Conditioned Changes in Ultrasonic Vocalizations to an Aversive Olfactory Stimulus are Lateralized in 6-Day-Old Rats

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ABSTRACT: Using a soft rubber plug to block airflow in one naris, Kucharski, Johanson, and Hall (1986) found that some forms of olfactory memory (e.g., odor preferences) were lateralized in young rats while other forms (e.g., conditioned activation and mouthing) were not. The present experiments extended that research by showing that conditioned increases in ultrasonic vocalizations were also lateralized. That is, when exposed to an odor that was previously paired with footshock, 6-day-old rats significantly increased their rate of vocalizing. This response only occurred, however, when the naris open at training was also open at test. The use of the developing rat as a natural split-brain preparation appears to be an effective procedure with which to broaden current approaches to the analysis of learning, memory, and emotion. © 2000 John Wiley & Sons, Inc. Dev Psychobiol 37: 121–128, 2000

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In recent years, increasing empirical and theoretical attention has been directed toward the experimental analysis of the development of learning and memory in rats. One impetus for this surge of interest is that the developing rat can be seen as being a “naturally lesioned” adult rat (see Fanselow & Rudy, 1998). That is, particular neural structures may not be fully functional early in development. Performance of developing rats on certain learning tasks may, therefore, be similar to the performance of adult rats with lesions of those structures. From this perspective, the developmental and experimentally induced lesion approaches to the analysis of the neural bases of learning and memory are complimentary; converging lines of evidence can be produced by considering data obtained from the two different approaches.

The developing rat does indeed appear to provide a natural split-brain preparation, at least for olfactory information. In other words, during the first week postpartum it is possible to restrict access to learned associations about olfactory stimuli to one hemisphere of the brain, even without doing any surgical procedures to separate the two hemispheres (Kucharski & Hall, 1988). This is possible for two reasons. First, cells in the nasal epithelium of each naris project only to the ipsilateral olfactory bulb (Schwob & Price, 1984). This, of course, is in stark contrast to other sensory systems where peripheral cells send both ipsi- and contra-lateral projections to the CNS. Second, the
anterior commissure (AC), a bundle of fibers connecting the two hemispheres, is not functional until sometime after the first week postpartum. It is via the AC that the two hemispheres normally communicate about odors. Therefore, restricting olfactory information to one naris during the first week of life leads to that information being represented only in the ipsilateral hemisphere, and to that information being inaccessible to the contralateral hemisphere.

More specifically, Kucharski and Hall (1988) did an elegant series of experiments showing that the developing rat can be used as a natural split-brain preparation. They demonstrated that several forms of olfactory memory could be functionally localized to one side of the brain by restricting the olfactory CS to one naris. In those experiments, 6-day-old rat pups were given odor–milk pairings while one naris was blocked with a soft, removable plug. At test, rats showed a preference for the odor only when tested with the trained naris open. When the pups were tested with the trained naris closed they performed no differently from subjects receiving the odor and milk in an unpaired fashion. That is, olfactory preference memories appear to be lateralized in 6-day-old rat pups. However, Kucharski and Hall (1988) found that 12- and 18-day-old rats responded bilaterally to the CS under the same experimental conditions. The older pups respond in this way because by 12 days of age the AC fibers have matured, whereas in 6-day-olds these fibers are still functionally immature (Schwob & Price, 1984). Support for this idea is provided by the finding that surgically cutting the fibers of the AC produced lateralized olfactory memories in 18-day-olds (Kucharski & Hall, 1988).

Lateralized memory for conditioned odor preference has been shown in several studies with 6-day-olds (Kucharski, Burka, & Hall, 1990; Kucharski & Hall, 1988; Kucharski et al., 1986). Not all forms of appetitive conditioning are lateralized at this age, however. For instance, conditioned mouthing (consummatory or ingestive responses) is only partially unilateral and conditioned activation (arousal state) is bilateral (Kucharski et al., 1986).

In contrast to this systematic exploration of lateralized appetitive conditioning, there has been very little research on the laterality of aversive conditioning. Indeed, there has been only one experiment that investigated lateralized odor aversion (Kucharski, Arnold, & Hall, 1995). In that study, 6-day-old rats received pairings of an odor (lemon or wintergreen) with a 0.6 mA footshock and were later tested for avoidance of those odors. The results showed that conditioned avoidance was lateralized in the 6-day-old rat. It is unclear whether aversive olfactory memories would also be lateralized if a different measure than odor avoidance was used. Given this, we examined whether conditioned odor aversion was lateralized when changes in ultrasonic vocalizations (USVs) served as the measure.

