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Sujith Swarna April 8, 2019

The Role of the Amygdala in Memory for Social and Nonsocial Odors

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Abstract

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Background: The basolateral amygdala (BLA) plays a key role in memory enhancement for emotional events. However, it is unclear how the BLA plays a role in modulating affective salience or the motivational significance of a stimulus to an individual. Because social information carries more affective salience than nonsocial information, the BLA may play a role in the prioritization of social information but not nonsocial information.

Purpose: The purpose of this project is to investigate the relationship between the BLA and social recognition memory. The project also assesses the role of the BLA in preferences for social stimuli.

Methods: A group of nine female Long Evans rats performed novel odor recognition tasks using other female social odors or nonsocial odors. These subjects also performed in a habituation-dishabituation task to new female social or nonsocial odors. Finally, preference tests were conducted to assess the preferences of these females for a) female social and nonsocial odors and b) female social and male social odors. Prior to each of these tasks, the BLAs of these subjects were infused with either muscimol or saline.

Results: Two-tailed paired-samples t-tests suggest that BLA inhibition may result in impairment of recognition memory performance in nonsocial trials on the NOR task. Three-way repeated measures ANOVA showed a significant effect of trial number in the habituation-dishabituation task as well as a significant interaction of trial number and odor type. Finally, two-tailed one-sample t-tests suggested no preference for female social odors over nonsocial odors in the preference test, but a strong preference for male odors over female odors. A two-tailed paired-samples t-test found that BLA inhibition significantly increased male preference.

Conclusion: The affective salience of an object is one of the primary influences of exploratory behavior in rodents. As such, levels of exploration serve as a good measure of the affective salience of a stimulus. This project suggests that BLA inhibition results in dysregulation of affective salience attribution that causes the rodents to explore objects abnormally more or less than they typically would.

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Introduction

The Prioritization of Memory

From a memory perspective, not all stimuli are equal. Certain types of information are processed and stored more easily than other types of information. In particular, some studies suggest that information relevant to promoting overall fitness is prioritized over comparatively neutral or random information (Kang et al., 2008; Nairne et al., 2007; Öhman and Mineka, 2001). This phenomenon allows for organisms to acquire and retain important information relevant to food storage, mating, and normal social functioning (Clayton, 1995; Kim et al., 2012; Klein et al., 2009).

The Amygdala and Emotional Memory

Details regarding emotional events tend to be remembered more vividly and distinctly than neutral events (Bohannon, 1988; Brown and Kulik, 1977; Cahill and Mcgaugh, 1995; Christianson and Loftus, 1990). This effect is thought to occur due to an enhancement in encoding, consolidation, and retrieval processes (Kensinger, 2009). Arousing information tends to capture and hold attention more than non-arousing information, aiding in the encoding process (Carretié et al., 2001, Christianson et al., 1991). In consolidation, arousal assists in the construction of more durable memories that are less resistant to memory decay (Labar and Phelps, 1998; Cahill, 2003). Emotional arousal also influences the prioritization of information retrieval and consequent decision-making (Damasio, 1994; Koenigs and Tranel, 2007).

The amygdala, an emotion-processing center in the brain, is heavily involved in the enhancement of all three of these processes (Richardson et al., 2004; Mcgaugh, 2002; Smith et al., 2006). However, while emotion can enhance memory via the amygdala, these memory

enhancement processes can occur independently of emotional events through different mechanisms than those underlying the subjective emotional experience (Inman et al., 2017). Indeed, a component of emotion called affect is sufficient to engage the amygdala (Fitzgerald et al., 2006; Garavan et al., 2001). Affect refers to the motivational significance of a stimulus that elicits somatic changes in the organism and consists of two primary dimensions: level of arousal and valence, the pleasantness or averseness of a stimulus (Russell, 1980). Emotion refers to the organism's perception of and behavioral responses to these changes.

Studies have shown that greater affective salience of a stimulus correlates with greater amygdala activation and concurrently greater memory for that stimulus (Dolcos et al., 2004; Hamann et al., 1999; Sharon et al., 2004). Furthermore, direct stimulation of the amygdala via either pharmacological agents or direct electrical stimulation has been shown to enhance memory for specific objects (Barsegyan et al., 2014; Inman et al., 2017; Bass et al., 2012). However, the amygdala has more than a supplementary role in affective-dependent memory benefits; it is essential to it. Indeed, patients with selective bilateral amygdala damage have been shown to demonstrate impairment of the acquisition of affective-dependent memory (Adolphs et al., 1997). Specifically, inhibition of the basolateral amygdala (BLA) eliminates this affective-dependent benefit and electrical stimulation further enhances it (Inman et al., 2017; Roozendaal and Mcgaugh, 1997).

