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The effect of lesioning the basolateral amygdala on odor preference and related memory in adult male rats

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ABSTRACT

Background: It has been shown that the basolateral amygdala (BLA) plays an important role in emotional behaviors, olfactory preference, and related memory in rats, such that inactivation of this area changes these behaviors. In the present study, the effect of BLA lesion on olfactory preference (relative to the urine of male, female, and immature rats) in male rats and their affected memory was evaluated.

Materials and Methods: Adult male Wistar rats (n=16) were used. Bilateral BLA lesions were created by passing a 1.5 mA current for 7 seconds. Animals were exposed to four different odors, including male urine, female urine, immature rat urine, and water. In each trial, the time spent near each odor, the number of visits to each odor, and the distance traveled in each area related to each odor were recorded.

Results: The results showed that the control group rats showed the highest olfactory preference for female urine and the lowest preference for water in combination with a neutral odor. BLA-lesioned rats showed an altered response of olfactory preference. In them, the first priority of odor preference shifted from female rat urine to immature rat urine. Spatial memory related to learning the location of olfactory sources was also impaired in these groups.

Conclusion: In conclusion, our findings suggest that the BLA plays a role in changing olfactory preference related to urinary chemical signals and their affected memory.

Keywords: Olfactory Preference, Memory, Basolateral Amygdala, Rats.

Introduction

In animals, particularly rodents, the ability to detect various odors and pheromones, along with the memory related to these scents, plays a crucial role in their behaviors, as it regulates vital survival behaviors. Numerous studies indicate that olfactory memories have a greater impact on recalling various events compared to visual or verbal memories (1). Rats extensively utilize their sense of smell, for instance, the odor of urine, for communication (2) . The scent of rodent urine is a rich source of information that can be explored in various processes, including the identification of other species, assessment of stress levels, age, sex, reproductive status, sexual experience, and different diseases (3).

In mate selection, which is one of the most important behavioral traits in animals, pheromones and scents play a significant role. Studies have shown that the urine of female rats contains attractive compounds for males that can stimulate neurons in the amygdala nucleus (2) . A high level of 2-heptanone, 4-methylphenol, and 4-ethylphenol in the urine of female wild rat compared to males attracts male attention (4). Male wild rat can distinguish between the scents of urine from males, females, and between females at different stages of the estrous cycle (5). Furthermore, female rats tends to prefer heavier males with larger testes and those with high testosterone levels for mating, demonstrating the ability to differentiate between males with high and low testosterone levels. The volatile compounds present in male rat urine activate the neurons in the amygdala of female wild rat; indeed, female rats use scents alone as a stable and strong factor for determining preference (6). Studies have shown that female rats prefer the odor of male rats urine and immature male rats urine to the scent of female rats, as well as the odor of healthy male urine to that of castrated males (7).

The basolateral amygdala (BLA) plays a crucial role in generating emotional responses, encoding information associated with emotional aspects, and in memory and learning processes, decision-making, fear, sexual behaviors, emotional responses, and preferential behaviors (8). This area primarily receives sensory information from the thalamus and cortex; the information is then processed by the basolateral complex, and its output is sent to the hippocampus, striatum, and central amygdala (9). Studies have confirmed the role of the BLA in conditioned sexual reward and in Vomero-nasal-olfactory rewards in males, which are related to the rewarding properties of female urine odor (10). Chemical ablation of the BLA in male rats leads to a significant reduction in sexual behaviors associated with conditioned visual cues (11). Indeed, alterations in sexual behaviors along with fear-related behaviors have been established as major indicators of severe amygdala damage in studies involving cats, monkeys, and rodents (12). Lesions in the basolateral amygdala lead to impairments in avoidance learning and neophobia responses; past studies have also demonstrated reduced learning and memory resulting from feeding behaviors in rodents with BLA dysfunction (13).

Various factors influence the performance of rodents in preferential behaviors and related learning, and the animal's relative preference for different odors, which typically affects their learning and memory, also impacts other behaviors. Therefore, the aim of the present study is to investigate the preferential behavior of male rats when exposed to the urine odor of female and immature wild rats, and the effect of basolateral amygdala lesions on olfactory preference and its associated learning, using a preference testing method.

Materials and Methods

Animals

In this experimental study, 16 adult male Wistar rats (n = 16), weighing an average of 200 to 250 grams, were obtained from the breeding and maintenance center for laboratory animals at Kerman University. The animals were housed in specific cages under conditions of 12-h light/12-h dark cycle at a temperature of (23 ± 2) degrees Celsius in the animal house of Shahid Bahonar University of Kerman, and had free access to water and food. Each animal was used only once, and ethical principles for working with laboratory animals were fully observed throughout all stages of the research (IR.UK.VETMED.REC.1398.018). Food and water were available ad libitum before behavioral testing, and no food deprivation protocol was applied because the study evaluated spontaneous olfactory preference rather than food-motivated behavior.

