Foraging behavioural changes induced by conspecific and heterosubspecific odours in two strains of wild mice

C. Jacquot *, C. Baudoin

Laboratoire d’Ethologie Expérimentale et Comparée-CNRS ESA 7025, Université Paris-Nord, 99 Av. J.B. Clément, 93430 Villetaneuse, France

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Abstract

Mice in wild populations of the two subspecies Mus musculus domesticus and Mus musculus musculus may potentially compete for food. Because of the importance of olfaction in mice, we hypothesised that the presence of unfamiliar conspecific or heterosubspecific chemical cues could play a role in access to and use of food resources. We used an experimental design that tested this assumption with males from two strains, originated from wild populations of these subspecies, as subjects. Exploratory activity, latency of food approach, time and frequency on the food area, number of seeds eaten and foraging rate (number of seeds eaten/time on the food area × 100) were compared for three different categories of odours (own, same strain and other strain odours) in both strains. In a foraging context, unfamiliar odours induced behavioural changes in male mice, especially an increase in exploratory activity from the more (same strain) to the less similar odour (different strain), and a reduction of time spent in the food area. Odour similarity related to genetic proximity in Mus and the cost-benefit ratio of an encounter are two possible explanations for the different processes involved in the treatment of odours in these two strains of mice. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: Foraging behaviour; House mouse; Odour effect; Strain effect

1. Introduction

In mammals, individuals receive information from conspecifics and also from individuals of other sympatric species that could be either competitors or predators. Signals carrying this information may have chemical, visual or acoustic origins (Halpin, 1986). In mice, they are often conveyed by olfactory cues. Species, sex, and the motivation of an individual can be determined through these signals (reviewed by Halpin, 1980). Many studies reported the great importance of olfactory signals from conspecific individuals on the regulation of social behaviour (Yamazaki et al., 1976; Hurst, 1987, 1989, 1990a,b,c; Drickamer and Mikesic, 1990; Penn and Potts, 1998) and in intrasexual competition (Hurst, 1990a, 1993; Gosling et al., 1996; Drickamer, 1997). Urine, faeces, and secretions of specialised glands are laid by male house mice throughout their territory...
(Crowcroft and Rowe, 1963; Brown, 1985) to advertise their competitive ability to other males (Hurst, 1993). Odours from other species can also be informative for mice and influence their behaviours. For example, odours of predators are avoided by mice (Dickman, 1992) or induce fear-associated behavioural responses (Dell’Omo and Alleva, 1994; Berton et al., 1998). Olfactory cues from heterospecific competitors (i.e. other species of rodents) may also be present in the environment but their functions are less investigated.

Because of the importance of olfaction in rodents, we may hypothesise that the presence of chemical cues from conspecific or heterospecific origin would have an impact in the access to and use of food resources. An animal searching for food has to select a foraging area, decide how much time to stay in the area, and what type of food to eat. Optimal foraging theory predicts that these decisions will evolve under natural selection to enhance fitness (Charnov, 1976; Krebs and Davies, 1978). The presence of conspecific competitors can affect decision rules: common shrews become risk-sensitive to variation in food reward rate (Barnard and Brown, 1985) whereas central place foragers, as the eastern chipmunks, reduce their seed-collecting rate (Giraldeau et al., 1994). Within a social group, a conspecific demonstrator can also influence food preferences (rats: Galef and Wigmore, 1983; mice: Valsecchi et al., 1996). Moreover, the presence of heterospecific competitors can also modify access to and use of food sites (hummingbirds: Pimm et al., 1985; bank vole and wood mouse: Canova, 1993).

Scent-marking around a food site may have a deterrent effect by discouraging intrusions (mice: Jones and Nowell, 1974) or denoting an unprofitable patch (least chipmunks: Devenport et al., 1999), but scent-marks can also facilitate food detection and selection by group members (rats: Galef and Beck, 1985; spiny mice: Rozenfeld et al., 1994) and by unfamiliar conspecifics (soft-furred field-rats: Soni and Prakash, 1987). Moreover, marked foraging sites may slightly affect the detection (ground squirrels: Livoreil, 1994) or the food collection by heterospecific individuals (spiny mice: Baudoin and Haim, 2000).