When isolated from the home cage, young rats emit USVs (Blumberg, 1992; Blumberg & Alberts, 1990; Hofer, Masmela, Brunelli, & Shair, 1999; Hofer & Shair, 1978; Shair, Masmela, Bruneil, & Hofer, 1997). Many have taken this to be indicative of distress (Hofer et al., 1999; Hofer & Shair, 1978; Shair et al., 1997), and preliminary experiments in our lab found that an odor paired with shock increased USVs in rats 6, 12, and 18 days of age. Therefore, in the present study we examined whether this increased USV rate in 6-day-old rats is lateralized or not. It might be expected that USVs would not be lateralized because USVs are more indicative of a general state response such as behavioral activation, rather than a specific, stimulus-oriented response such as avoidance.

**GENERAL METHOD**

**Subjects.** Experimentally naive, 5-day-old (at time of training), Sprague-Dawley rats obtained from the breeding colony in the School of Psychology at the University of New South Wales were used. All rats were housed in litters of eight with their mother in plastic boxes (65 x 40 x 22 cm; L x W x H) kept in a room with a 12-hr light/dark cycle (lights on at 6 am). Food and water were available ad libitum. Both sexes were included in the experiments and rats were not handled prior to training. Training and testing occurred between 9 am and 5 pm. All animals were treated in accord with the principles of animal use maintained by the American Psychological Association, and the Animal Care and Ethics Committee at the University of New South Wales approved all procedures.

**Apparatus.** A rectangular, clear, Plexiglas chamber (13 x 9 x 9 cm; L x W x H) with a stainless steel grid floor (each 2 mm in diameter and 5 mm apart) and raised 5 cm above a table top was used for training and testing. Electric shock (1.5 mA; 1 s in duration; from a Coulbourn constant currant shocker, model S13-02) could be manually delivered to the grid floor.

**Odors.** One milliliter of liquid grape odorant was used as the CS+ (Grape #182380019, Wild Flavours, Heidelberg). Lemon odor (1 ml; Lemon # 181505/22,
Wild Flavours, Heidelberg, Germany) was used as an alternative stimulus in order to facilitate conditioning in young rats (see Kucharski & Spear, 1984). Each odor was individually placed ~5 cm below the grid floor on a small piece of paper toweling (~3 cm × 3 cm) in a petri dish. The petri dish containing the odor was covered with a glass lid between trials and fresh odors were used for each litter at training and at test. The room was adequately ventilated and the air temperature was kept at 22°C.

**Nose Plug.** To restrict olfactory information to one nasal cavity during training and testing, a soft rubber plug was inserted into one naris (method based on Kucharski & Hall, 1988). The plug was made from a 6 mm piece of silastic tubing (0.025 cm, outside diameter) with a 4.0 silk thread knotted and inserted into the lumen to block air flow and to allow for easy removal. The plug was coated in petroleum jelly and gently inserted into the rat’s naris. The pups were then returned to the nest with the mother and litter for 30 min prior to training or testing. After 30 min, the mother and pup appeared to pay little attention to the presence of the plug. The naris that was blocked (left or right) was counterbalanced between litters and was switched for the closed naris groups prior to testing. The open groups had the plug inserted into the same naris for training and testing.

**Ultrasound Vocalizations.** A bat detector (S-25, Ultrasound Advice) set at 42.5 kHz and equipped with a high frequency microphone was placed on the tabletop, next to the chamber grid. Headphones were connected to the bat detector allowing the experimenter to count the number of vocalizations during testing.

**Training.** The training procedure was the same for both Experiments 1 and 2. The pups were kept in a separate room with the mother and litter in their home cage during the 30-minute nose plug acclimation period. Each pup was carried individually to the training/testing room and placed into an incubator that was maintained at 32°C. Pups were trained according to either a “Paired” or “Unpaired” condition in two phases that were separated by 60–90 min. Paired animals received grape–footshock pairings and Unpaired animals received both footshock and grape, but in an explicitly unpaired fashion.