The Amygdala and Social Cognition

However, artificial stimulation of the BLA does not necessarily reflect its function in the natural world. While emotional stimuli do carry affective salience, there are a number of other stimuli that do so as well. Several studies suggest the existence of a network designed to specifically process social cues, information obtained from conspecifics (Greene et al., 2009;

Harris et al., 2007; Song et al., 2016; Wood et al., 2003). The amygdala is thought to play a role in that network. Individuals with abnormal amygdala functioning, as in the cases of individuals with autism and patient SM, demonstrate impaired social information processing (Adolphs et al., 1994; Baron-Cohen et al., 2000). Certain social cues, like facial expressions for humans and chemosignals for rodents, have been found to differentially activate different parts of the amygdala (Leonard et al., 1985; Meredith et al., 2008; Mujica et al., 2009; Rutishauser et al., 2011). In particular, neurons in the BLA selectively respond to social cues and infusion of certain pharmacological agents into this area induces anxiety in tests that measure social interaction (Gonzalez et al., 1996; Peterson and Wenstrup, 2012; Sajdyk and Shekhar, 1997).

The current study aimed to address the question of what role the BLA plays in the prioritization of social information. We hypothesized that, due to the dual nature of the BLA in processing certain social cues and enhancing memory, the BLA may play a role in modulating social recognition memory. We predicted that inhibition of the BLA of female rats during a modified version of the novel object recognition task would impair recognition memory for social cues, cues that carry information between conspecifics, but not nonsocial cues, neutral cues that do not carry relevant information. Because GABAergic influences exist within the BLA, we used muscimol, a $GABA_A$ agonist, to inhibit it (Berlau and Mcgaugh, 2006; Helmstetter and Bellgowan, 1994; Mcdonald 1985; Wellmann et al., 2005). We also hypothesized that social stimuli were so salient to our subjects that they would require more time to habituate to those odors compared to the nonsocial odors. We predicted that the habituation rates of our rats to social odors in a habituation-dishabituation test would be lower than their habituation rates to nonsocial odors and that the BLA modulated the social habituation rates. Specifically, we predicted that inhibition of the BLA would increase the habituation rates to the

social odors, but not nonsocial odors. Finally, we conducted two separate preference tests to assess the preferences of our female subjects for social versus nonsocial odors and for male social versus female social odors. We hypothesized that the BLA modulated the processing of information most salient to our subjects: social in the first test and male social in the second. We predicted that BLA inhibition would decrease their overall interests in these respective scents.

Experiment 1

Method

Subjects

Subjects consisted of nine adult female Long Evans rats from Charles River Laboratories initially pair-housed in rectangular polycarbonate cages in the same cubicle. Subjects were individually housed for Experiments 2-4 as some had begun to gnaw on their cage mates guide cannula. We used female rats as subjects to avoid aggression-motivated or reproduction-motivated behaviors that are inherent to male-male and male-female interactions (Taylor et al., 1987). Access to food and water was unrestricted. All subjects were on a 12-hour light/dark cycle and all behavioral testing occurred during the light cycle. All studies were approved by Emory University's Institutional Animal Care and Use Committee, and all experimenters were on the following IACUC protocol: 201700501.

Surgeries

General anesthesia was induced and maintained by isoflurane (1-2%) mixed with oxygen. Pre-operative subcutaneous injections of buprenorphine (0.03mg/kg) were provided. The subjects were then placed in a stereotaxic frame and their scalps excised. Anchor screws were inserted and guide cannula implanted in the BLA (Coordinates: A/P -3.5mm, M/L 5.1mm, D/V -

8.9mm). Subjects received post-operative subcutaneous injections of buprenorphine (0.05mg/kg) and Metacam (1mg/kg) immediately after the surgery. Subjects were also provided subcutaneous injections of buprenorphine (0.05mg/kg) up to 3 days after surgery and Metacam (1mg/kg) 1 day after surgery. Subjects were given at least seven days of rest to recover before testing.

Olfactory Stimuli

To assess social recognition memory, many studies have used other conspecifics instead of objects in the NOR (Engelmann and Landgraf, 1994; Popik et al., 1992). However, this method introduces a number of variables that may not necessarily be social-related but could still activate the amygdala. For example, animate objects tend to garner more attention than inanimate objects leading some to suggest a possible involvement of the amygdala (Calvillo and Hawkins, 2016). To control for this along with several other potential confounds like the sociability of the conspecific being explored, we decided to use odors rather than objects or conspecifics in our NOR.