Experimental Groups

In this experimental study, the animals were randomly divided into three groups:

1. **Control group (Control):** This group did not undergo stereotaxic surgery or electrolytic lesioning and did not receive any drugs.
2. **Sham group (Sham):** This group underwent stereotaxic surgery, and electrodes were placed in the target area without creating any lesion.
3. **Basolateral Amygdala Lesion group (BLA-lesion):** This group underwent stereotaxic surgery, and their BLA region was electrically lesioned. After one week of recovery, they were tested.

Each experimental group consisted of 16 rats (Control, n=16; Sham, n=16; BLA-lesion, n=16).

Additionally, urine samples were collected from female rats in the proestrus stage to assess preferential behavior. Female urine was collected exclusively during the proestrus phase because this stage is associated with maximal estrogen secretion and the highest concentration of attractive urinary pheromones. Restricting urine collection to a single estrous stage reduced biological variability and ensured consistency among odor samples used in behavioral testing (4).

Stereotaxic Surgery and Electrolytic Lesioning

A stereotaxic apparatus was used to identify and electrically lesion the BLA region and to study the experimental groups. Initially, before surgery, the animals were anesthetized via intraperitoneal injection with a mixture of 10% ketamine and 2% xylazine. After anesthesia and fixation of the animal in the stereotaxic apparatus, the electrode for placement in the BLA was positioned in the appropriate location on the apparatus, and the zero coordinates of the apparatus in the anterior-posterior, lateral, and dorsal-ventral directions were noted.

Subsequently, the surgical site was disinfected with industrial alcohol, and then the hair in the area of interest was shaved with scissors and a clipper. The area was thoroughly cleaned with 70% alcohol, and the coordinates of bregma (the intersection of the frontal and parietal bones) and lambda (the intersection of the occipital and parietal bones) were measured. The coordinates of the vertical axis of the bregma and lambda points were also determined.

If the height of both points was the same, the coordinates of the BLA region were determined using the Paxinos-Watson atlas (14) and compared with the zero coordinates of the apparatus, and the corresponding coefficients were applied. A hole was drilled with a dental drill, and an electrode with a tip diameter of 125 µm (Teflon-coated stainless steel) was lowered to the depth of the target region using the stereotaxic apparatus. Then, an electrical current of 1.5 mA was applied to the BLA region for 7 seconds using an electrolytic lesion device(15) . After surgery and lesioning of the target area, the animals were kept in individual cages and allowed a one-week recovery period before being prepared for experimental tests.

Histological Verification of Lesions

Histological examination of the lesion was performed, just after decapitation, the rats' brain was removed and stored in 10% formalin for at least three days. Also, serial transverse sections (30 µm) were cut, and the lesion sites were determined according to a rat brain atlas (14).

Odor Preference Test

To evaluate the behavioral responses related to odor preference, urine samples from male and female Wistar rats, immature male rats (3-5 weeks old), and water as a neutral substance were used. Distilled water was selected as the neutral stimulus because it does not contain biologically relevant volatile compounds or pheromonal cues that could influence odor preference, thereby providing an appropriate control condition. Equal amounts of each were applied to a designated piece of cotton. In this study, to assess odor preference across different groups, a preference testing device for food, drug, and odor was employed.

This device consists of walls and a base made of black-colored Plexiglas, with dimensions of 30 × 60 × 60 cm (length × width × height), mounted on a movable platform and covered with a transparent Plexiglas lid. The device has four sides, each featuring a unique visual shape, including: a food access port (4 × 4 cm), a water access port (4 × 4 cm), and an odor port (2 × 2 cm). Each port can be covered with lids measuring 5 × 4 cm (for the food and water ports) and 3 × 2 cm (for the odor port) when necessary.

During the odor preference assessment, the number of visits to each port was recorded using infrared sensors. The duration of the animal's presence in each area and the distance traveled were measured and analyzed using four load cells symmetrically placed beneath the device, each corresponding to one area. Data were collected in real-time during the experiment and after its completion, saved as text files, and accessible through Notepad for review (16).

Protocol for Odor Preference Evaluation and Its Effect on Memory in Rats

After the recovery period following surgery, the rats were tested according to the following stages:

Habituation Stage

Two days before the main test, rats were allowed 15 minutes to freely explore all areas of the device. During this period, all ports were empty.

