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The behavioural response of mice to predator odours

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The ability to detect and react to a predator odour is crucial for prey species. In the present study 10 mice (*Mus musculus*) were used to test the behavioural response of mice towards two predator odours (3-methyl-1-butanethiol and 3-mercapto-3-methyl-butan-1-ol) and one fruity odour (n-pentyl acetate). All three odours were tested against a near odourless blank stimulus (diethyl phthalate). The animals were individually placed in a test chamber of two equally sized compartments divided by a vertical Plexiglas wall with a semicircular opening. Their proximity to the odours, placed beneath the floor in petri dishes in each compartment, was measured continuously with stop watches. The mice spent less time in proximity to 3-methyl-1-butanethiol and n-pentyl acetate compared to diethyl phthalate ($P<0,05$). The mice did not prefer any specific compartment in the test with 3-mercapto-3-methyl-butan-1-ol compared to diethyl phthalate ($P>0,05$). The avoidance of 3-methyl-1-butanethiol and n-pentyl acetate can be explained either by neophobia, or in the case of 3-methyl-1-butanethiol that it contains sulphur. The lack of behavioural response towards 3-mercapto-3-methyl-butan-1-ol may be due to its loss of intensity over time. From this study it is not certain if mice have an innate fear of predator odours.

Nyckelord/Keyword:
Predator odour, prey speceis, neophobia, habituation.

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1 Abstract

The ability to detect and react to a predator odour is crucial for prey species. In the present study 10 adult male mice (*Mus musculus*) were tested for their behavioural response towards two predator odours (3-methyl-1-butanethiol and 3-mercapto-3-methyl-butan-1-ol) and one fruity odour (n-pentyl acetate). All three odours were tested against a near odourless blank stimulus (diethyl phthalate). The animals were individually placed in a test chamber of two equally sized compartments divided by a vertical transparent wall with a semicircular opening. Their proximity to the odours, placed beneath the floor in each compartment, was measured continuously with stop watches. The mice spent less time in proximity to 3-methyl-1-butanethiol and n-pentyl acetate compared to diethyl phthalate ($P<0,05$). The mice did not prefer any specific compartment in the test with 3-mercapto-3-methyl-butan-1-ol compared to diethyl phthalate ($P>0,05$). The avoidance of 3-methyl-1-butanethiol and n-pentyl acetate can be explained either by neophobia, or in the case of 3-methyl-1-butanethiol that it contains sulphur. The lack of behavioural response towards 3-mercapto-3-methyl-butan-1-ol may be due to its loss of intensity over time. From this study it is not certain if mice have an innate fear of predator odours.

2 Introduction

The ability to detect a predator before it detects you is a crucial ability for prey species. Avoiding a predator is the best way to ensure survival. The odour of an animal plays an important role in this interaction, functioning as a possible cue for both predator and prey (Hughes et al. 2010; Ferrero et al. 2011). Previous studies show that prey species react faster with aversive behaviour when presented with odours from their natural predators compared to unknown predator odours (Kavaliers, 1990; Apfelbach et al. 2005). However, unknown predator odours still elicit behavioural responses in prey species, indicating that certain compounds in predator odours are distinguishable for prey species even if no prior contact has been made with the predator (Dickman, 1992; Nolte et al. 1994). Differences in behavioural responses are also apparent considering what type of predator odour is used in studies with prey species. Stronger behavioural responses have been observed for mice (*Mus musculus)* when using a complete predator odour, compared with using only individual substances or compounds known to be constituents of predator odours (Zhang et al. 2007).

Predator odour compounds are not thought to be species specific (Mason et al. 1994; Nolte et al. 1994). There are several different compounds that result in aversive behaviour of prey species (Zhang et al. 2007). Sulphur-containing compounds are thought to serve as repellents for prey species (Mason et al. 1994; Nolte et al. 1994; Apfelbach et al. 2005; Zhang et al. 2007). The carnivorous diet of a predator results in protein digestion, which in turn leads to the creation of sulfurous metabolites in feces and urine (Mason et al. 1994; Nolte et al. 1994). It is therefore crucial for prey species to be able to distinguish and interpret these odours as threats.

