



Male and female mound-building mice, *Mus spicilegus*, discriminate dietary and individual odours of conspecifics

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(Received 14 February 2005; initial acceptance 23 April 2005;
final acceptance 2 November 2005; published online 22 June 2006; MS. number: 8467R)

Individual body odour is known to provide information to conspecifics about both the identity of the donor and its biological state (e.g. reproductive condition, age, diet). It is not clear whether information related to individuality and biological state is evaluated collectively or separately. To gain insight into this subject, we examined the effect of a change in diet on conspecific recognition of individual chemical signatures in mound-building mice, *Mus spicilegus*. The diet change consisted of the addition of an aromatic concentrate to the drinking water. We used two different procedures based on spontaneous responses of mice to the presentation of odorous stimuli: the habituation–dishabituation procedure and the habituation–generalization procedure. Mice of both sexes were able to perceive the two types of information contained in the modified chemical signature of the donor, that is, they were able both to perceive the change in diet and to identify the chemical signature of the donor.

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Chemical communication is widespread in the animal world and constitutes, in rodents, a prominent mode of communication. Olfaction represents the main sense by which rodents recognize individuals and conspecifics and acquire knowledge about their social environment (Brown 1979). The study of individual recognition by chemical cues presents an interesting problem at the evolutionary level: species specificity requires a high degree of homogeneity from one individual to another whereas individual identification requires that each individual has a chemical signature that differs from conspecifics (Halpin 1980).

The individual chemical signature may be defined as the complete set of odorants produced by the body of a given individual that allows unambiguous identification. Individual characteristics, conveyed by these odorous productions, allow the recognition of an individual (Gheusi et al. 1994, 1997; Johnston & Jernigan 1994) at both cognitive and functional levels (Gosling 1990; Gosling & McKay 1990; Randall 1991). This property of the individual chemical signature is predicted to be related to an individual's genomic structure. Many studies have suggested a link between the individual chemical signature and a precise section of the genome (reviewed in Brennan 2004).

Odours are known to convey information about the state of an individual (e.g. reproductive state, age, diet). Several studies have shown the influence of diet on olfactory cues. In meadow voles, *Microtus pennsylvanicus*, for example, an increase in protein content of the diet increased the attractiveness of odorous marks (Ferkin et al. 1997). In rats, *Rattus norvegicus*, genetic differences in the major histocompatibility complex (MHC), bacterial flora and diet interact to produce the individual chemical signature (Brown & Schellinck 1992; Brown 1995). Rats found it easier to discriminate between urinary odours of two MHC-congenic mice after the mice consumed different diets (Brown et al. 1996). It was also easier for these rats to remember the differences between the urinary odours of genetically identical mice maintained under different diets than to remember the differences between MHC-congenic mice sharing the same diet (Schellinck et al. 1997). To be functional, however, the individual chemical signature depends on stability. Indeed, any sudden change in this individual chemical signature could disturb the normal social relationship of an established group (Halpin 1980). Consequently, one may ask whether individuality is the result of information related to the biological state (e.g. reproductive condition, age, diet) and the genetic identity of the individual, and whether biological state and genetic identity are distinct. To gain insight into this subject, we investigated whether a change in diet could disturb the recognition of the individual chemical signature by a conspecific in mound-building mice, *Mus spicilegus*.

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Mus spicilegus, a mouse of eastern and central Europe (Sokolov et al. 1998), differs dramatically from other species of mice. It is monogamous (Patris & Baudoin 1998, 2000; Dobson & Baudoin 2002; Patris et al. 2002; Gouat & Féron 2005) and characteristically builds mounds during autumn (Orsini et al. 1983; Garza et al. 1997) where individuals over winter. During this winter cloistering, mice become familiar with each other, and this familiarity is responsible for the inhibition of their reproduction at this time (Gouat et al. 2003a). In spring, individuals leave the mounds and start to breed after pairing with unfamiliar individuals (Gouat et al. 2003b). Given the importance of individual recognition in *M. spicilegus*, this species seemed appropriate for our proposed study. Furthermore, male *M. spicilegus* are able to discriminate between the olfactory signatures of two conspecific males (Gouat et al. 1998). In the present study, we used different habituation procedures to test whether a change in diet can be detected by mice, and whether, in spite of this change in diet, mice are still able to recognize an individual chemical signature. We used males and females as experimental animals and males as donors. Because females are thought to play a prominent role in mate choice (Andersson 1994), we predicted that females would discriminate between individual signatures of males.