Testing Stage

- **First Phase:** A cotton swab soaked with male rats' urine odor was placed in position A of the device (this is the designated choice). The other ports remained empty and closed. The animal was released into the device from the central area without any specific orientation and was tested for 3 hours. At the end of the test, the number of visits, time spent in each area, and the distance traveled were recorded.
- **Second Phase:** After resting in its usual cage, the animal was tested again with a cotton swab soaked in female rats urine in position B, following exactly the same procedures. Data were recorded during the 3-hour period.
- **Third Phase:** Similarly, the cotton swab soaked in urine from immature rats was placed at position C, and the cotton soaked in water at position D, with all steps repeated exactly the same.

Final Phases

- **Phase 5:** All ports were left open, and all cotton swabs soaked with each type of urine or water were simultaneously presented in their previous designated ports (A with urine A, B with urine B, etc.). The animal's preference was observed based on which port it visited more.
- **Phase 6:** All ports were closed, without any stimuli present. The animal was placed in the device, and it selected a port based on visual cues above each port and the memory formed. The software recorded the number of visits, time spent, and distance traveled toward each olfactory port, thus assessing olfactory preference and related memory.

All behavioral experiments were performed during the light phase between 09:00 and 12:00 to minimize the influence of circadian rhythms on exploratory and olfactory behaviors.

Statistical analysis

Data are presented as means ± standard error of the mean. Statistical analysis comprised one-way analysis of variance followed by post hoc Tukey's test. The p-value < 0.05 was considered statistically significant.

Results

Data analysis revealed that the average number of visits to the areas associated with male and female urine odor significantly decreased ($p<0.01$ and $p<0.001$) in the BLA-lesioned group compared to the control group. However, there was no significant difference in the number of visits to the immature rat's urine area between the control and BLA-lesioned groups. In the control group, the number of visits to the area associated with female urine significantly increased ($P<0.05$) compared to the area associated with immature rats' urine. Conversely, in the BLA-lesioned group, visits to the immature rat's area showed a significant increase ($P<0.05$) compared to the areas with male and female urine odor (Figure 1).

The results showed that in the BLA-lesioned group, rats spent significantly less time in the area associated with the urine odor of immature rats, males, and females compared to the control group ($p<0.001$) (Figure 2). In the control group, the time spent in the area associated with the female urine odor showed a significant increase ($p<0.01$) compared to the immature rats and male urine areas. However, in the BLA-lesioned group, the most time was spent in the area with the urine odor of immature rats.