The intensity of a predator odour also affects the behavioural response of prey species. Even if the initial presentation of a predator odour induces an aversive behaviour, prey species may assess the situation differently if a predator odour loses intensity over a prolonged period of time (Sullivan et al. 1985). This is not to be confused with habituation. Habituation is characterized by the decrease of a specific

behaviour during regular exposure to a constant stimulus over time, where the behaviour initially was triggered by the aforementioned stimulus. The behaviour does not have to be avoidance of the stimulus, but can also be non-vigilante such as grooming, exploration or foraging (Takahashi et al. 2005). The intensity of a predator odour plays a major role in habituation. Habituation to an intense odour is less likely to occur compared to a weak odour.

The behavioural response of the house mouse (*Mus musculus*) to different predator odours has been studied extensively (Dickman, 1992; Berton et al. 1998; Apfelbach et al. 2005; Zhang et al. 2007). Some studies addressing the question whether behavioural responses of rodents towards predator odours are innate or not led to contradicting findings. Some studies show an innate response to predator odour (Coulston et al. 1992; Nolte et al. 1994; Apfelbach et al. 2005; Takahashi et al. 2005; Punzo, 2007; May et al. 2012), whereas others indicate the opposite (Dickman, 1992; Hogg and File, 1994; Stoddart, 1976).

The goal of this study was to examine the behavioural response of mice to predator odours. Two sulphur-containing odorants known to be constituents of certain predator odours were used (Cavallini et al. 1980; Mattina et al. 1991; Wood et al. 1991; Wood et al. 2002; Miyazaki et al. 2006). To ensure that a possible repellent effect was not due to neophobia, and to present the animals with an odour not linked to predators, an odorant commonly found in fruit was used as a control odour (Maarse, 1991). Each of these three odours was then individually matched against a blank stimulus (a solvent) in a test chamber containing two compartments. The animals were then tested for their response to the presentation of these odours. All tested mice were predator-naïve, and the control odorant is found in fruit that is not a common food source for the mice.

3 Materials & methods

3.1 Animals and housing

10 adult male CD-1 mice (*Mus musculus*) 16 months of age were used in this study. They were kept in standard Plexiglas cages (35x20x13 cm) including wood shavings as bedding, nest material and cardboard rolls as enrichment. Food (standard rodent pellets) and water were supplied *ad libitum*. All mice were kept in a room with a temperature of 20 °C (± 1°C). A 12:12 hour light/dark regime was used with lights on at 07.00 AM. The animals were kept at the Annex (CBR5), Campus Valla, Linköping. All mice were predator-naïve.

3.2 Odourants

Four different odours were used in this study. One fruity odour (n-pentyl acetate), two predator odours (3-methyl-1-butanethiol and 3-mercapto-3-methyl-butan-1-ol) and one solvent odour (diethyl phthalate).

3.2.1 Diethyl phthalate

Diethyl phthalate is a near odourless liquid harmless to inhale and be exposed to. It was used as a control odour in every test and was used to dilute the other odours.

3.2.2 n-pentyl acetate

n-pentyl acetate is a known constituent of odours commonly found in fruits. It was diluted to 1:1000 with diethyl phthalate.

3.2.3 3-methyl-1-butanethiol

3-methyl-1-butanethiol is a known constituent of certain predator odours. It is found in the anal scent gland of the striped skunk (*Mephitis mephitis*) and the anal sac secretion of the hooded skunk (*Mephitis macroura*) and spotted skunk (*Spilogale putoruis*) (Cavallini et al. 1980; Wood et al. 1991; Wood et al. 2002). All aforementioned skunks are natural predators of mice. It was diluted to 1:100 000 with diethyl phthalate.

3.2.4 3-mercapto-3-methyl-butan-1-ol

3-mercapto-3-methyl-butan-1-ol is a known constituent of certain predator odours. It is found in the urine of cats (*Felis catus*) and bobcats (*Lynx rufus*) (Mattina et al. 1991 and Miyazaki et al. 2006). Both animals are natural predators of mice. It was diluted to 1:10 000 with diethyl phthalate.