The highly sensitive olfactory system in rodents is a powerful tool to use in studying memory (Eichenbaum, 1998). Some studies have used odors to assess recognition memory in rodents (Feinberg et al., 2012; Ramus and Eichenbaum, 2000). In the Feinberg study, the researchers used spices for their nonsocial odors. Similarly, for our experiment, we used aromatherapy oils for our nonsocial odors, which presumably were interesting to our rodents but did not carry social information. For our social odors, we used urine from other rats. Rats can acquire a wealth of information from the urine of other rats including their sex, reproductive status, and health status (Beynon and Hurst, 2004). As such, rats are capable of discriminating between the urine odors of different individuals (Brown, 1988).

All stimuli were presented on 1 1/4 ” wooden blocks. All subjects were habituated to the wooden blocks before testing to ensure any exploration observed was elicited by the odors on the blocks rather than the blocks themselves. Nonsocial odors consisted of 1% dilutions of various aromatherapy oils in mineral oil from spectrum chemical MFG. CORP, New Brunscwick, NJ. 4uL of the diluted compound was then pipetted on to each face of the block shortly before testing. Social odors were collected by retrieving urine from female Sprague Dawley and Long Evans rats completely isolated from the subjects. Within trials, donor urine was paired with donor urine from the same strain of rat. 4uL of each urine sample were pipetted on to each face of the block shortly before testing.

Infusions

All infusions were performed in rats briefly anesthetized with isoflurane (1-2%). A volume of either 1uL muscimol (0.5ug/uL) or saline was infused bilaterally and simultaneously into the BLA at a rate of 0.25uL/min to ensure the BLA would be sufficiently inactivated if muscimol was present (UltraMicroPump; World Precision Instruments, Sarasota FL). As the lab has done in the past, infusion needles remained in place for an additional 2 minutes following the infusion before being removed to ensure the full volume had been infused (Bass et al., 2014). Behavioral testing began 30 minutes after infusion.

Behavioral Testing

To assess recognition memory, we used a modified version of the commonly used novel object recognition task (NOR) (Antunes and Biala, 2011). When presented with a novel object and a familiar object that was previously presented, many animals, including rats, tend to explore the novel object more (Ennaceur, 2010). As mentioned previously, for our paradigm, we used different odors rather than different objects to assess memory in a group of female Long Evans

rats.

To assess the role of the BLA in social and nonsocial recognition memory, the female subjects performed the NOR. Before beginning the NOR, the rats were infused with either saline or muscimol. The NOR consisted of two phases - Study and Test – which were separated by either a very short delay or a 5-minute delay. Both phases took place in the same rectangular polycarbonate cage. During the Study phase, two wooden blocks, both containing either a social (female) or nonsocial odor, were presented in opposite corners of the cage. The rats were allowed two minutes to explore these blocks making them familiar. During the Test phase, two new wooden blocks were placed in the same positions as the previous wooden blocks. One block was scented with the previously presented odor (familiar) and the other was scented with a novel odor. The rats were again allowed to explore for two minutes. The location of the novel and familiar odors was counterbalanced during the Test phase.

Behavioral Scoring and Data Analysis

All experiments were recorded on video and scored using BORIS, an event logging software (Friard and Gamba, 2016). Exploration time consisted of solely sniffing and whisking time directed towards the stimuli. Biting, gnawing, and playing with the block were not considered to be exploration. One-sample t-tests and paired-samples t-tests were conducted using IBM SPSS Statistics 24.

Results

To assess memory performance on the NOR, a discrimination index (DI) was used. DI = ((novel-familiar)/total exploration time)*100. A DI of 0 would represent no evidence of memory, while more positive DIs would represent better memory. Figure 1 shows the mean DI scores for