The assumption that cues from potential competitors of different origins may be used in a foraging context was tested in the present study. Mus musculus domesticus and Mus musculus musculus are widely distributed, respectively, in Western and Eastern Europe and share a natural narrow hybrid zone stretching from Denmark to the Black Sea (Boursot et al., 1993). They are considered either as two subspecies (Boursot et al., 1993) or as two distinct species (Sage et al., 1993).

We studied two mice strains, DDO and MDH, respectively originated from wild populations of Mus m. domesticus and Mus m. musculus (see Christophe and Baudoin, 1998). As in wild populations, males of both subspecies potentially compete not only for females, but also for food, we used an experimental paradigm to test the influence of unfamiliar conspecific and heterospecific odours on mice foraging behaviour. As social interactions between individuals differ in the two strains (Christophe et al., 1997) and as DDO and MDH have different olfactory preferences in a sexual context (Christophe and Baudoin, 1998), we may predict dissimilarities in the behaviour of the two strains. The dominance of Mus m. domesticus over Mus m. musculus individuals was observed in several studies (Thuesen, 1977; Van Zegeren and Van Oortmerssen, 1981) and confirmed in DDO and in MDH male mice (Christophe et al., 1997). We may then expect that heterospecific odours should have a stronger effect in the subordinate strain, viz. Mus m. musculus (MDH). It is nevertheless difficult to predict either an inhibitory or a stimulating odour effect on foraging behaviour as both aspects were previously reported in various rodent species (see above).

2. Methods

2.1. Subjects

Mice were adult males Mus m. domesticus (DDO) (n = 38) and Mus m. musculus (MDH) (n = 35) produced in our laboratory and never used in previous experiments. The original stock
of mice was established with animals collected near the hybrid zone in Denmark (in Odis for DDO and in Hov for MDH) in 1988–1989 by F. Bonhomme and coworkers (UMR CNRS 5555, Montpellier, France). Individuals from both strains bear genes of the other subspecies (Vanlerberghe et al., 1988) and were bred in laboratory for some 15 generations.

All animals were maintained in the same room at 22–24 °C, 40–50% humidity, L: 14, D: 10 photoperiod, and light off at 12:00 h. Although the two strains were spatially separated in this room, we cannot exclude that individuals experienced heterospecific odours through volatiles before the study.

Animals were weaned at 21 days and then reared in same-sex groups in polycarbonate cages (26 × 16 × 14 cm) containing cotton nesting material and sawdust. Two weeks before testing, male mice were isolated. At this time, they were aged 182.9 ± 6.1 days (n = 73). Food (standard lab chow) and water were available ad libitum. During the 2 days prior tests mice were exposed to a small quantity of alpist seeds (Phalaris canariensis) to familiarise them with this type of food.

2.2. Procedure

Food was removed at the beginning of the dark phase on the test day. Two hours later, tests were carried out under a dim red light. The test arena (70 × 40 × 50 cm) made with laminated wood contained a sand patch (a Petri dish of 8 cm diameter with 40 g sand washed with bleached water). Lines drawn on the laminated wood floor delimited 12 identical areas (Fig. 1).

Mice were familiarised to the arena during 75 min before the test and, by this way, scent-marked the arena and the dish. Then, we waited for 10 min before to begin the test.

In each strain, three independent groups were made:

– The control group or ‘Own odour group’ (DDO males: n = 12, MDH males: n = 11): males were tested in presence of their own odours.

– ‘Unfamiliar odour from a same strain individual’ group (DDO males: n = 13, MDH males: n = 11): the source donor was a male from the same strain, unfamiliar and unrelated (relatedness coefficient < 0.05) to the tested mouse.

– ‘Unfamiliar odour from another strain’ group (DDO males: n = 13, MDH males: n = 13): the source donor was an unfamiliar male from the other strain.

Forty alpist seeds were added for the test to the sand patch and mixed.

Two animals were tested simultaneously. In the control group, mice were tested in the same arena they had previously scent-marked with 40 seeds added. In the two other groups, the experimental mice were transferred in the other arena already marked by the other subject.