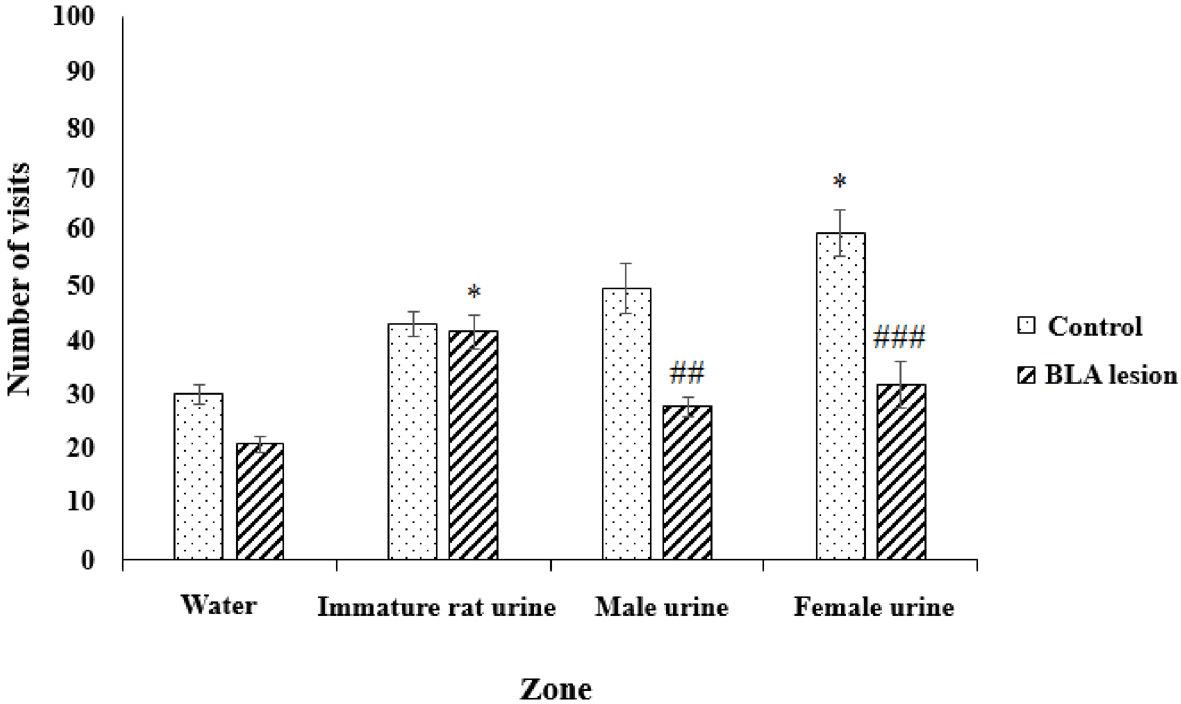

Figure 1. Comparison of the number of visits to the areas associated with male, female, and immature rat urine odor, and water, between the experimental groups. *p<0.05 compared to the immature rat urine odor in the control group, and ##p<0.01 and ###p<0.001 compared to the control group. The graphs are based on mean ± standard error (n=16).

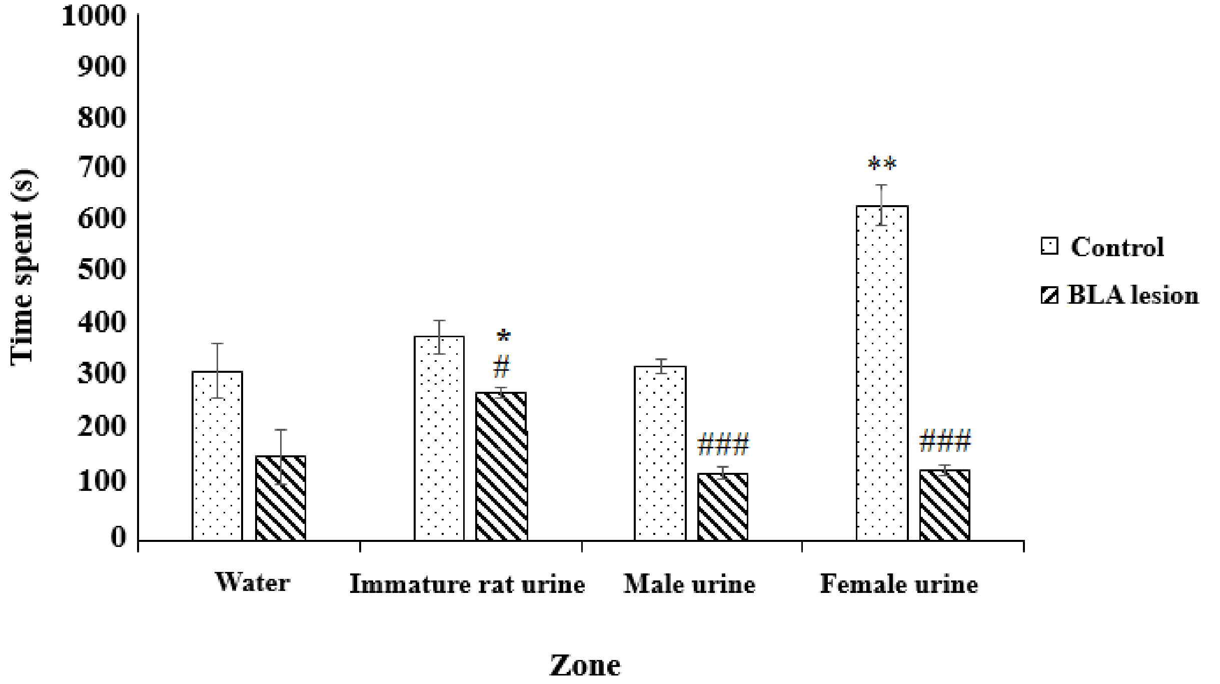

Figure 2. Comparison of the time spent in the areas associated with male, female, and immature rat urine odor, and water, between the experimental groups. **p<0.01 compared to the urine odor of immature rats and males in the control group, and *p<0.05 compared to the urine odor of male and female rats in the BLA-lesioned group. #p<0.05 and ###p<0.001 compared to the control group. The graphs are based on mean ± standard error (n=16).