METHODS

Animals and Breeding Conditions

The mice derived from 80 wild animals caught in Hungary in 1999 (Gouat et al. 2003a), and reared in captivity for five generations. We used 32 adult males and 22 adult females, 3–11 months old bred from 20 different breeding pairs. The mice were kept under controlled laboratory conditions (20°C, 14:10 h light:dark cycle). During the dark phase, the room was lit by a dimmed red light (two neon tubes, 35 W) allowing observation. The mice were housed in standard polycarbonate cages (26 × 14 cm and 16 cm high) with sawdust (Special Diet Services, Witham, Essex, U.K.). Experimental mice were kept in pairs and donors singly. Cotton wool was provided for nesting material. Food (type M20, Special Diet Services, Witham, Essex, U.K.) and water were supplied ad libitum.

The mice were weaned at 28 days of age, and, 1 week later, they were placed in same-sex sibling groups. At this time, when an animal was left alone (i.e. when there was only one male or one female in a litter), we placed it with another sibling group of the same age and sex. One week before the experiment, we took experimental individuals from these sibling groups and placed them in same-sex pairs in new clean cages. Individuals were identified by hair clipping. Odour donors and subjects were different animals.

Samples

As the odorous stimulus, we used soiled sawdust, referred to below as 'sawdust samples', with urine and droppings from donor mice, which has been shown to

convey chemical signatures (Gouat et al. 1998; Maslak & Gouat 2002). Donors were isolated 1 week before the experiment. Only adult males were used as donors because isolation may modify the reproductive state of females (Féron & Gheusi 2003). The diet change involved the addition of an aromatic concentrate (Antésite with an anise aroma, Antésite S.A, Voiron, France) to the drinking water. We used anise aroma for this because it is well tolerated by mice (F. Tourrain & P. Gouat, unpublished data), and contains neither alcohol nor sugar. Therefore, the diet was not modified by caloric intake, which could influence the attractiveness of odorous marks (Ferkin et al. 1997). The amount used (1.33 g/litre) corresponded to the concentration recommended by the manufacturer. The control diet included plain water without the anise aroma (Water diet).

We collected sawdust samples over a 2-week period. First, mice were placed in a clean cage with clean sawdust and received plain water. After 3 days the soiled sawdust was collected in a freezer bag, closed hermetically and placed at –10°C until required. Afterwards, the mice were placed in a new cage with clean sawdust and received the Anise diet. After another 3 days, we collected sawdust samples again, in the same way. As a consequence, samples from mice on the Water diet were frozen for longer (i.e. 3 days) than those from mice on the Anise diet. To avoid possible bias caused by this difference in freezing time, we carried out a third series of sawdust sampling after the mice had been on the Anise diet. This time, the mice were placed in the same cage with clean sawdust and received the Water diet. To eliminate anise residues which could persist just after this change in diet, the sawdust and cages were changed the following day. Three days later, we collected sawdust samples again in the same way. For each experiment, the two Water sawdust samples were used alternately. No effect of freezing time was detected, so we pooled the data from the two types of Water sawdust samples. Sawdust samples were used within 2 weeks of collection.

Procedures

The procedures we used were based on spontaneous responses of mice to the presentation of odorous stimuli. Under these circumstances, animals respond only to stimuli that have importance for them. These procedures are recognized to be ecologically and functionally valid (Schellinck & Brown 1994; Schellinck et al. 1995); they are based on simple designs and have already been used successfully with wild animals (Vaché et al. 2001), including *M. spicilegus* (Gouat et al. 1998; Heth et al. 2001, 2003).

In experiments 1 (on males) and 4 (on females), our aim was to determine whether mice respond to the change in diet as reflected by the donor's odorous stimuli. For these experiments we used a habituation–dishabituation procedure (Halpin 1980; Johnston et al. 1993). Subjects were presented with sawdust soiled by a donor on the Water diet for three successive trials (habituation phase). We always used the Water diet during the habituation phase because this stimulus was less novel for the subject, as they had not been exposed to the odour of anise. On

the fourth trial (dishabituation phase), we presented sawdust soiled by the same donor but on the Anise diet.