In Phase 1, one trial for the Paired subjects comprised a grape–footshock pairing separated by a lemon exposure. That is, a pup was taken from the incubator and placed on the grid floor of the shock apparatus for 30 s with the lemon odor underneath. The pup was then returned to the incubator for 30 s before being placed back on the grid floor for 30 s in the presence of grape odor. During this 30-second period with grape, two 1 s, 1.5 mA shocks were given, one at the 14th second and one at the 29th second. The pup was then returned to the incubator for 30 s before the next trial began. One trial for the Unpaired animals in Phase 1 comprised the same proceedings as for the Paired animals; however, neither grape nor lemon were presented. That is, the pup was taken from the incubator and placed on the grid floor for 30 s in the absence of odor. It was then returned to incubator for 30 s before it was placed back on the grid to receive the two footshocks in the absence of odor. All pups received five consecutive trials, with two shocks per trial.

Phase 2 involved the same process as Phase 1, with two exceptions. Firstly, no shocks were given to rats in either condition. Secondly, the Unpaired group received alternating presentation of the odors, as the Paired group had in Phase 1.

At the end of each phase, the pups were placed back in the home cage with the mother and litter. Throughout the training period, every rat had one naris blocked and plugs were removed before subjects were returned to the litter.

**Testing.** Testing occurred 24 hrs (± 2 hrs) after training. Plugs were inserted 30 min prior to test while subjects remained with the mother and litter. Half of each group was tested with the trained naris open and half with the trained naris closed. Thus, four conditions were tested: a Paired–Open (i.e., a Paired subject tested with the trained naris open), Paired–Closed, Unpaired–Open, and Unpaired–Closed. The pups were taken from the litter after the 30-minute acclimation period and placed in the incubator for 30 s before being placed into the apparatus that was used for training. The number of USVs per min were recorded for the baseline period (2 min in Experiment 1 and 5 min in Experiment 2) and then for 5 min in the presence of the grape odor (CS+). For each subject, the number of USVs per test min was calculated as a percentage change from the number of USVs made in the last baseline min (i.e., ((T−B) / B) × 100, where T is the test minute score and B is the baseline score). Any pup that emitted less than 10 USVs in the final baseline minute was replaced.

**EXPERIMENT 1**

This experiment examined whether aversive odor memories are lateralized in 6-day-old rats when
changes in USVs are used as the measure of conditioning.

**Method**

**Subjects.** Forty-eight rats were trained at 5 days of age and tested at 6 days of age. Half of the animals received grape–shock pairing and half received explicitly unpaired pairings of grape and shock (see General Methods). Four conditions were tested (Paired Open, Paired Closed, Unpaired Open, Unpaired Closed) with 12 subjects in each. No more than one subject from any litter was included in a condition. During the testing phase, the numbers of USVs per min were recorded for a total of 7 min. The first 2 min served as a baseline measure. At the beginning of the 3rd minute, the CS+ (grape odor) was placed under the grid for 5 test min. There were seven subjects that emitted less than 10 USVs in the 2nd baseline min and were replaced. Two of these came from the Paired Open condition, two from the Paired Closed condition and three from the Unpaired Closed condition.

**Results and Discussion**

There were no differences among the groups on baseline scores (see Table 1). When the odor was presented the Paired Open group showed a gradual increase in the number of USVs emitted, whereas the Paired Closed group performed similarly to the unpaired controls, all of which decreased the number of USVs emitted across the test period (see Figure 1).

Statistical analysis confirmed that no groups were different on baseline scores \((F < 1)\). There was a significant effect of time on baseline scores because all groups emitted fewer USVs in the second minute of the baseline period (see Table 1; \(F(1,44) = 75.52, p < 0.001\)). There was no time-by-group interaction effect on the baseline scores \((F < 1)\).

When the CS+ was introduced, a repeated measures ANOVA confirmed that there was a significant difference among groups \((F(3,44) = 15.11, \ p < 0.001)\). There was no effect of time \((F < 1)\), but there was a significant interaction of time by group \((F(12,176) = 2.87, \ p = .001)\). That is, as the Paired Open group increased its rate of ultrasounding across the test period, the Paired Closed and both unpaired groups decreased their rate of ultrasounding. Pairwise comparisons, with the Newman Keuls procedure \((p < 0.05)\), showed that the Paired Closed and the two unpaired groups were not significantly different at any time point whereas the Paired Open group was significantly different from all other groups at 2–5 test min (see Figure 1).