3.3 Experimental setup

The test chamber (35x20x13 cm) was a modified standard cage, divided into two equally sized compartments by a Plexiglas wall, fixed to the lid, with a semicircular opening of 4 cm width which allowed an animal to switch between the two compartments (Fig. 1). A perforated metal floor was placed three centimetres above the test chamber bottom.

Underneath the perforated floor, in each compartment, a petri dish with filter paper (5,1 cm in diameter) was placed. During the experiments 100 µl of the specific odorant was added to the filter paper in the designated petri dish using a micropipette. A blank stimulus (the near odourless solvent) was present in the other petri dish in every test. After each test, the test chamber was thoroughly cleaned with ethanol. All 10 mice were tested once a day. Each odour was tested six times, making it a total of 18 days of observations. After every third mouse the filter papers and odours were replaced to make sure that the effect of the odours did not wear off.

Prior and after the experiments with odours, a test with the near odourless blank stimulus present in both compartments was performed. The purpose was to see if the mice displayed any spontaneous preference towards a certain compartment and to habituate them to the test chamber. All ten mice were tested twice, once before performing the actual study and once after the study had been performed.

Fig. 1. Test chamber used in the experiment, centred on a table with lights directly above as not to create a bias for any of the two compartments.

3.4 Data collection

A mouse was placed in the middle of the test chamber and the lid was closed. The location of the mouse was recorded continuously during ten minutes with two stop watches, one for each compartment. The number of switches between compartments was also recorded.

3.5 Statistics

A paired two-tailed t-test was used to assess possible compartment preference by the animals in the time that the animals spent in proximity to or away from diethyl phthalate.

Paired Wilcoxon tests were used to assess possible differences in the time that the animals spent in proximity to or away from a given odour. n-pentyl acetate versus diethyl phthalate, 3-methyl-1-butanethiol versus diethyl phthalate and 3-mercapto-3-methyl-butan-1-ol versus diethyl phthalate were all matched against each other.

The Spearman signed rank correlation test was used to assess possible correlation between the number of switches that occurred over time across the six test sessions for each of the odours.

4 Results

4.1 Preference test with the control odour

The mice spent more time in compartment A in 11 out of 20 trials. No significant difference was found between the time spent in compartment A (4:54 ± 0:54) and the time spent in compartment B (5:06 ± 0:54), both containing diethyl phthalate (Fig. 2, $P>0,05$).

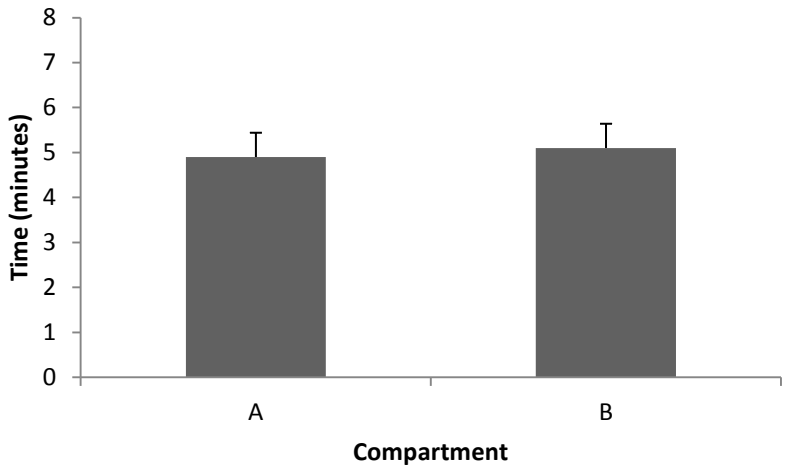

Fig.2. Average time (mean ± SD) spent in the compartments containing diethyl phthalate.