the social and nonsocial odors in the immediate tests. In the control (PBS) condition, rats appeared to demonstrate recognition memory performance for nonsocial odors, though this performance was not statistically significant (mean DI ± SEM = 27.32 ± 14.84, one-sample t-test versus chance (DI = 0 ± 0): $t(8) = 1.84$, $p = 0.10$, $d = 0.61$). In the muscimol condition, rats demonstrated robust performance (mean DI ± SEM = 39.59 ± 9.71, one-sample t-test versus chance (DI = 0 ± 0): $t(8) = 4.08$, $p = 0.004$, $d = 1.36$), though there was no statistically significant difference between their performance in both conditions (paired-samples t-test versus chance: $t(8) = 0.72$, $p = 0.49$, $d = 0.24$). Rats did not perform well on social trials in the control condition (mean DI ± SEM = 6.30 ± 10.87, one-sample t-test versus chance (DI = 0 ± 0): $t(8) = 0.58$, $p = 0.58$, $d = 0.19$) as well as in the muscimol condition (mean DI ± SEM = 18.51 ± 11.37, one-sample t-test versus chance (DI = 0 ± 0): $t(8) = 1.63$, $p = 0.14$, $d = 0.54$). There was no significant difference between their performance in both conditions (paired-samples t-test versus chance: $t(8) = 0.82$, $p = 0.44$, $d = 0.27$). Figure 2 shows the mean DI scores for the social and nonsocial odors in the 5-minute recognition memory test. In the control condition, rats demonstrated robust recognition memory performance for nonsocial odors (mean DI ± SEM = 39.17 ± 13.49, one-sample t-test versus chance (DI = 0 ± 0): $t(8) = 2.90$, $p = 0.02$, $d = 0.97$). In the muscimol condition, the performance of the rats was low (mean DI ± SEM = 4.86 ± 12.45, one-sample t-test versus chance (DI = 0 ± 0): $t(8) = 0.39$, $p = 0.71$, $d = 0.13$) but not significantly different from their performance in the control condition (paired-samples t-test versus chance: $t(8) = 2.01$, $p = 0.08$, $d = 0.67$). Rats did not perform well on social trials in the control condition (mean DI ± SEM = 15.14 ± 17.25, one-sample t-test versus chance (DI = 0 ± 0): $t(8) = 0.88$, $p = 0.41$, $d = 0.29$) and in the muscimol condition (mean DI ± SEM = 21.28 ± 15.31, one-sample t-test versus chance (DI = 0 ± 0): $t(8) = 1.39$, $p = 0.202$, $d = 0.46$) There was no statistically

significant difference between their performance in both conditions (paired-samples t-test versus chance: $t(8) = 0.31$, $p=0.76$, $d = 0.10$).

Interim Discussion

We conducted the immediate test to ensure that muscimol was not affecting the capacity of our rats to smell other odors. Because it was not a particularly challenging memory task, we did not expect to see any effects of muscimol in this test. As such, our prediction was that memory performance would be robust and high in the immediate test across all trials and equivalent between muscimol and control conditions. We also conducted the 5-minute test, as it was a more accurate measure of memory performance. We predicted a lower DI for rats in the muscimol condition undergoing social trials but not nonsocial trials.

Although, when in the control condition for the immediate test, rats did not perform above chance in the nonsocial trials, their robust performance in the 5-minute test suggests that the experiment may not have had enough power to fully observe that effect in the immediate test. In the 5-minute test, we observed a downward trend in memory performance for subjects in the muscimol condition in the nonsocial trials, suggesting that BLA inhibition may have a general effect on memory itself. It is difficult to extend any of these conclusions to the social trials as rats in the control condition in both the immediate and 5-minute tests did not discriminate between novel and familiar odors. Interestingly, overall exploration time was about equal in the social and nonsocial trials. This led us to hypothesize that the rats may require more time to habituate to social scents than nonsocial scents.

Experiment 2

Method

To determine whether rats habituate more slowly to social scents than nonsocial scents and to determine the role of the BLA in this habituation, we conducted a habituation-dishabituation test (Rankin et al., 2009). In this paradigm, subjects are repeatedly exposed to the same stimulus over a fixed number of trials. During this time, it is expected that the subjects will demonstrate decreased interest in the stimulus over the course of these trials. In the final trial, a new stimulus is introduced. Subjects tend to explore this new stimulus much more than the repeatedly presented stimulus in the previous trial.

The same female subjects were used in this paradigm. The infusion protocol used was the same as in Experiment 1. In this task, a trial consisted of exposure to a single wooden block scented with either a social or nonsocial odor. Rats were allowed to explore each block for up to 1 minute before beginning the next trial. The first 5 trials consisted of exposure to blocks freshly scented with the same social or nonsocial odor. In the 6^{th} (novel) trial, the rats were presented with another block scented with a new social or nonsocial odor and again allowed to explore up to 1 minute.

Using IBM SPSS Statistics 24, three-way (odor type; infusion condition; habituation/dishabituation trial number) repeated measures ANOVA were separately performed on the data for all 6 trials and the first 5 trials (habituation phase) and a two-way (odor type; infusion condition) repeated measures ANOVA was performed on the data for the 6^{th} trial (dishabituation).