The mouse was introduced in the area on the opposite side of the food patch (S in Fig. 1) and video recorded for 15 min. Data were recorded afterwards using a PSION WORKABOUT. We recorded the latency before reaching the area containing the food patch, the time spent on the food area, the number of visits to the food area, the duration of a visit to this area and the number of seeds eaten. The number of squares visited was recorded to estimate the general activity (locomotion/exploration) of the mouse during the test. Because of test conditions (red light + video recording), it was not possible to determine when mice began to eat.

A foraging rate was calculated as the ratio of number of seeds eaten to time spent on the food

![Fig. 1. Experimental arena.](image-url)
Table 1

Behavioural parameters observed in *Mus m. domesticus* (DDO) (mean ± SE) and comparison among the three types of odours

<table>
<thead>
<tr>
<th></th>
<th>Own odour (1), n = 12</th>
<th>Unfamiliar DDO odours (2), n = 13</th>
<th>Unfamiliar MDH odours (3), n = 13</th>
<th>Statistical comparison</th>
</tr>
</thead>
<tbody>
<tr>
<td>Latency to reach the patch (s)</td>
<td>48.06 ± 19.17</td>
<td>21.65 ± 8.90</td>
<td>12.51 ± 4.07</td>
<td>Tendency, F&lt;sub&gt;2,35&lt;/sub&gt; = 2.75</td>
</tr>
<tr>
<td>Number of crossed areas</td>
<td>184.75 ± 30.88</td>
<td>243.77 ± 24.02</td>
<td>258.38 ± 28.35</td>
<td>NS, F&lt;sub&gt;2,35&lt;/sub&gt; = 1.87</td>
</tr>
<tr>
<td>Number of food area visits</td>
<td>18.08 ± 3.34</td>
<td>23.42 ± 2.64</td>
<td>27.54 ± 2.31</td>
<td>Tendency, F&lt;sub&gt;2,35&lt;/sub&gt; = 2.82</td>
</tr>
<tr>
<td>Duration of a visit to the food area (s)</td>
<td>121.30 ± 47.74</td>
<td>41.79 ± 2.84</td>
<td>30.98 ± 1.46</td>
<td>*&lt;sup&gt;1&lt;/sup&gt;, F&lt;sub&gt;2,35&lt;/sub&gt; = 4.49 (1)-(2), * (2)-(3), NS (1)-(3), *</td>
</tr>
<tr>
<td>Total time in the food area (s)</td>
<td>450.33 ± 64.52</td>
<td>311.98 ± 39.26</td>
<td>308.18 ± 40.25</td>
<td>*&lt;sup&gt;1&lt;/sup&gt;, F&lt;sub&gt;2,35&lt;/sub&gt; = 3.41 (1)-(2), * (2)-(3), NS (1)-(3), tendency</td>
</tr>
<tr>
<td>Number of seeds eaten</td>
<td>15.5 ± 2.59</td>
<td>11.23 ± 2.05</td>
<td>15.04 ± 2.61</td>
<td>NS, F&lt;sub&gt;2,35&lt;/sub&gt; = 0.89</td>
</tr>
<tr>
<td>Foraging rate (seeds/s × 100)</td>
<td>3.22 ± 0.42</td>
<td>3.21 ± 0.46</td>
<td>4.73 ± 0.39</td>
<td>***&lt;sup&gt;1&lt;/sup&gt;, F&lt;sub&gt;2,35&lt;/sub&gt; = 7.32 (1)-(2), NS (2)-(3), *** (1)-(3), ***</td>
</tr>
</tbody>
</table>

NS, not statistically different.
*<sup>1</sup> P ≤ 0.05; ***<sup>1</sup> P ≤ 0.005; tendency: 0.05 < P ≤ 0.077.

area (in seconds) per cent. This rate may theoretically vary between 0 and ∞, but we never observed a foraging rate above 10, which might be the practical limit of this rate (mice may not be able to eat quicker).

2.3. Statistical analysis

Normality and homogeneity of variance were first checked for each parameter. When at least one of these tests failed, a square root transformation was done (Lehner, 1996). This was sufficient to regularise our data (in normality and/or homogeneity). An ANOVA was performed afterwards within each strain.