4.2 Odourants

4.2.1 3-methyl-1-butanethiol

The mice spent more time in the compartment containing diethyl phthalate in 46 out of 60 trials. Accordingly, a significant difference was found between the time spent in the compartment containing 3-methyl-1-butanethiol and the time spent in the compartment containing diethyl phthalate (Fig.3, $P<0,05$).

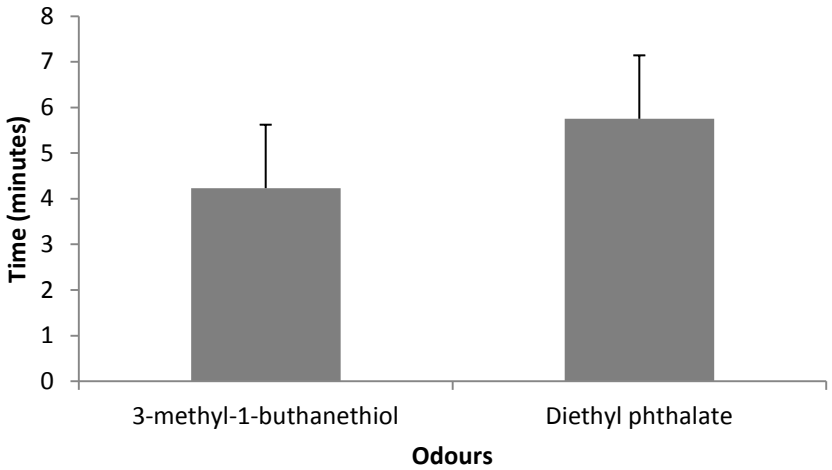

Fig.3. Average time (mean ± SD) spent in the compartment containing 3-methyl-1-butanethiol and in the compartment containing diethyl phthalate.

4.2.2 n-pentyl acetate

The mice spent more time in the compartment containing diethyl phthalate in 40 out of 60 trials. Accordingly, a significant difference was found between the time spent in the compartment containing n-pentyl acetate and the time spent in the compartment containing diethyl phthalate (Fig. 4, $P<0,05$).

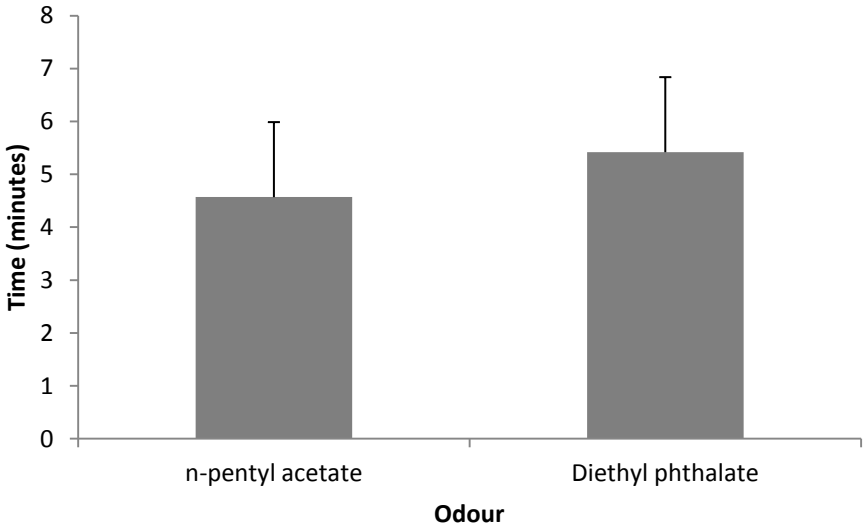

Fig. 4. Average time (mean ± SD) spent in the compartment containing n-pentyl acetate and in the compartment containing diethyl phthalate.

4.2.3 3-mercapto-3-methyl-butan-1-ol

In 32 out of the 60 trials the mice spent more time in the compartment containing diethyl phthalate. No significant difference was found between the time spent in the compartment containing 3-mercapto-3-methyl-butan-1-ol and the time spent in the compartment containing diethyl phthalate (Fig. 5, P>0,05).

