Series	Recipients (number, sex)	Age of pup transfer to house mouse female, days	Odor sources	Odor investigation time (average, min–max), s	Number of experiments		P
					with longer investigation	total	
1	2♂♂ 3♀♀	1	♂ HM ♂ MBM	10.2, 1–14 11.3, 2.2–11.5	8 3	12	NS
2	5♂♂ 2♀♀	2	♂ HM ♂ MBM	8.4, 1.1–24.7 9.2, 1–27.7	13 14	27	NS
3	5♂♂ 2♀♀	2	♀ HM ♀ MBM	10.5, 2–24 11.7, 1.1–32	7 5	16	NS
4	1♂ 3♀♀	7	♂ HM ♂ MBM	10.6, 2.5–31.2 11.2, 2–43	5 7	12	NS
5	1♂ 3♀♀	7	♀ HM ♀ MBM	17.7, 4–47 6.8, 2–15	5 1	6	<0.05

between four weeks of age and the onset of sexual maturity, and the experiments started when the mice were two months old. Four house mouse males and three females used in the experiments were fostered by mound-building mouse females from three days of age, and four males were fostered from six days of age. Two mound-building mouse males and three females were fostered by house mouse females from one day of age; five males and two females, from two days of age; and one male and three females, from seven days of age. Animals reared by females of a closely related species were used in several series of experiments (Table 1, series 1, 2 and 3–6; Table 2, series 2, 3 and 4, 5). The

intervals between the series of experiments were six to seven days. The age of pups at the time of transfer and the number of experiments in each series are listed in Tables 1–3.

A detailed description of the two-choice test used in the present study in which urine odor presented in Petri dishes was given in earlier publications (Sokolov et al., 1983; Kotenkova and Naidenko, 1999). The procedure is described below. Individual animals were placed into glass chambers (30 × 20 × 20 cm) with a mesh lid and sawdust (2-cm layer) and a piece of cotton wool for nest building at the bottom. The animals

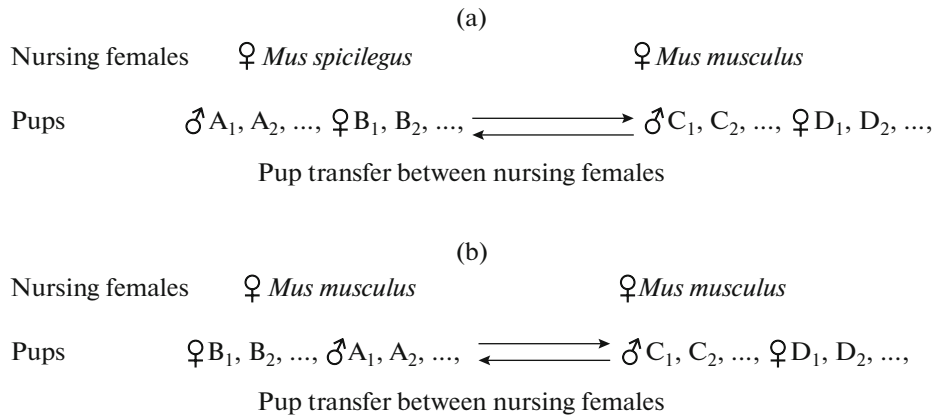


Fig. 1. Scheme of pup transfer between females for cross-fostering. (a) Pup cross-fostering by house and mound-building mouse females; (b) pup cross-fostering by house mouse females (control).

stayed in the chambers throughout the experimental period. The experiments were performed in the same chambers during the period of maximal evening activity of the mice (between 20:00 and 4:00) once every four to seven days with weak artificial illumination. A round plastic pedestal (diameter 130 mm, height 30.5 mm) was placed near one end of the chamber, and two Petri dishes (40 mm in diameter) were placed on the pedestal. Two square pieces of cellophane (10 × 10 mm) with drops of donor urine (~20 µL) were placed into the Petri dishes immediately prior to the beginning of the experiment. The urine samples in each Petri dish were derived from a single donor. The Petri dishes were placed onto the pedestal, so that the distance between them was ~30 mm. The time of sniffing each odor source after natural awakening of the animal and exit from the nest was recorded using a stopwatch for three instances of odor investigation. The observer was blinded to the origin of the urine in the Petri dishes during the trial.