The results of this experiment show that a conditioned aversive odor increases USVs, and that this response is lateralized. That is, rats in the Paired condition emitted more USVs only when the naris open at test was the same naris that was open during training. When the naris that was open at test was the naris that was closed during training, paired subjects responded no differently than the unpaired control groups. Therefore, it appears that aversive odor memories are lateralized when either avoidance responding (Kucharski et al., 1995) or number of USVs (present experiment) are used to assess conditioning.

Even though the Paired Open group showed an increase in USVs across the test period, both the Unpaired groups and the Paired Closed group showed substantial decreases in USVs. Decreases in USVs over these sorts of time periods have been reported elsewhere (Kehoe & Boylan, 1992). However, we wanted to determine if the results obtained in Experiment 1 were due, at least in part, to the decrease in USVs in the Paired Closed and Unpaired groups. To do this we replicated Experiment 1 with an increased baseline period.

**Table 1. Mean (± SEM) Number of USVs Emitted during the Baseline Period for All Groups in Experiment 1**

<table>
<thead>
<tr>
<th>Group</th>
<th>Minute 1</th>
<th>Minute 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Paired Open</td>
<td>82.6 (±9.3)</td>
<td>48.7 (±6.0)</td>
</tr>
<tr>
<td>Paired Closed</td>
<td>69.6 (±8.4)</td>
<td>41.6 (±8.3)</td>
</tr>
<tr>
<td>Unpaired Open</td>
<td>80.3 (±11.7)</td>
<td>46.8 (±7.3)</td>
</tr>
<tr>
<td>Unpaired Closed</td>
<td>76.8 (±10.0)</td>
<td>50.1 (±6.5)</td>
</tr>
</tbody>
</table>
EXPERIMENT 2

We did the present experiment to determine whether increasing the duration of the baseline phase would reduce the decline in control group USVs reported in Experiment 1 whilst retaining the significant increase in USV emissions by the Paired Open group. Based on the results of Experiment 1, extending the baseline phase from 2 to 5 min seemed sufficient to produce stability in USV emissions in all groups.

Method

Subjects. Rats from 30 litters were trained at 5 days of age and tested at 6 days of age. All rat pups received either grape–shock pairings or explicitly unpaired presentations of grape and shock during training (see General Methods). In this experiment only one unpaired condition was used, where half were tested with the trained naris open and half with the trained naris closed. No more than two animals from each litter were used for a single condition and when two animals from one litter were used, the scores for these animals were averaged (to minimize litter effects), thereby producing 10 final scores for each group. During the testing phase, the numbers of USVs per min were recorded for a total of 10 min. The first 5 min served as a baseline measure and at the beginning of the 5th minute the CS+ (grape odor) was placed under the grid for 5 test min. There were four subjects that ultrasounded less than 10 times in the 5th baseline min and were replaced. Two of these came from the Paired Closed group and two came from the Unpaired group.

Results and Discussion

There were no differences among groups on baseline scores. The baseline scores for all groups declined over the 5-min period (see Figure 2); nevertheless, all groups were emitting between 33–45 USVs per min by the last baseline minute. When the grape odor CS+ was presented the Paired Open group emitted more USVs, while the animals in the Paired Closed and the Unpaired group did not (see Figure 3).

Statistical analysis confirmed that all three groups did not differ significantly on number of USVs emitted during the 5-min baseline period ($F < 1$), but there was a significant effect of time ($F(4,108) = 106.11, p < 0.001$). That is, during the 5-minute baseline period all groups significantly decreased their rate of ultrasounding (Figure 2). There was no interaction effect of group by time on baseline USVs ($F < 1$).

During the test phase there was a significant difference among groups ($F(2,27) = 7.32, p < 0.001$), and a significant effect of time ($F(4,108) = 2.74, p = .03$); that is, the Paired Open group emitted significantly more USVs than the other two groups. There was no significant interaction effect of group by time ($F(8,108) = 1.19, p = .31$). Pairwise comparisons, with the Newman Keuls procedure ($p < .05$), showed that the Paired Closed group was not significantly different from the Unpaired group at any time point whereas the Paired Open group was significantly different from both these groups at test minute 5.