If the time spent investigating the soiled sawdust increased significantly between the third and fourth trials in experiments 1 and 4, we could conclude that mice perceived the change in diet. To test whether mice were able to recognize the chemical signature of a donor in spite of a change in diet, we carried out another experiment (experiment 2 on males) using a habituation–generalization procedure (Todrank et al. 1998) with two donors and a change in diet. During the habituation phase, subjects were presented with sawdust soiled by a donor on the Water diet. On the fourth trial, we presented simultaneously sawdust soiled by the habituation donor and sawdust soiled by an unknown donor, both on the Anise diet. If subjects spent more time investigating the sawdust soiled by the second donor, we could conclude that subjects considered that odours of the new donor on the Anise diet differed more from the habituation stimulus than odours of the habituation donor on the Anise diet. This result would suggest that mice were able to recognize the individual chemical signature in spite of the change in diet.

However, the investigation time might not increase significantly with the change in diet. When a habituation–dishabituation procedure is used, a null result is difficult to interpret. An absence of response may be caused by lack of interest or an inability to discriminate. A systematic lack of response to the stimuli could not be considered as an absence of detection (Schellinck & Brown 1994), but may reveal that the subject does not respond to the stimuli in this context (Todrank & Heth 2003). To distinguish between these interpretations, we used a different type of habituation–dishabituation procedure in experiment 5. During the habituation phase, subjects were presented with sawdust soiled by a donor on the Water diet. On the fourth trial, we presented simultaneously two dishes of sawdust soiled by the habituation donor, one on the Water diet and the other on the Anise diet. This two-stimulus test paradigm should be easier for the subject than a single stimulus trial: the subject can compare the two stimuli directly rather than compare the novel stimulus to the memory of the habituation stimulus (Johnston & Peng 2000). If subjects spent significantly more time investigating the Anise diet stimulus than the Water diet stimulus, we could conclude that they perceived the change in diet.

The procedure was the same for both males and females. However, because discriminative responses of *M. spicilegus* females have not been studied in this paradigm before, we first tested whether females respond to a change of donor on the Water diet by using a habituation–dishabituation procedure (experiment 3). All females were in anoestrus during the experiments as shown by their closed vagina (Féron & Gheusi 2003).

Experimental Conditions

We carried out discrimination trials during the beginning of the dark phase (first 5 h). Ten minutes before the

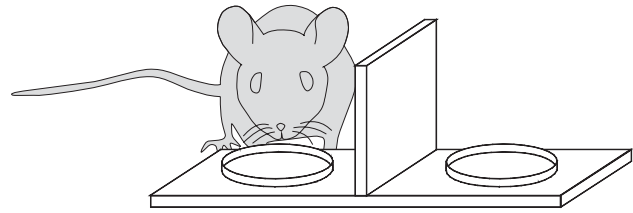


Figure 1. The test device with a mouse investigating the dish on the right side.

trial, we took and defrosted only the necessary quantity of soiled sawdust. Experiments were carried out in the home cage of the experimental mouse to avoid possible bias from the stress of a transfer to a new environment (Burman & Mendl 2002). Subjects were housed in pairs, and the nontested individual was taken out of the cage 10 min before the trial and placed in a clean cage without sawdust. At the end of the trial, this mouse was returned to the cage and was tested the next day. All the mice were tested in the same way but they were not tested with the same donors or with donors of similar origins. Donors were assigned to an experimental mouse at random following the rule that the animals were unfamiliar and from different parents. In a given experiment each combination of parents of a subject and donors was used only once.

Immediately before each trial, we placed two plastic dishes (3.5 cm diameter), fixed to a support (Fig. 1), so that the mice could not displace or overturn them, in the cage of an experimental mouse opposite the nest (Maslak & Gouat 2002). Two dishes with one or both containing soiled sawdust, were always presented whatever the procedure. When only one odour stimulus was presented, the second dish contained clean sawdust. The clean sawdust was a control for the stimulus presented (first trial) and showed that an increase in investigation time observed in the fourth trial was for the soiled sawdust only. A trial lasted 5 min and started when the mouse left its nest and moved towards the support. We used a stop watch to record how long the mouse spent investigating the sawdust during each trial. Experiments were also monitored by a video camera. We defined investigation as occurring when the nose of the mouse was 1 cm or less above the dish, or when the mouse was scratching in the dish.