Sexually mature male and female mice not familiar to the animals tested were used as urine donors. Urine was collected two to three days prior to the experiments or on the day of the experiments by placing the animals into small mesh cages with 60-mm Petri dishes under the bottom for 2–4 h. The urine was stored frozen and thawed only once, 1 h prior to the beginning of the experiment. At least three urine donors from each species were used in each series. The sexual cycle stage was identified according to the standard procedure of vaginal swab analysis (Kirshenblat, 1971) prior to urine collection.

RESULTS AND DISCUSSION

Several series of experiments were performed in order to characterize the influence of the early olfactory experience on the subsequent reaction of house mice to con- and heterospecific odors (Tables 1, 2). There was no significant difference in the reactions to

conspecific and foster species odors in house mice fostered by mound-building mouse females from three days of age, regardless of the sex of urine donors (series 1 and 2). Male and female house mice fostered by mound-building mouse females from six days of age investigated longer the urine odor from foster species females (series 3), but there were no significant differences between the time of investigation of the male odor from different species (series 4). These mice showed no significant difference in the times of the male mound-building mouse and female house mouse odor investigation when these odors were presented in pairs (series 5), but the time of odor investigation for the female mound-building mouse was significantly longer than that of conspecific male odor investigation when these odors were presented simultaneously (series 6). Mound-building mice fostered by house mouse females from any age did not show a significant difference in the times of sniffing house and mound-building mouse odor sources in all experiment series but one (Table 2). The series that formed an exception was performed with mound-building mice transferred to a house mouse female at seven days of age. These mice took significantly more time to sniff urine from foster species females than conspecific urine (series 5).

Sexually mature house mice fostered by rat females from 7–12 days of age investigated significantly more time the conspecific odor as compared to the odor of foster species (Sokolov and Kotenkova, 1987). The discrepancy between the results may be due to the greater similarity between the odors of house and mound-building mice (as compared to rat odor) related to the phylogenetic similarity of the species. Moreover, Sokolov and Kotenkova (1987) reported summarized data for mice fostered by rats from 7–12 days of age. This could have introduced a bias into the experiment results if the critical period for odor imprinting occurred at an age earlier than 10–12 days and the number of mice fostered by rats from 10–

Table 3. Time of investigation of urine odor of conspecific and closely related species by house and mound-building mice (control experiments)

Series	Recipients (number, sex)	Age of pup transfer (or no transfer) to another conspecific female, days	Odor sources*	Odor investigation time (average, min–max), s	Number of experiments		P
					with longer investigation	total	
1	6♂♂ HM	5–6	♀ HM ♀ MBM	11, 3.1–22.5 4.8, 1.2–19.3	7 1	9	<0.05
2	7♂♂ HM	–	♀ HM ♀ MBM	9.1, 1.3–23.1 3.3, 1.1–7.3	11 2	13	<0.01
3	12♂♂ MBM	–	♂ HM ♂ MBM	3.7, 0.8–10.5 10.1, 8.0–13.7	3 16	23	<0.01
4	12♂♂ MBM	–	♀ HM ♀ MBM	7.2, 3.3–9.1 16.2, 13.1–17.3	1 14	16	<0.01

* Anestrous female in the first series; estrous female in the second series.

12 days of age exceeded the number of mice fostered from seven days of age.

The results of control trials are presented in Table 3. Sexually mature house mouse males fostered by conspecific females other than biological mothers from five to six days investigated significantly longer the urine odor from conspecific anestrous females as compared to the odor of mound-building mice females (series 1). The males reared by biological mothers investigated longer the urine odor from conspecific estrous females (series 2). Similarly, to house mice, male mound-building mice reared by their biological mothers investigated significantly more time the conspecific odor as compared to the heterospecific odor (series 3 and 4). The results of these experiments are in agreement with the earlier results. As mentioned above, we have shown that male and female house and mound-building mice always investigated significantly longer the conspecific odor as compared to the odor of closely related mouse species, regardless of the pairwise combinations used for odor presentation (Kotenkova et al., 1989; Sokolov et al., 1990; Kotenkova and Naidenko, 1999). Other authors have reported a similar directionality of behavioral responses to conspecific odors and the odors of closely related species upon pairwise presentation of odor sources to house and mound-building mice (Heth et al., 2001).