A principal effect ANOVA was realised to show Strain and Odour effects and multiple comparisons using Newman–Keuls’ post-hoc tests were conducted. We used STATISTICA software to carry out this statistical analysis.

Results are expressed as mean ± standard error.

3. Results

3.1. Comparison of *Mus m. domesticus* (DDO) groups

DDO mice had a tendency reaching quicker the food patch when the odour was different from their own (F<sub>2,35</sub> = 2.75; P = 0.077; Table 1) and visiting it more often (F<sub>2,35</sub> = 2.82; P = 0.073).

The duration of a visit to the food area and the overall time spent on this area differed according to the odour (respectively, F<sub>2,35</sub> = 4.49; P = 0.018 and F<sub>2,35</sub> = 3.41; P = 0.044; Table 1). Visits to the food area were longer and the overall time spent was higher when mice were tested with their own odours compared to odours from an unfamiliar DDO male (P = 0.025 for the duration of a visit; P = 0.030 for the time spent) or with MDH odours (P = 0.020 for the duration of a visit; tendency (P = 0.065) for the time spent).
The number of crossed squares was also lower when they were tested with their own odours but no significant difference was demonstrated ($F_{2,35} = 1.87; \ P = 0.17$; Table 1).

The number of seeds eaten during the test did not differ statistically among the three groups ($F_{2,35} = 0.89; \ P = 0.42$). However, DDO males ate slightly fewer seeds in an arena with same strain odours than in an arena scent-marked by the tested animal or by a MDH male. This variation of the number of seeds eaten coupled to differences in time spent on the food area led to different foraging rates of DDO individuals ($F_{2,35} = 7.32; \ P = 0.002$; Fig. 2). A higher foraging rate was observed for individuals tested in an arena scent-marked by MDH males ($4.73 \pm 0.39$) as compared to individuals tested either with their own odours ($3.22 \pm 0.42; \ P = 0.004$) or with same DDO odours ($3.21 \pm 0.46; \ P = 0.004$).

3.2. Comparison of Mus m. musculus (MDH) groups

Latency in reaching the food area did not statistically differ according to the type of odour ($F_{2,32} = 0.91; \ P = 0.41$), even if, on average, mice tested with same strain odours reached later the food area (Table 2).

There was also no difference in the number of visits to the food area ($F_{2,32} = 1.98; \ P = 0.154$), although visits were, on average, more numerous with unfamiliar odours. The duration of a visit to the food area and the overall time spent on this area differed among the three groups ($F_{2,32} = 3.19; \ P = 0.05$ for the duration of a visit; $F_{2,35} = 3.83, \ P = 0.032$ for the time spent on the food area; Table 2). Visits to the food patch were shorter in duration when mice were tested in an arena scent-marked by a DDO male compared to their own odours ($P = 0.045$). The time spent on the food area during the whole test was higher in the control group than it was in an environment scent-marked by a male from a different strain ($P = 0.03$). Time with a same strain odour was in between these two situations.

The number of squares crossed ($F_{2,32} = 1.96; \ P = 0.16$; Table 2) did not differ according to odours.

The seed intake did not statistically differ among the MDH groups ($F_{2,32} = 1.51; \ P = 0.24$).