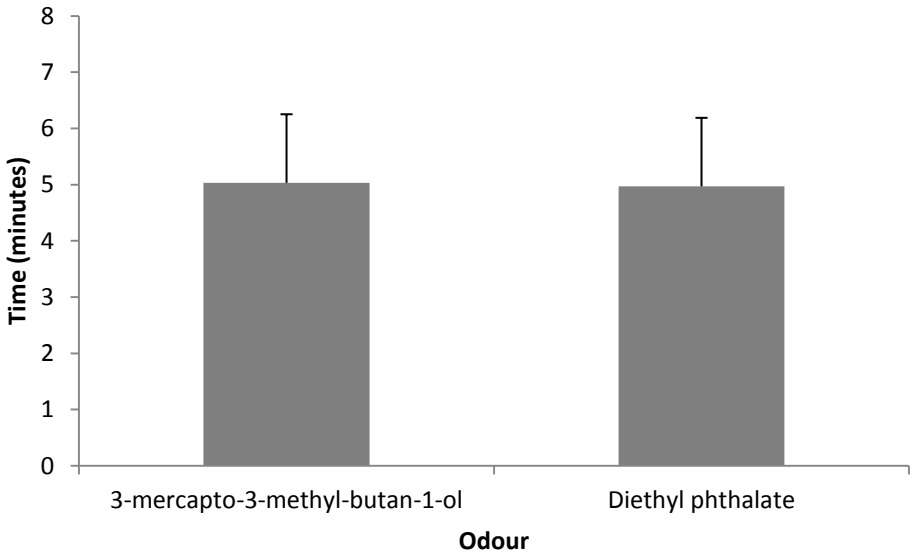

Fig. 5. Average time (mean ± SD) spent in the compartment containing 3-mercapto-3-methyl-butan-1-ol and in the compartment containing diethyl phthalate.

4.3 Switches between compartments

4.3.1 Average number of switches per odour and test session

The average number of switches between compartments for a given odour generally decreased across the six test sessions (Table 1).

Table 1. Average number of switches per odour and test session

Odour	Test session					
	1	**2**	**3**	**4**	**5**	**6**
3-methyl-1-butanethiol	35,3	31,4	32,1	23,2	23,2	19,2
n-pentyl acetate	30,7	29,8	27,0	23,1	23,7	22,8
3-mercapto-3-methyl-butan-1-ol	31,7	31,2	27,6	25,6	24,5	24,5

4.3.2 Total number of switches between compartments per odour

The total number of switches between compartments per odour across all six test sessions was similar between the three odours (Table 2).

Table 2. Total number of switches between compartments per odour

Odour	Switches
3-methyl-1-butanethiol	1644
n-pentyl acetate	1571
3-mercapto-3-methyl-butan-1-ol	1651

4.3.3 3-methyl-1-butanethiol

A significant negative correlation was found for the number of switches across the six test sessions. Switches between compartments decreased across the six test sessions (Fig. 6, r_s=-0,42; P<0,05).