Even though the Paired Open group is only significantly different from the two other groups at the last time point (whereas in Experiment 1 the Paired Open group was significantly different from the Paired Closed and the two Unpaired groups at time points T2 to T5), it should be noted that the pattern of USVs emitted by the Paired Open group in both
experiments was almost identical. That is, when the Paired Open group was first presented with the CS+, the number of USVs decreased by about 15%. By the fourth minute, the number of USVs had increased by 20%, and then by 40% by the end of the fifth test minute (See Figures 1 and 3).

With the extended baseline phase in Experiment 2, the decrease in Unpaired and Paired Closed group USVs across the test period was not as great as the decrease seen in these groups in Experiment 1. That is, in Experiment 1 the Paired Closed and the Unpaired groups showed about a 55% decrease, whereas these groups only showed about a 20% decrease in Experiment 2. Nevertheless, it should be noted that by the last test minute the Unpaired groups and the Paired Closed groups were still emitting an average of 20 USVs per min in Experiment 1 and about 23 USVs per min in Experiment 2. Therefore, lengthening the baseline period from 2 to 5 min produced a more stable estimate of the USV rate prior to the introduction of the odor CS+.

**DISCUSSION**

The results of this study replicate Kucharski et al.'s (1995) finding that aversive odor memories in 6-day-old rat pups are lateralized. It extends their finding of lateralized odor avoidance by showing that conditioned increases in USVs are also lateralized. In both experiments of this study, presentation of the odor CS increased the number of USVs in rats in the Paired condition only if the trained naris was open during the test period. Rats in the Paired condition with the trained naris closed during the test phase performed no differently than unpaired control groups.

Kucharski and Hall (1988) reported that olfactory memories were no longer lateralized by 12 days of age. By the second week of life, the anterior commissure had matured and allowed for inter-hemisphere communication. In other words, rats of 12 days of age, and older, could access the training memory whether the trained or the untrained naris was open at test. As noted in the introduction, research in our laboratory has shown that an olfactory CS previously paired with shock increases USVs in rats 6, 12, and 18 days of age (unpublished data). Therefore, one would predict that the same pattern of results reported by Hall and Kucharski would also be observed when USVs are used as the measure of conditioning. That is, 6-day-old rats should exhibit conditioned increases in USVs only when the trained naris is open at test whereas rats 12 days of age, or older, should exhibit conditioned increases in USVs when either naris is open at test.

The results of the present study provide strong support for the first part of this prediction, but unfortunately, we were unable to obtain evidence concerning the second part of the prediction. In several attempts to examine this issue, we consistently found that the nose plug was irritating to 12-day-old rats. This resulted in the subject directing persistent, intense behavioral activity toward the plug, which, in many cases, led to it being pulled out of the naris. In those instances where the plug was still in place after the adaptation period, the subjects continued to be preoccupied with attempting to remove this object from their naris, making it impractical to test them.

In addition to supporting the idea that olfactory memories can be lateralized in the very young rat, the results of the present study also show that USVs can be used to assess classical conditioning to olfactory stimuli in young rats. To date, only one other study has measured changes in USVs as a conditioned response during development (Barr, Wang, & Carden, 1994). In that study, aversive conditioning of USVs to an odor was demonstrated by pairing lemon with administration of a k opioid receptor agonist. They too found that rat pups (3- and 7-day-olds) significantly increase USV emissions to an aversive CS; however, the pattern of responding was different to that of the present study. In the study by Barr and colleagues, USV emissions increased rapidly in the first minute and then dropped to control levels for the rest of the 6-minute test period, whereas in our study USVs gradually increased throughout the test period. The difference in response patterns could be due to a number of factors, namely, the US (k opioid agonist vs shock), the CS (lemon odor vs grape odor), the ambient temperature during test (31°C vs. 22°C), or the testing procedure (they did not have a baseline measure). Measuring changes in USVs might be a particularly useful procedure for measuring learning in the very young rat. The results of the present study certainly suggest that changes in USVs to an aversive olfactory CS are a very reliable method of indexing classical conditioning given that the means obtained for the Paired Open group were almost identical in the two experiments.