*Fig. 2. Foraging rate in DDO and MDH strains (mean ± SE).*
Table 2

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Own odour (1), n = 11</th>
<th>Unfamiliar MDH odours (2), n = 11</th>
<th>Unfamiliar DDO odours (3), n = 13</th>
<th>Statistical comparison</th>
</tr>
</thead>
<tbody>
<tr>
<td>Latency to reach the patch (s)</td>
<td>25.21 ± 8.31</td>
<td>36.99 ± 10.14</td>
<td>21.74 ± 4.80</td>
<td>NS, F(_{2,32}) = 0.91</td>
</tr>
<tr>
<td>Number of crossed squares</td>
<td>152.45 ± 25.07</td>
<td>243.18 ± 47.81</td>
<td>274.23 ± 46.86</td>
<td>NS, F(_{2,32}) = 1.96</td>
</tr>
<tr>
<td>Number of food area visits</td>
<td>15.00 ± 2.51</td>
<td>25.45 ± 4.41</td>
<td>24.31 ± 3.88</td>
<td>NS, F(_{2,32}) = 1.98</td>
</tr>
<tr>
<td>Duration of a visit to the food area (s)</td>
<td>84.31 ± 16.85</td>
<td>90.76 ± 21.70</td>
<td>45.04 ± 19.69</td>
<td>* , F(_{3,32}) = 3.19 (1)-(2), NS (2)-(3), NS (1)-(3)</td>
</tr>
<tr>
<td>Total time in the food area (s)</td>
<td>517.92 ± 64.52</td>
<td>427.44 ± 43.74</td>
<td>303.62 ± 52.84</td>
<td>* , F(_{3,32}) = 3.83 (1)-(2), NS (2)-(3), NS (1)-(3)</td>
</tr>
<tr>
<td>Number of seeds eaten</td>
<td>27.73 ± 3.92</td>
<td>26.59 ± 3.38</td>
<td>18.92 ± 3.91</td>
<td>NS, F(_{2,32}) = 1.51</td>
</tr>
<tr>
<td>Foraging rate (seeds/s × 100)</td>
<td>5.08 ± 0.59</td>
<td>5.92 ± 0.72</td>
<td>4.86 ± 0.94</td>
<td>NS, F(_{2,32}) = 0.42</td>
</tr>
</tbody>
</table>

NS, not statistically different. * P ≤ 0.05; tendency: 0.05 < P ≤ 0.077.

As a decrease in time spent on the food area was associated to a decrease in the number of seeds eaten, only weak variations of the foraging rate in relation to odours were observed (F\(_{2,32}\) = 0.42; P = 0.66; Fig. 2): the foraging rate was 5.08 ± 0.59 for the own odour group, 5.92 ± 0.72 for the unfamiliar MDH group and 4.86 ± 0.94 for the unfamiliar DDO group.

3.3. Principal effects comparison

3.3.1. Strain effect

Whatever was the odour, MDH males ate more seeds during the test than DDO males (F\(_{1,69}\) = 7.68; P = 0.007) and they had a higher foraging rate (F\(_{1,69}\) = 8.24; P = 0.005; Fig. 2).

However, no difference was found for the duration of a visit to the food area (F\(_{1,69}\) = 1.10; P = 0.30), for the total time spent on this area (F\(_{1,69}\) = 2.04; P = 0.16), for its number of visits (F\(_{1,69}\) = 0.22; P = 0.64), for the number of crossed squares (F\(_{1,69}\) = 0.25; P = 0.87), or for the latency to reach the food patch (F\(_{1,69}\) = 0.67; P = 0.42).

3.3.2. Odour effect

There was an Odour effect for the duration of a visit to the food area (F\(_{2,69}\) = 6.16; P = 0.0034), for the total time on it (F\(_{2,69}\) = 6.69; P = 0.002), for the number of visits (F\(_{2,69}\) = 4.22; P = 0.019) and for the number of crossed squares (F\(_{2,69}\) = 3.81; P = 0.027).

Whatever was the strain, males tested with their own odours crossed less squares compared to an unfamiliar odour (P = 0.047 compared with same strain odour and P = 0.027 with other strain odour) and did less visits to the food area (P = 0.028 compared with the same strain odour and P = 0.020 with the other strain odour).

Duration of a visit to the food area was also shorter with their own odours than with another strain odour (P = 0.025) but the overall time spent on it was greater (P = 0.024 compared with same strain odour and P = 0.018 with other strain odour).

However, no difference was found for the number of seeds eaten (F\(_{2,69}\) = 0.86; P = 0.43), the foraging rate (F\(_{2,69}\) = 0.51; P = 0.60), or the latency to reach the food patch (F\(_{2,69}\) = 2.12; P = 0.13).
4. Discussion

The presence of individual chemical cues belonging to the same strain or to another one was sufficient in our study for inducing foraging behavioural changes both in *Mus m. domesticus* (DDO) and in *Mus m. musculus* (MDH) males. In these two strains, the behaviour of male mice differed according to the odours in the foraging area (own, same strain, or other strain odours; see Tables 1 and 2). So the solely presence of unfamiliar odours can play a role in access to and use of food resources. A primary function of these odours could be to inform individuals that the area is inhabited. But behavioural changes observed in male mice (compared to regarding their behaviour with their own scent-marks) were more pronounced with other strain odours than with same strain odours. So, these two strains seemed to process differently unfamiliar odours from a same strain individual and from another strain individual. A gradual response was indeed noticed with many variables and in both strains from the most similar odour (own odour) to the less similar one (other strain odour) (see Tables 1 and 2). In particular, *Mus m. domesticus* (DDO) and *Mus m. musculus* (MDH) males gradually increased their locomotory/exploratory activity.