Ethical Note

Donors were isolated for a 3-week period (1 week before, and 2 weeks during, collection of samples). To bring adult mice back to their sibling groups after 3 weeks of isolation may have caused a high level of aggression. To avoid this, we killed donors by asphyxiation with carbon dioxide at the end of the collecting period. The samples were kept for 2 weeks in the freezer, and we collected enough soiled sawdust to be used in all the experiments. As a result, we used only 11 males as donors in the five experiments. The number of combinations of the origins of donors and subjects was sufficient to avoid pseudoreplication problems.

All the experimental procedures were approved by the Ile-de-France Regional Ethics Committee in Animal Experiment number 3.

Data Analysis

Because of the small number of animals in each group ($N \leq 15$), we used nonparametric statistics and exact procedures (Mundry & Fischer 1998). Tests were two tailed and carried out with StatXact (Cytel Software Corporation, Cambridge, MA, U.S.A.). Two types of comparisons were made according to the question. For paired comparisons we used a permutation test, which gives the exact probability of occurrence of the same or more extreme distributions than the observed distribution.

To see whether habituation occurred, we compared investigation time for soiled sawdust during the first and the third trials. For habituation–dishabituation procedures (experiments 1, 3 and 4), we compared the duration of investigation of soiled sawdust between the third and the fourth trials to determine the effect of change (donor change or diet change). The duration of investigation on the third trial was used twice. To prevent a type I error we used the sequentially rejective Bonferroni procedure (Holm 1979), and the threshold of significance was lowered to $\alpha = 0.025$ for two comparisons. In experiments 2 and 5, we tested the difference in duration of investigation between the two samples of soiled sawdust presented on the fourth trial. Before these two paired comparisons, we carried out a Friedman analysis of variance (exact procedure) on the complete set of investigation times used.

RESULTS

Males

Experiment 1: same donor on two diets

Twelve subjects were tested (five different sets of parents) with the odours of six donors (six different sets of parents). The investigation time across the three trials was significantly different (Friedman ANOVA: $\chi^2_{r22} = 12.17$, $P = 0.002$; Fig. 2). Investigation time for soiled sawdust decreased significantly between the first and the third trials

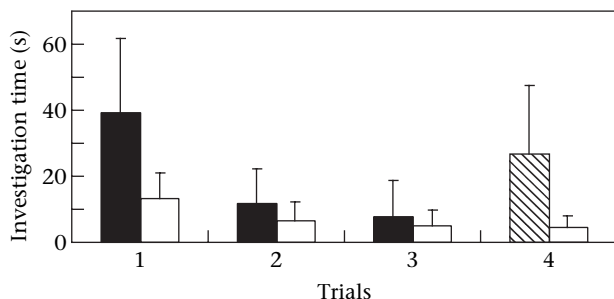


Figure 2. Mean + SD time spent by male mound-building mice ($N = 12$) investigating sawdust stimuli during a habituation–dishabituation procedure with one donor and a change in diet. □: Clean sawdust; ■: sawdust soiled by a donor male on the Water diet; ▨: sawdust soiled by the same donor male on the Anise diet.

of the habituation phase (permutation test: $P = 0.004$). Experimental animals significantly increased their investigation time for soiled sawdust during the fourth trial ($P = 0.013$).

Experiment 2: two diets and two donors

Nine males were tested (four different sets of parents) with the odours of five donors (five different sets of parents). The investigation time across the three trials was significantly different (Friedman ANOVA: $\chi^2_{r16} = 16.73$, $P < 0.001$; Fig. 3). Habituation occurred between the first and the third trials (permutation test: $P = 0.020$). During the fourth trial, males spent more time investigating the sawdust soiled by the unknown donor than the sawdust soiled by the habituation donor, despite the change in diet ($P = 0.004$).