Our results prove that the reaction of house and mound-building mice to the odors of conspecific and foster species is modified by the early olfactory experience. However, it is necessary to note that some earlier experiments that involved house mice yielded contradictory results. Both the design of the experiment and the specific methodological approaches were different in four experimental studies that addressed the effect of fostering by heterospecific females on the subsequent reaction to odors of conspecific and foster species in house mice (Quadagno and Banks, 1970; Kirchhof-Glazier, 1979; Sokolov and Kotenkova,

1987; Wuensch, 1992). The differences were the following: different rodent species were used as foster species; different modifications of the method were used to assess the individual reactions to odor, and the genetic background of the experimental animals varied (different mouse strains and animals captured in the wild were used). All these facts determined the differences in the study results.

Some authors reported, that adult male and female mice fostered by hamsters of the genera *Baiomys* or *Peromyscus* or Norway rats *Rattus norvegicus* investigated longer the odor of foster species or preferentially stayed in a chamber compartment with this odor as compared to conspecific odor (Quadagno and Banks, 1970; Sokolov and Kotenkova, 1987). The results of other studies were inconsistent with those listed above (Kirchhof-Glazier, 1979).

The results of experiments that involved fostering of house mice by Norway rats can be mentioned as an example of discrepancies related to the use of different variants of two-choice tests. Some series of experiments did not reveal a difference in the time of rat and mouse odor source sniffing by mice fostered by rats, but a difference was observed in a series of experiments performed according to a modified method (Sokolov and Kotenkova, 1987). Sexually mature male and female laboratory mice fostered by rats from two to three days significantly more time investigated the female rat odor as compared to conspecific female odor if the urine was placed onto slides and the experiments were performed on a neutral territory, but the time of investigation of urine samples presented in glass tubes in the home cage was the same. The different reactions to odors could have been due to the difference in odor presentation variants and the degree of familiarity of the testing area to the experimental animals in this case. The assessment of the informative significance of the odor signals by mice moved to a neutral territory and brought into direct contact with

the odor source (upon urine placement onto slides) might have been more efficient.

Control male mice reared by conspecific females sniffed significantly longer the sources of female mouse odor, regardless of the method variant used. The inconsistency of data for golden hamsters *Mesocricetus auratus* was reported for some experiments that used different modifications of two-choice test (Johnston, 1981).

Mouse pups were transferred to rat females at a later age in order to identify the critical period during which the reaction to a certain odor could change. House mice fostered by rats from 7–12 days of age investigated significantly more time conspecific female urine odor as compared to urine odor from females of the foster species (Sokolov and Kotenkova, 1987). This demonstrates the coincidence of the critical period and the synaptogenesis period and agrees with other data on identification of the critical period in rodents (Voznessenskaya et al., 1999). Overall, the studies demonstrated changes in the reaction of house mice to con- and heterospecific odors under the influence of early olfactory experience. Sometimes the direction of the reaction was opposite to that observed in the unfostered animals.

Quadagno and Banks (1970) experimented with cross-fostered pups transferred between the house mouse and the northern pygmy mouse (*Baiomys taylori*) on postnatal day 1. The cross-fostered individuals were grown to adulthood and tested for odor preferences in a Y-shaped maze. House mouse female odor was supplied to one of the maze arms, and northern pygmy mouse odor, to the other arm (both females were dioestrous). House mouse males and females fostered by northern pygmy mouse females spent significantly less time in a chamber with conspecific odor as compared to unfostered (control) individuals of the same species; thus, cross-fostered house mice stayed longer in the chamber with heterospecific female odor. Sexual differences were observed, as females showed a stronger preference for the northern pygmy mouse female odor than the males. Similar sexual differences were also observed in laboratory mice: in contrast to males, female mice fostered by rats from one to three days of age sniffed significantly more time urine odor sources from unfamiliar females of the foster species than the odor sources of unfamiliar conspecific females (Sokolov and Kotenkova, 1987).