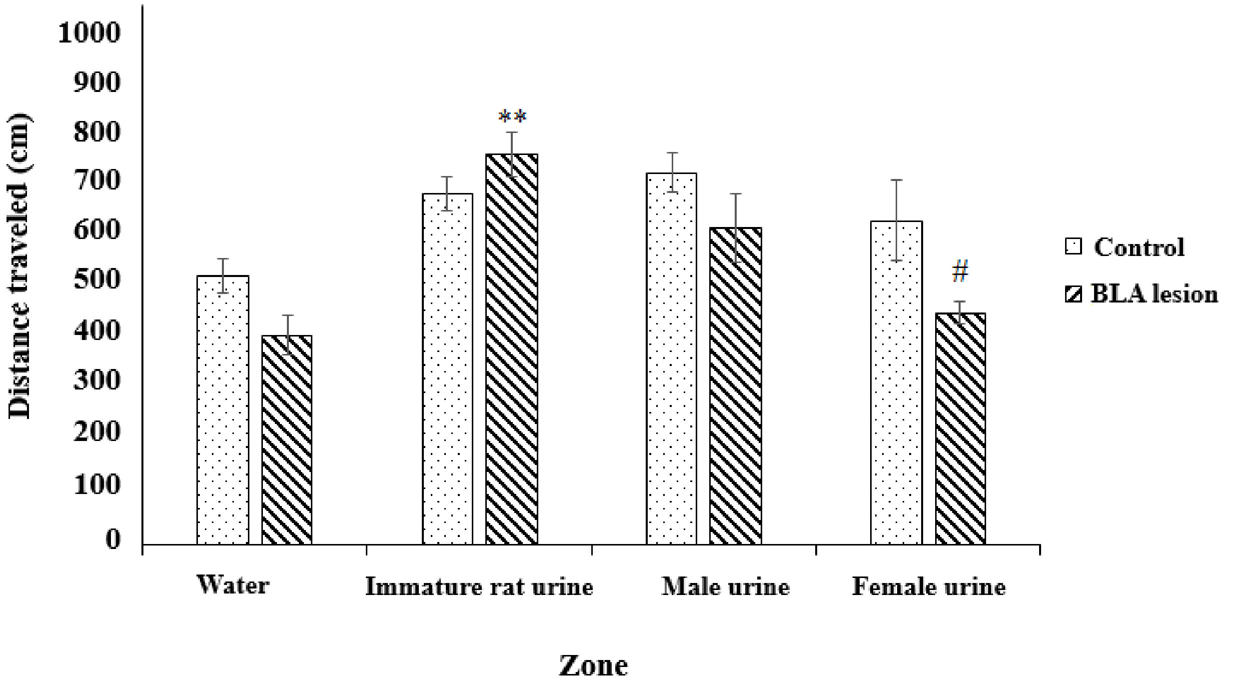

Figure 3. Comparison of the distance traveled in the areas associated with male, female, and immature rat urine odor, and water, between the experimental groups. **p<0.01 compared to the female urine odor in the BLA-lesioned group, and #p<0.05 compared to the control group. The graphs are based on mean ± standard error (n=16).

The mean distance traveled in the different areas is shown in figure 3. According to the figure, the distance traveled by the rats in the areas related to the urine odor of adult male rats, immature male rats' urine, and water did not show a significant difference between the lesioned and control groups, while the distance traveled in the female urine odor area in the BLA-lesioned group was significantly reduced ($p<0.05$) compared to the control group.

The total distance traveled by the animal is shown in Figure 4. The total distance in the BLA destruction group was significantly reduced compared to the control group ($p<0.01$).

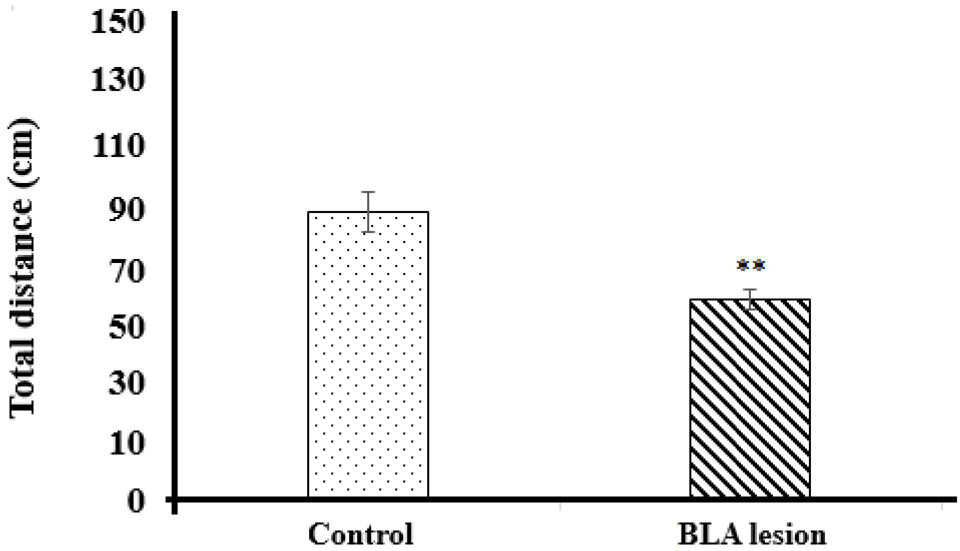

Figure 4. Comparison of the total distance traveled between the experimental groups. **p<0.01 compared to the control group. Graphs are plotted based on mean ± standard error (n = 16).