Females

Experiment 3: different donors

Seven females were tested (six different sets of parents) with the odours of six donor males (six different sets of parents). The investigation time across the three trials was significantly different (Friedman ANOVA: $\chi^2_{r12} = 10.29$, $P = 0.004$; Fig. 4). The decrease in investigation time for soiled sawdust between the first and the third trials showed that females habituated to the odour of the first donor on the Water diet (permutation test: $P = 0.016$). During the fourth trial, females increased their investigation time for sawdust soiled by the second donor ($P = 0.031$).

Experiment 4: same donor on two diets

The odours of five donors (five different sets of parents) were used to test eight females (four different sets of parents). The investigation time across the three trials was significantly different (Friedman ANOVA: $\chi^2_{r14} = 9.75$, $P = 0.005$; Fig. 5). Habituation occurred between the first and the third trials (permutation test: $P = 0.023$) but no

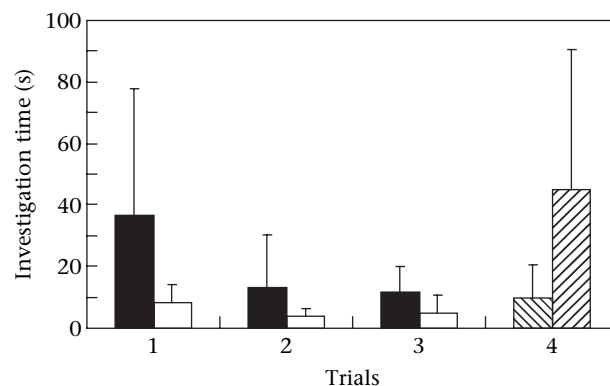


Figure 3. Mean + SD time spent by male mound-building mice ($N = 9$) investigating sawdust stimuli during a habituation–generalization procedure with two donors and a change in diet. □: Clean sawdust; ■: sawdust soiled by male donor A on the Water diet; ▨: sawdust soiled by male donor A on the Anise diet; ▩: sawdust soiled by male donor B on the Anise diet.

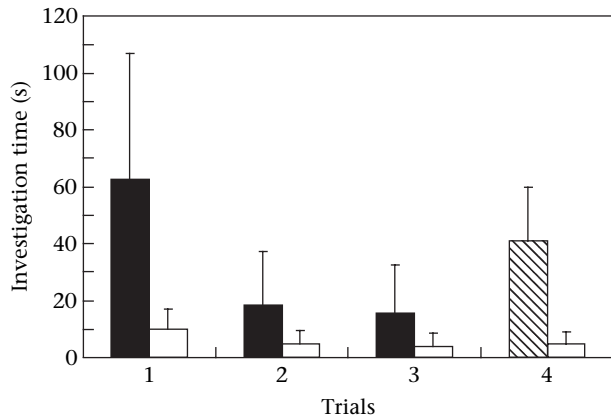


Figure 4. Mean + SD time spent by female mound-building mice ($N = 7$) investigating sawdust stimuli during a habituation–dishabituation procedure with two donors on the Water diet. □: Clean sawdust; ■: sawdust soiled by male donor A; ▨: sawdust soiled by male donor B.

increase was detected in the fourth trial ($P = 0.305$). Investigation time decreased in five of the eight tested females (four different origins).

Experiment 5: change of diet

Seven females (six different sets of parents) were tested with the odours of five donors (five different sets of parents). The investigation time across the three trials was significantly different (Friedman ANOVA: $\chi^2_{12} = 14.91$, $P < 0.001$; Fig. 6). Females habituated to the odour of the first donor on the Water diet, as was shown by the decrease in investigation time of soiled sawdust between the first and the third trials (permutation test: $P = 0.016$). In the fourth trial, females spent more time investigating the sawdust soiled by the donor on the Anise diet than on the Water diet ($P = 0.047$).

DISCUSSION

The change in diet was clearly perceived by males in experiment 1 (Fig. 2). The results of experiment 2

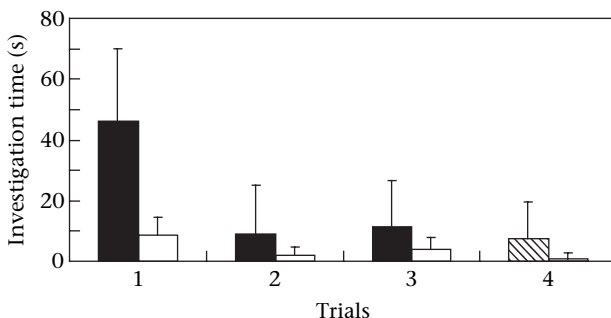


Figure 5. Mean + SD time spent by female mound-building mice ($N = 8$) investigating sawdust stimuli during a habituation–dishabituation procedure with one donor and a change in diet. □: Clean sawdust; ■: sawdust soiled by a donor male on the Water diet; ▨: sawdust soiled by the same donor male on the Anise diet.