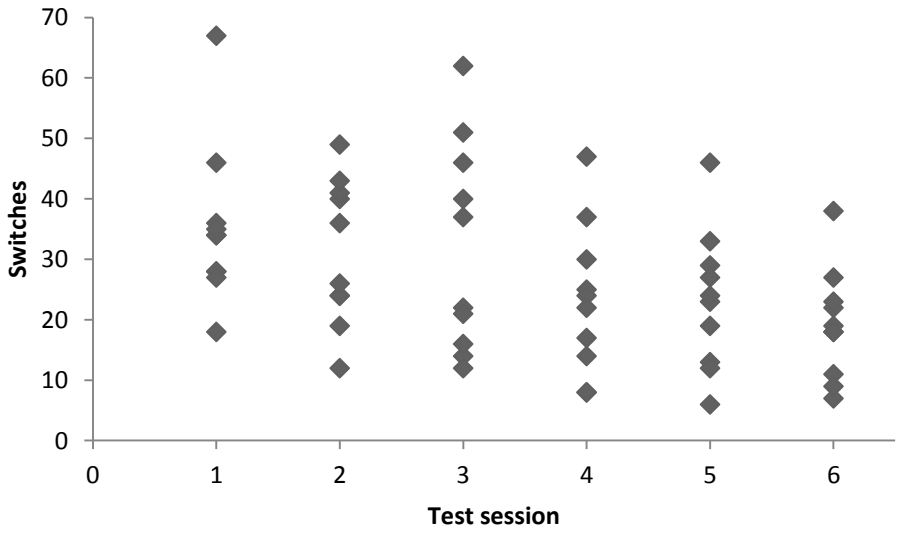

Fig. 6. Number of switches between the 3-methyl-1-butanethiol compartment and the diethyl phthalate compartment across the six test sessions.

4.3.4 n-pentyl acetate

A significant negative correlation was found for the number of switches across the six test sessions. Switches between compartments decreased across the six test sessions (Fig. 7, r_s=-0,26; P<0,05).

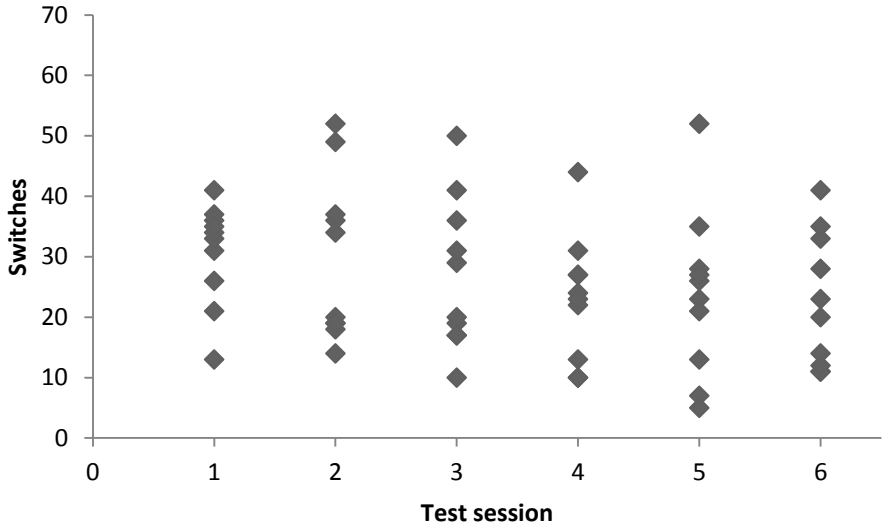

Fig. 7. Number of switches between the n-pentyl acetate compartment and the diethyl phthalate compartment across the six test sessions.

4.3.5 3-mercapto-3-methyl-butan-1-ol

No significant correlation was found for the number of switches across the six test sessions.(Fig. 8, r_s=-0,23; P>0,05).

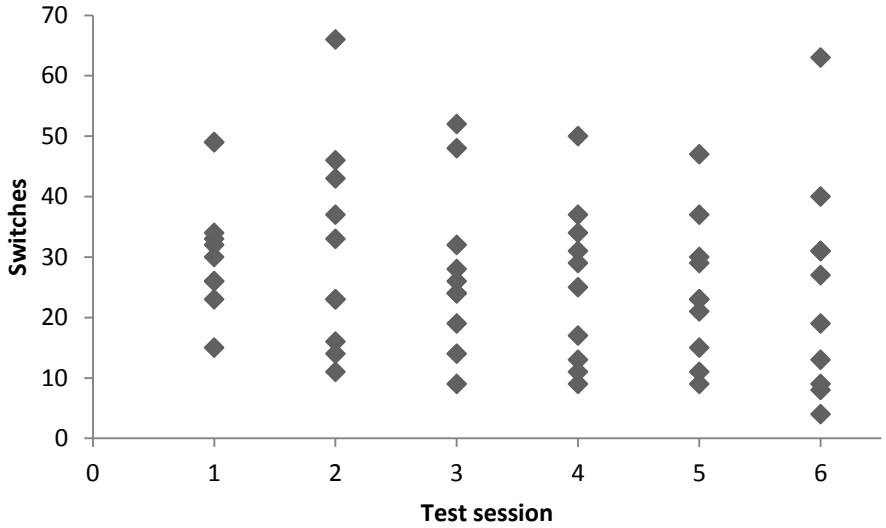

Fig. 8. Number of switches between the 3-mercapto-3-methyl-butan-1-ol compartment and the diethyl phthalate compartment across the six test sessions.