We interpret the increase in USVs observed in this study as a conditioned fear response. However, this observed change in USVs could be due to one of two, possibly intertwined, processes. For example, some have interpreted isolation-induced USVs in young rats to be an indicator of emotional distress or anxiety (e.g., Hofer & Shair, 1978; Shair et al., 1997, 1999). That is, isolated rat pups experience a loss of familiar cues, such as thermal, olfactory, and tactile cues, which results in separation anxiety (Hofer, 1996). This type
of interpretation of USVs can be applied to the present study if one assumes that the presentation of the olfactory CS for shock heightens the separation anxiety being experienced, and thus producing an increase in USVs. However, others have suggested that rather than being a distress call, isolation-induced USVs are the consequence of a series of physiological events that aid thermoregulation (Blumberg 1992; Blumberg & Alberts, 1990; Blumberg, Solokoff, & Kent, 1999; Kirkby & Blumberg, 1998; Solokoff & Blumberg, 1997). Specifically, an isolated young rat is faced with a thermoregulatory challenge and in order to meet this challenge it must maintain cardiovascular function and oxygen transport to the lungs. Blumberg and colleagues (Blumberg et al., 1999; Kirkby & Blumberg, 1998) conclude that rats recruit a response termed the “abdominal compression reaction” (ACR) that propels blood back to the heart during extreme cold when blood viscosity is high. These abdominal contractions coupled with laryngeal braking (a respiratory maneuver that assists in enhancing oxygen transport to the lungs and possibly augments the ACR generation of intraabdominal and intrathoracic pressure), appear to coincide with the emission of ultrasound.

However, one could not suggest that the odor-elicited changes in USVs in the Paired–Open subjects in the present study are entirely a consequence of a thermoregulatory challenge—all subjects were tested at the same ambient temperature. Additionally, the fact that USVs are lateralized in young rats suggests that USVs are likely to be a stimulus-oriented response rather than a general activation response. As mentioned previously, Kucharski and colleagues (1986) found that conditioned preference and ingestive responses were lateralized, whereas conditioned activation was not. If USVs were nothing more than general state response, for example, a response that regulates body temperature, then it might be expected that conditioned increases in USVs would not be lateralized in 6-day-old rats. Since USVs are lateralized in 6-day-old rats, like conditioned preference and ingestive responses are, then this suggests that the conditioned increase in USVs observed in subjects in the Paired Open condition are stimulus-oriented and not just a response to temperature.

It is possible, however, that one of the mechanisms identified by Blumberg and his colleagues for producing isolation-induced USVs (i.e., laryngeal braking) is also involved in the present context. That is, the rats in the Paired–Open condition may have increased their oxygen intake in response to the aversive olfactory CS in order to ready themselves for “flight or fight.” This respiratory maneuver then produced, as a by-product, increased numbers of USVs.

Given that in our study an aversively conditioned, novel odor increases USVs in 6-day-old rats, and that this finding has also been demonstrated in rats 12 and 18 days old, it is important to consider that some studies have found a reduction of USVs to a biologically relevant, aversive olfactory stimulus. That is, exposure to an anesthetized, unrelated adult male not only elicits freezing responses and elevates corticosterone levels in 12- and 14-day-old rats (both signs of fear or distress), it also reduces USVs (Takahashi, 1992, 1994). Further, the reduction in USVs under these conditions is abolished when the subjects are rendered anosmic (Shair et al., 1999). However, Takahashi (1992) also found that rats aged 3, 6, and 9 days did not alter the number of USVs emitted when exposed to the anaesthetized male rat. He suggested that this was due to the functional immaturity of the inhibitory system responsible for reducing USVs in rats 9 days of age and younger. The interpretation offered for the reduced USVs in 12- and 14-day-old rats to a biologically relevant olfactory stimulus is that the young rat inhibits its USVs in order to reduce the likelihood of attracting the attention of a potential predator. Why, then, does an odor paired with shock produce an increase in USVs? Do these different odors have different effects on USVs because one is conditioned and the other is unconditioned? Or is it the case that young rats recognize why an aversive odor is aversive (i.e., this one potentially predicts a predator while that one potentially predicts a painful experience)?

Whatever the mechanism responsible for the changes in USVs the results of the present study show that USVs can be used as a reliable measure of conditioning to olfactory stimuli in 6-day-old rats. Nevertheless, it is clear that additional research is required to determine (1) the mechanism(s) involved in this effect, and (2) the conditions in which aversive odors inhibit USVs and those in which aversive odors increase USVs.

REFERENCES