Comparison of the fifth stage of the experiment (where all odors were available to the animal) with the sixth stage (where all ports lacked olfactory stimuli) showed that the control group exhibited the highest preference for the odor of female urine. The greatest number of references and time spent in this group were related to the area with the odor of female urine. There was no significant difference between the fifth and sixth stages in the number of references and time spent in the control group, while in the BLA destruction group, a significant difference ($p<0.05$, $p<0.01$, and $p<0.001$) was observed between the fifth and sixth stages (Figure 5).

Discussion and Conclusion

In the present study, the effect of lesioning the basolateral amygdala on olfactory preference related to urine odor and its pheromones, which are actually the main and primary stimuli for inducing animal behaviors, including sexual, care-seeking, and territory-marking behaviors, was assessed in male rats using a new device and protocol. In this study, several parameters, including time spent, number of references, and distance traveled in each area, were measured as indicators of odor preference assessment. According to the results, the highest preference of the control group rats was for the odor of adult female rats urine, while the BLA-lesioned group showed the highest preference for the odor of immature male rat urine.

In this study, male rats preferred the urine odor of female rats to the urine odor of male rats, immature rats, and distilled water. These results are consistent with the research of Lydell et al. (1972) (17) Olfactory stimuli play an important role in the expression and modulation of sexual behaviors in rats, such that pheromones and olfactory stimuli that are naturally present in the urine of female rats are highly attractive to males (18). The odor of female urine increases luteinizing hormone levels and increases testosterone in male rats. It also increases the expression of Fos protein in brain structures, including the olfactory bulb, nucleus accumbens, preoptic area, stria terminalis, amygdala, and ventral tegmental area (19).

Urine odor provides important information about gender, health, social status, and reproductive status in rodents (20). Previous studies have shown that inactivation of the basolateral amygdala changes the spontaneous preference of female rats for the urine odor of other female rats, but BLA lesions do not generally impair the mouse’s ability to detect odors (20). Therefore, it cannot be said that the reason for the change in odor preference in the BLA-lesioned group in the present study is related to a disorder in odor perception. The animal’s olfactory preference generally changed in the lesion group, such that the highest preference in this group was for the odor of immature rats’ urine, or in other words, immature rats, which was completely different from the control group.