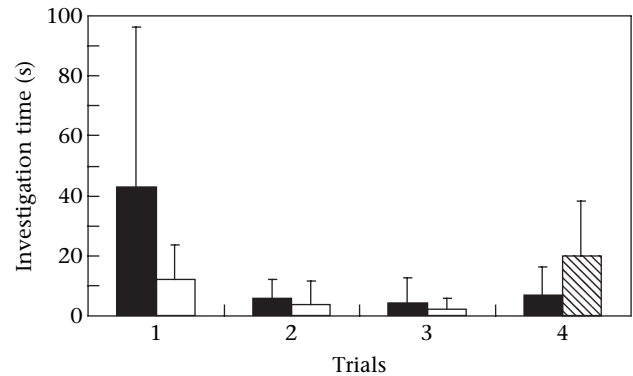


Figure 6. Mean + SD time spent by female mound-building mice ($N = 7$) investigating sawdust stimuli during a habituation–dishabituation procedure with one donor and two diets. □: Clean sawdust; ■: sawdust soiled by male donor A on the Water diet; ▨: sawdust soiled by male donor A on the Anise diet.

suggested that, despite the change in diet, males perceived the change in donor during the generalization phase (Fig. 3).

In experiment 3, females reacted to the change in donor on the Water diet and consequently were able to discriminate between the olfactory signatures of two donor males (Fig. 4). Females responded similarly to males in previous tests (Gouat et al. 1998). Nevertheless, responses of females to a change in diet of the donor (experiment 4, Fig. 5) differed from the responses of males confronted with a similar change (experiment 1, Fig. 2). Females did not respond to the change in diet of the donor, and their investigation time of the soiled sawdust even tended to decrease. Although this decrease in investigation time of the soiled sawdust between trials 3 and 4 was far from significant, this result was similar to that observed when the habituation phase included four trials or more (Gouat et al. 1998; Maslak & Gouat 2002). Females behaved as though the chemical signature of the donor was not altered by the change in diet. A problem with the samples of soiled sawdust can be excluded, because the same sawdust samples were successfully used in other experiments with both male (experiments 1 and 2) and female (experiment 5) subjects. In experiment 5, nevertheless, females were able to discriminate between the two types of diet when the two stimuli were presented in the same trial (Fig. 6). These results suggest that during experiment 4, the two types of information were perceived by the females, but that females simply did not respond to the changes presented, an inherent problem with experimental tests that depend on spontaneous responses. These difficulties are overcome, however, through examining the two sets of results together; in this case it becomes clear that, despite this change in diet, both males and females were able to identify the chemical signature of the habituation donor.

Our results showed that mound-building mice were able to react, in a relatively independent way, to information about individuals and diets simultaneously evident in conspecific odours. The fact that mice were able to perceive this information in parallel provides important

insights into the multiple functions of individual odours. Variation in hormonal level, diet and bacterial flora affects individual odours (Brown 1987). In addition, in several rodent species close genetic relatedness (i.e. genetic similarity) between individuals is associated with closer perceptual similarity in their odours ('odour-gene covariance') but each individual odour is as unique as the individual genotype (Todrank & Heth 2003). Every odorant directly linked with a part of the genome, especially those parts with a high level of polymorphism, may contribute to the production of a chemical signature (Brennan 2004). Our results, in conjunction with those of previous studies (reviewed in Todrank & Heth 2003), suggest that individual odours are perceived as composites that provide multiple types of information simultaneously. Future neurophysiological studies are necessary to determine how the brain processes and sorts the various types of information available in individual odours.

Acknowledgments

Nicolas Busquet and Jo Todrank provided helpful comments on the manuscript and Lavinia Bruneau and Sonia Kleindorfer helped revise the English. We thank Simone Demouron for her help in caring for animals.

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