5 Discussion

This study found inconclusive results as to how mice respond to predator odours. The mice spent less time in proximity to one of the predator odours (3-methyl-1-butanethiol) and the fruity odour (n-pentyl acetate) compared to the near odourless blank stimulus (diethyl phthalate). The mice did not prefer any specific compartment in the test with the other predator odour (3-mercapto-3-methl-butan-1-ol) compared to the near odourless blank stimulus (diethyl phthalate).

A mouse is not a human. The concentrations of the three odours used in this study were all chosen by a human. The intention was to choose concentrations that were of equal subjective intensity and which were, at least for a human nose, not too intense, but also not too weak. That said, what a human may perceive as a moderate intensity may not apply for a mouse. Worth mentioning in this context is that the olfactory sensitivity of mice for the two predator odourants is not known, whereas the olfactory detection threshold for the fruity odour has been determined at 5 ppt (parts per trillion) (Walker and O'Connell, 1986).

The results from the preference test with the control odour, performed before and after the actual tests, confirms that the mice show no preference for either compartment ($P>0,05$). This validates the results from this study, which therefore can be credited to the behavioural response of the mice to the predator odours, not the test chamber.

The results of the test with the first predator odour (3-methyl-1-butanethiol) gave a significant difference as to where the mice positioned themselves in proximity to the odours ($P<0,05$). The compartment containing the near odourless blank stimulus (diethyl phthalate) was preferred over the compartment containing the predator odour in 46 out of 60 trials. In accordance with previous studies, this is not unexpected (Coulston et al. 1992; Nolte et al. 1994; Apfelbach et al. 2005; Takahashi et al. 2005; Punzo, 2007; May et al. 2012). 3-methyl-1-butanethiol is a sulphur-containing compound, derived from natural predators of the house mouse (Cavallini et al. 1980; Wood et al. 1991; Wood et al. 2002). For rodents, the avoidance of sulphur-containing compounds is adaptive and increases their survival chances (Mason et al. 1994). However, due to the current experimental setup, the results cannot confirm that the avoidance of this predator odour is due to an innate behaviour. The avoidance can be due to neophobia or the sulphur-containing compound itself.

Across the six test sessions with 3-methyl-1-butanethiol the mice decreased the number of switches between compartments ($P<0,05$). However, the mice did not increase the time spent in proximity to the predator odour. This is a possible sign of habituation. By remembering the predator odour, the need for exploration decreased throughout the test sessions. This, however, is a sign of habituation towards the situation the mice are exposed to, not towards the predator odour itself. The mice continuously throughout the test sessions deemed the predator odour to be a threat. By decreasing the number of switches between compartments the mice also decreased the number of encounters to what they deemed to be a threat. Again, if the avoidance was due to the predator origin of the odour, neophobia or the sulphur-containing compounds remains to be tested.

The result of the test with the fruity odour (n-pentyl acetate) also gave a significant difference as to where the mice positioned themselves in proximity to the odours ($P<0,05$). The compartment containing the near odourless blank stimulus (diethyl phthalate) was preferred over the compartment containing the fruity odour in 40 out of 60 trials. n-pentyl acetate is not a sulphur-containing compound and is a constituent of fruit odours (Maarse, 1991). There are several different explanations as to why the mice chose to avoid it. It could be that the mice had never before experienced this smell so neophobia is a possibility. n-pentyl acetate was also the least diluted of the three odours (1:1 000) and had a very intense smell. In comparison with the other two odours, this odour was by far the one that maintained its intensity the most. Every odour was changed every third mouse (approximately after 45 minutes of usage), and n-pentyl acetate kept its intensity fairly regular throughout this time, which the predator odours did not. These are, however, personal observations, and once again, mice are not humans.