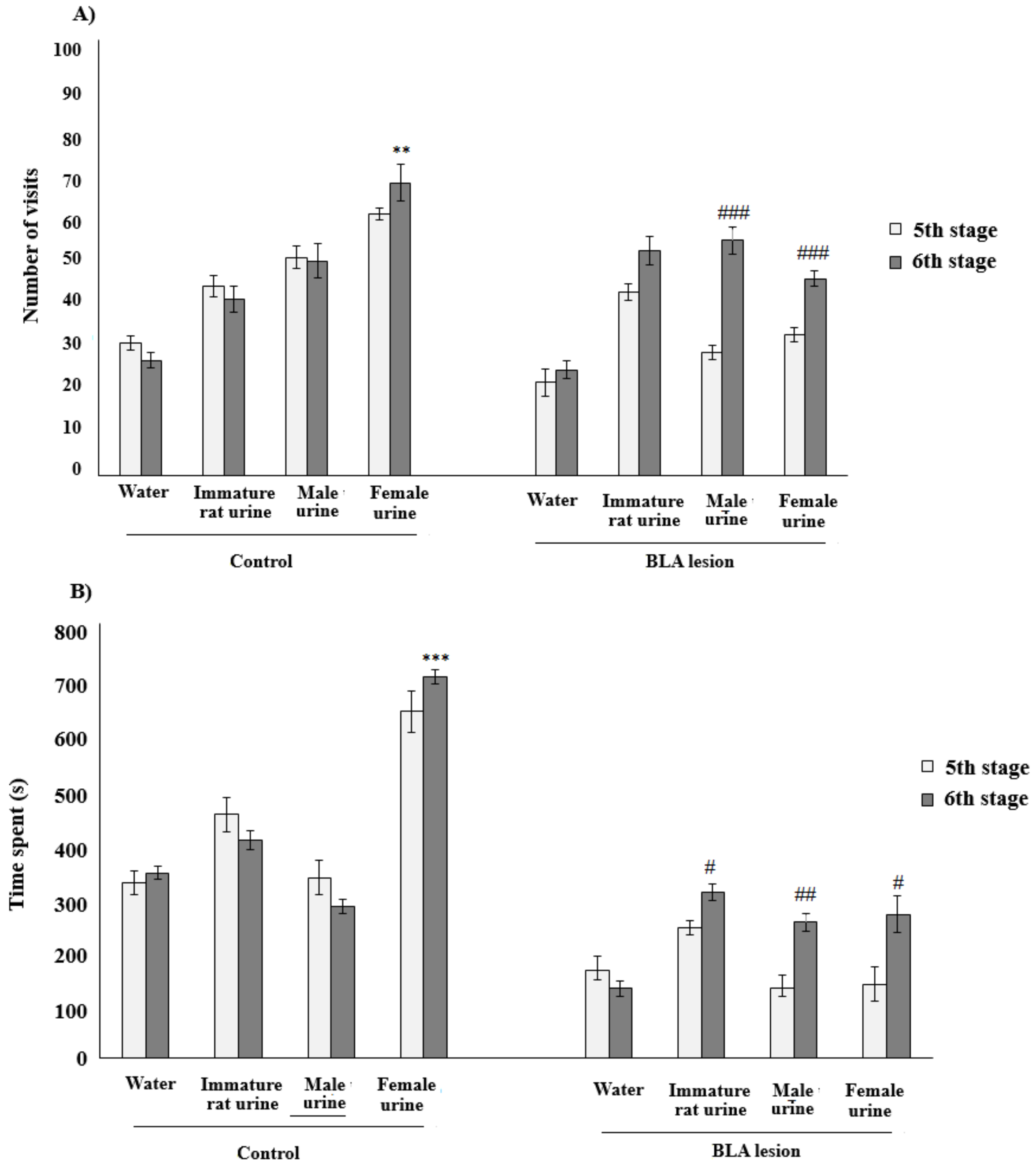

Figure 5. A) Comparison of the fifth stage (all odors were available to the animal) and the sixth stage (all ports were odorless) in the number of references B) and the time spent between the experimental groups. *p<0.01 and ***p<0.001 compared to the odor of immature rats' urine in the control group in the sixth stage, and #p<0.05, ##p<0.01, and ###p<0.001 compared to the fifth stage. Graphs are plotted based on mean ± standard error (n=16).

Although the BLA-lesioned rats exhibited a significant reduction in total locomotor activity, the observed changes in odor preference are unlikely to be explained solely by decreased exploratory behavior. If reduced locomotion were the primary determinant, a proportional decline in exploration across all odor compartments would be expected. Instead, the lesioned animals displayed a selective redistribution of odor preference, characterized by a marked reduction in preference for female urine together with a relative increase in preference for immature rat urine. Moreover, the number of visits to the immature urine compartment did not significantly differ from the control group despite the overall reduction in locomotor activity. These findings suggest that BLA lesion primarily altered the motivational and emotional processing of biologically relevant olfactory cues rather than producing a nonspecific reduction in exploratory behavior (20).

One possible explanation for this unexpected shift in odor preference is that the basolateral amygdala is critically involved in assigning emotional and motivational significance to biologically relevant sensory stimuli rather than in primary odor detection itself. The BLA integrates olfactory information received indirectly from the olfactory cortex and medial amygdala with contextual and reward-related information from the hippocampus and nucleus accumbens (21). Therefore, lesioning this structure may disrupt the normal evaluation of the rewarding value of female urinary pheromones while preserving basic olfactory perception.

Consequently, odors that are normally less preferred, such as those from immature rats, may become relatively more attractive because the neural circuitry responsible for assigning incentive salience to reproductively relevant odors has been impaired. In addition, the BLA has extensive reciprocal connections with the hypothalamus and other limbic regions involved in social and reproductive behaviors (22). Disruption of these pathways may alter the balance between approach and avoidance responses toward different social odors, resulting in the altered odor preference observed in the present study.

In one study, BLA lesions in postpartum female rats did not show any changes in their natural maternal behavior (23), but another study observed significant deficits in maternal behavior in female rats with BLA lesions (24). Lee et al. (1999) found that electrical lesioning of the BLA is associated with changes in paternal behavior and relatively minor deficits in maternal behavior. In the present study, lesioning this area increased the number of times male rats visited the port related to the odor of immature rats. It is obvious that here, both types of behavior exist in BLA-lesioned rats, but a change in the animal’s performance is seen in the behavioral tendency. In one study, electrical lesioning of the BLA in male rats led to neuronal damage and changes in paternal behavior, whereas in female rats, BLA lesioning reduced the activity of nerve fibers and, consequently, reduced offspring care behavior (25).