The results of Kirchhof-Glazier (1979) did not agree with those described above, since the author did not detect the influence of early olfactory experience on the behavioral or physiological reactions in laboratory mouse females (line CjL/C) fostered by deer mice *Peromyscus maniculatus* from the first day of life. Cross-fostered house mice tested by the author stayed near a conspecific odor source for a longer time, and the odor of unfamiliar deer mouse males did not cause accelerated sexual maturation of young females, sex-

ual cycle synchronization, or pregnancy block in these animals. However, conspecific male odor evoked these physiological reactions in the female mice. The author concluded that early olfactory experience did not affect subsequent behavioral and physiological reactions to con- and heterospecific odors. We believe that this discrepancy in the data cannot be explained solely by differences in the experimental methods (different variants of two-choice test). Moreover, it is hardly possible that the reaction to con- and heterospecific odors would change after fostering by certain species, but remain unaffected after fostering by another species, although such a phenomenon is possible in theory (it can be related to species-specific odor features, such as the degree of aversion of intact heterospecific individuals to the odor). An aversion of house mice to the odor of deer mice cannot be ruled out. Mice of the CjL/C might have certain strain-specific genetic features, such as anosmia to certain components of deer mouse urine.

The aim of the studies performed by Wuensch (1992) was to identify the factors that evoked early olfactory experience-related changes in the behavioral reactions to con- and heterospecific odors, to test for changes in the time of foster species and conspecific odor investigation, and to find out whether the species-specific features of maternal behavior could affect the directionality of behavioral responses. The author studied male wild house mice fostered by Norway rats or deer mouse *P. maniculatus bairdi* from the first day of life. The presentation of three, rather than two, odors to the mice was a distinctive feature of these experiments. The animals were placed into the central chamber of the experimental maze at 35 days of age. The maze had four arms joined to the central chamber. Odors of litter from mice, rat, and deer mice were presented in the three arms, and the clean sawdust placed in the fourth arm.

All males (regardless of the rearing conditions) spent the most time in the arm with conspecific odor in the first series of experiments. Males fostered by rats preferred the arm with rat odor to that with deer mouse odor, as shown by pairwise comparison of time spent in the arms, whereas the animals fostered by deer mouse preferred the arm with this odor. Control males did not show any difference in the reaction to these odors.

The males used in the second series of experiments could choose between two arms with rat odor and two arms with mouse odor. Similarly to the first experiment, the males preferred mouse odor regardless of the rearing conditions. However, the time spent in arms with rat odor was significantly higher for the animals reared by rats in a room where only rats were housed than in the two other experimental groups, namely, males reared by female mice in a room where a rat colony was housed and males reared by mice in a room where only mice were housed. These experi-

ments led to the conclusion that the early olfactory experience did not affect the reaction to conspecific odor in house mice, but had a considerable effect on the reaction to rat odor (Wuensch, 1992). The author supposed that species-specific features of maternal behavior in mice and rats, rather than early olfactory experience, could affect the reaction of mice to odors, since the reaction of mice to the rat odor did not change if these animals were reared by female mice in a room in which rats were kept. We believe that this interpretation of the results requires additional experimental verification.

We have used the same standardized method in studies performed over many years, and this permitted comparison of results obtained at different times. Thus, our data showed that cross-fostered house and mound-building mice can serve as model species for further studies of the effect of early olfactory experiences on the subsequent response to con- and heterospecific odors, both in research on behavioral mechanisms that underlie the formation of the response to species-specific odor in ontogeny and in research on learning mechanisms at the level of the central nervous system.

ACKNOWLEDGMENTS

This work was supported by the Russian Science Foundation, project no. 16-14-10269.

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Translated by S. Semenova