The increased level of mice activity is an odour effect and it may suggest that both strain mice would become more vigilant when, in a foraging context, the olfactory substrate is different from their own scent-marks. They may use their own odour as a referent in this process (self-referent phenotype matching; Heth et al., 1998). This mechanism might be used within populations and across species (Heth et al., 2001). So we can imagine that, in a foraging context, male mice may react quickly according to the characteristics of the olfactory environment, comparing these odours with their own. However, this may not solely explain the higher exploratory activity observed.

Males should be able to estimate the competitive ability of a potential opponent. This estimation might be possible without ever meeting the signaler by the way of intrinsic properties of olfactory cues (Hurst, 1993; Gosling et al., 1996). In this case, males might diversely behave according to the cost-benefit ratio of a potential encounter with the transmitter animal. As a consequence, an acute level of vigilance could be the expression of a sensitivity to risk incurred by agonistic contacts. It could be the case in these two strains of mice because encounters between unfamiliar males are generally agonistic (Thuesen, 1977; Van Zegeren and Van Oortmerssen, 1981; Christophe et al., 1997) and could be physically dangerous. Moreover, encounters between mice belonging to the same strain are less agonistic than that between males of *Mus m. domesticus* (DDO) and *Mus m. musculus* (MDH) (Christophe et al., 1997). In the present experiment, mouse food deprivation was weak (only few hours), which could correspond to the situation in a commensal environment where food is generally permanently available. The benefit supplied by the seed consumption on a different home range does not probably exceed the cost of an encounter with the resident male. In an environment scent-marked by a potential opponent, house mice would then increase their vigilance even more since the likely cost of the encounter is high. Relation among odour, vigilance and risk is more recurrent in a predation context (Kemble and Bolwahnn, 1997; Berton et al., 1998; Thorson et al., 1998), but this relation could also occur at another level, as subordinate mice may present an elevated level of risk assessment in response to unfamiliar male odours (Garbe and Kemble, 1994).

Besides the increase exploratory activity, our result displayed differences in the foraging characteristics of the two strains. The seed consumption and the foraging rate of MDH males are higher than those of DDO males. However, these differences are not correlated to differences in body mass between the strains (unpublished data).

Although foraging variables of both strains are affected by an unfamiliar odour, only *Mus m. domesticus* (DDO) males present significant differences between unfamiliar odours of the same strain and those of another strain. It is possible that a difference in the number of seeds eaten in the presence of another strain odour occurs as well in *Mus m. musculus* (MDH) males (see Table 2) but the small size of our groups and/or the limitation of the food patch to 40 seeds did not permit to display these differences.
Our experiment was only conducted on two strains. Apply our results to all *Mus m. domesticus* and *Mus m. musculus* populations might be uncertain. However, if the hypothesis of odours similarity correlated to genetic proximity was supported to explain the differences of exploratory activity, our results might be verified in other strains or populations. In other hand, if the cost-benefit ratio hypothesis was supported, results might differ as the agonistic interactions between two individuals might vary in other populations (Van Zegeren and Van Oortmerssen, 1981).

Our results on odour effect on foraging behaviour illustrate that unfamiliar scent-marks could carry information about an unfamiliar individual and this information is processed according to the odour origin. Our work did not demonstrate a clear inhibition or stimulation of food intake with a conspecific or a hetero(sub)specific odour as found in various species (Soni and Prakash, 1987; Devenport et al., 1999; Baudoin and Haim, 2000), but rather a rearrangement of foraging behaviour characteristics in mice well known for their behavioural adaptability.

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