The role of the basolateral amygdala in sexual behaviors has been investigated in several studies, such that lesioning this area reduces sexual behaviors in male rats (26), which is consistent with the present study regarding the decreased preference for female urine odor in the BLA-lesioned male rats group. Olfactory information plays a very important role in sexual behaviors, such that lesioning the olfactory bulb reduces the participation of male and female rats in sexual activity (27). Amygdala lesions, especially of the basolateral amygdala, have been associated with abnormalities related to taste and olfactory behaviors (28), such that lesioning this nucleus leads to changes in food preference and also impairs memory (16). In the present study, persistent memory regarding the previous location of odors was also impaired in the BLA-lesioned group.

In the control group, after training in the last stage, where memory testing was based on matching visual cues with odors, male rats chose the area related to the odor of female urine, which they had previously preferred. In fact, according to the unique visual cues in each area, the rats in the control group, after the training stages, chose the area where their previously preferred odor was located. Learning based on visual cues is a proven phenomenon in rats (29), and this type of learning is also used in the Morris water maze system (30). One of the most important areas involved in memory is the hippocampus, and studies have shown that pyramidal neurons in the dorsal and ventral hippocampus increase activity (31). The basolateral amygdala is an important region for memory formation, such that lesioning this area impairs memory, as in the present study, the BLA-lesioned groups failed to retrieve information in the memory test stage in the parameters of time spent and number of references to the target area. The interaction between the BLA and the hippocampus is necessary for social behaviors and memory. In fact, the transfer of information between these areas is necessary for stabilizing memories, and at this time, the population of neurons increases in these sections simultaneously with the recall of memories (32).

The impairment of odor-associated memory observed following BLA lesion may also be related to disruption of functional interactions between the basolateral amygdala and the hippocampus. Previous studies have demonstrated that the BLA modulates hippocampal-dependent memory processes through extensive anatomical and functional connections. The hippocampus plays a critical role in encoding spatial and contextual information, whereas the BLA contributes to assigning emotional and motivational significance to sensory experiences. Coordinated activity between these two regions facilitates the consolidation and retrieval of biologically relevant memories. Therefore, damage to the BLA may weaken hippocampal processing of odor-location associations, resulting in the impaired memory performance observed in the present study (21).

In this study, using a new and multi-purpose device and protocol to investigate olfactory preference behavior, considering multiple parameters, including time spent, number of references, and distance traveled in each area, we found that, consistent with previous studies, male rats showed the highest preference for the urine of female rats, while lesioning the basolateral amygdala led to a change in olfactory preference behavior in male rats and also their memory, such that the olfactory preference of male rats generally changed, and they showed the highest preference for the odor of immature rats.

One limitation of the present study is the use of electrolytic lesions to disrupt the basolateral amygdala. Unlike excitotoxic lesions, electrolytic lesions may damage not only neuronal cell bodies but also fibers of passage traversing the target region (33). Therefore, although the present findings strongly support the involvement of the basolateral amygdala region in olfactory preference and related memory, some of the observed behavioral alterations may also reflect disruption of neural pathways passing through this area (21). Future studies using more selective approaches, such as excitotoxic lesions, chemogenetic, or optogenetic techniques, are needed to further define the specific contribution of basolateral amygdala neurons.

The present findings provide further evidence that the basolateral amygdala contributes to the integration of emotionally relevant olfactory information with memory processes. These results may facilitate future investigations into the neural circuits underlying social odor processing, pheromone-guided behaviors, and neuropsychiatric disorders characterized by impaired olfactory function and emotional memory (21). Future studies employing selective neuronal manipulation techniques and functional neural circuit analyses may further clarify the specific mechanisms through which the BLA regulates odor-guided behavior.

In summary, it can be said that the basolateral amygdala nuclei play a key role in the preference and learning of information resulting from the chemical compounds of urine, especially pheromones, in rats. Discovering the exact mechanism of this phenomenon in rats requires the design and implementation of complementary research.

Author Contributions

M. Zamyad and M. Abbasnejad contributed 34% and 33%, respectively, to the conceptualization, methodology, supervision, formal analysis, and writing original draft. S. Esmaeili Mahani, A. Mohammadpour Rahimi, and S. Fazlabadi contributed equally (11% each) to methodology, investigation (data collection), writing review & editing, and final approval. All authors gave their final approval to the submitted manuscript.

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Data availability

The data supporting the findings of this study are available from the corresponding author upon reasonable request

Consent for publication

All authors have read and approved the final version of the manuscript and have given their consent for its publication.

Conflict of interest

The authors declare that there is no conflict of interest.

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Artificial intelligence (AI)-assisted technology

Artificial intelligence (AI) was used to assist with the paraphrasing and rewriting of sentences and to improve the scientific language and overall clarity of the manuscript.

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