Across the six test sessions with n-pentyl acetate the mice decreased the number of switches between compartments ($P<0,05$). However, as with the first predator odour, the mice did not increase the time spent in proximity to the fruity odour. This may be a sign of habituation as described above.

The result of the test with the second predator odour (3-mercapto-3-methyl-butan-1-ol) did not give a significant difference as to where the mice positioned themselves in proximity to the odours ($P>0,05$). The mice spent more time in the compartment containing the near odourless blank stimulus in only 32 out of 60 trials. While this is somewhat unexpected, there are several different possible reasons as to why this happened. The regime of changing the odours after every third mouse during the test sessions (approximately after 45 minutes of usage) was put into place due to the evaporative loss of intensity of the smell of 3-mercapto-3-methyl-butan-1-ol. Even though the initial intensity of the smell was strong directly after a change, it quickly lost its intensity. When the next change occurred the intensity of the smell had, to a great extent, disappeared, and was to the human nose hard to distinguish. This never happened with any of the two other odours.

If the mice experienced the same effect, it is not surprising that the results show no preference or avoidance towards any of the compartments. The predator odour could have been too subtle to be acknowledged as a threat. This explanation is somewhat strengthened by the fact that no sign of habituation was observed. The number of switches between compartments did not decrease throughout the test sessions for the second predator odour like it did for the other two odours ($P>0,05$). This indicates that the mice never experienced the second predator odour as they did the other two odours.

One could argue that they simply did not recognize the second predator odour as a threat and therefore ignored it. That, however, leaves the question of neophobia. If the mice avoided the fruity odour due to neophobia, why did they not avoid the second predator odour for the same reason? This indicates even more that the mice did not recognize the second predator odour. They avoided both the first predator odour and the fruity odour, but not the second predator odour. If the two former were avoided due to neophobia, sulphur-compounds (for the first predator odour) or intensity, it seems likely that the second predator odour would also be avoided for some of these reasons. Now that it was not avoided indicates that the lack of intensity played a large

role in the given results. Urine and its constituents from predators are highly aversive to prey species (Nolte et al. 1994), but no significant difference was found despite the origin of the second predator odour.

Ten mice were used in this study. Due to the short period of time available for data collection, the results are very sensitive to extreme values. I recognized large individual differences amongst the mice. Some seemed unaffected by human interaction, whereas others did not. Freezing behaviours were apparent for some of the mice, where they instantly upon being dropped in the test chamber ran to a corner and stayed there for a long period of time (2-3 minutes) without moving. When these mice later began to move, it was apparent that they started to pay attention to the odours and what compartment they were in (this did not apply for 3-mercapto-3-methyl-butan-1-ol). The initial choice of corner and compartment did, however, not seem to be influenced by what odours were present.

The forceful situation of being placed in a new environment with unfamiliar stimuli clearly affected some of the mice, and therefore also their behaviour. Stress due to the change in environment, human contact, novel sounds and lights may have affected the results negatively. This has been shown to be a limiting factor in previous studies (Berton et al. 1998). Not all individuals froze or displayed stretching, but due to the limited amount of data, the few mice that did may have had an effect.

In conclusion, the mice spent less time in proximity to the first predator odour (3-methyl-1-butanethiol) and the fruity odour (n-pentyl acetate) compared to the near odourless blank stimulus (diethyl phthalate). The mice did not prefer any specific compartment in the test with the second predator odour (3-mercapto-3-methyl-butan-1-ol) compared to the near odourless blank stimulus (diethyl phthalate). The decreased number of switches across the six test sessions indicates that the mice habituated to both the first predator odour and the fruity odour. Whether the aversive behaviours against these two odours were due to neophobia, the strong intensity of the odours or the sulphur (only in the predator odour) remains to be investigated. The mice did not decrease the switching between compartments for the second predator odour, indicating that they did not perceive this odour to its full extent. From this study it is not certain if mice have an innate fear of predator odours.

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