Results

Figure 3 shows the average exploration time of the rats for the social and nonsocial odors on the habituation-dishabituation task. For the analysis of all 6 trials, the three-way repeated measures ANOVA did not reveal any statistically significant main effect due to odor type (social versus nonsocial; $F(1,8) = 0.002$, $p = 0.97$, $\eta_p^2 = 0.0003$). No main effect was observed for treatment (muscimol versus PBS; $F(1,8) = 1.33$, $p = 0.28$ $\eta_p^2 = 0.14$). There was a significant main effect observed due to trial ($F(5,40) = 11.002$, $p = 0.000001$, $\eta_p^2 = 0.579$). There was a significant interaction between odor type and trial ($F(5,40) = 2.52$, $p = 0.05$, $\eta_p^2 = 0.239$). There was no significant interaction between odor type and treatment ($F(1,8) = 0.006$, $p = 0.94$, $\eta_p^2 = 0.001$) and between treatment and trial ($F(5,40) = 0.46$, $p = 0.80$, $\eta_p^2 = 0.06$). Finally, there was no observed interaction of all three variables ($F(5,40) = 0.79$, $p = 0.56$, $\eta_p^2 = 0.09$).

For the analysis of the first 5 trials, the three-way repeated measures ANOVA revealed no significant main effect due to odor type ($F(1,8) = 0.05$, $p = 0.830$, $\eta_p^2 = 0.01$) or treatment ($F(1,8) = 2.07$, $p = 0.19$, $\eta_p^2 = 0.21$), though there was a significant main effect due to trial ($F(4,32) = 7.92$, $p = 0.0001$, $\eta_p^2 = 0.50$). There was also a significant interaction between odor type and trial ($F(4,32) = 3.73$, $p = 0.01$, $\eta_p^2 = 0.32$). There was no significant interaction between odor type and treatment ($F(1,8) = 0.12$, $p = 0.74$, $\eta_p^2 = 0.02$) or between treatment and trial ($F(4,32) = 0.76$, $p = 0.56$, $\eta_p^2 = 0.09$). Finally, there was no observed interaction of all three variables ($F(4,32) = 0.58$, $p = 0.68$, $\eta_p^2 = 0.07$).

For the analysis of the final trial, the repeated measures ANOVA revealed no significant effects due to odor type (($F(1,8) = 0.25$, $p = 0.63$, $\eta_p^2 = 0.03$) or treatment ($F(1,8) = 0.37$, $p = 0.56$, $\eta_p^2 = 0.04$). There was no observed interaction between odor type and treatment ($F(1,8) = 0.85$, $p = 0.38$, $\eta_p^2 = 0.10$).

Interim Discussion

As expected, the rats habituated to both social and nonsocial scents in the first 5 trials normally. We also observed differences in habituation rates that depended on the type of odor presented but were independent of the treatment provided. Dishabituation was unaffected by odor type and treatment, indicating that the rats were still capable of discriminating between both social and nonsocial odors and could demonstrate memory for an odor previously presented. Contrary to our hypothesis, BLA inhibition appeared to have no effect on exploration time at any point in the task. However, it is possible that we were not able to observe the BLA's effects because of the differences in exploration times between nonsocial and social presentations on the first trial. Indeed, the rats appeared to explore the nonsocial odors much more than the social odors. Because we had initially hypothesized that social odors would carry more affect than nonsocial odors, we expected more exploration of the social odors. To directly compare the subjects' interests in social versus nonsocial odors, we conducted a preference test.

Experiment 3

Method

To assess the role of the BLA in the female subjects' preferences for social versus nonsocial odors, we conducted a preference test. Two blocks, one scented with a nonsocial odor and the other with a social (female) odor, were placed on opposite sides of a rectangular polycarbonate cage. The infusion protocol for muscimol and saline was the same as outlined in the previous two experiments. One-sample t-tests and paired-samples t-tests were conducted using IBM SPSS Statistics 24.

Results

In experiment 3, another discrimination index was created to assess the effects of muscimol on social preference. DI=((social-nonsocial)/total exploration time)*100. A DI of 0 would represent no preference for either type of odor. A more positive DI would represent greater social preference, while a more negative DI would represent greater nonsocial preference. Figure 4 shows the mean DI preference scores for social and nonsocial odors. Subjects demonstrated no preference for social odors in the control condition (mean DI ± SEM = -2.32 ± 13.27, one-sample t-test versus chance (DI = 0 ± 0): $t(8) = 0.18$, $p = 0.87$, $d = 0.06$), but showed a slight increase in nonsocial interest when in the muscimol condition (mean DI ± SEM = -16.70 ± 11.20, one-sample t-test versus chance (DI = 0 ± 0): $t(8) = 1.49$, $p = 0.17$, $d = 0.50$), though there was no statistically significant difference between performance in the two conditions (paired-samples t-test versus chance: $t(8) = 0.85$, $p = 0.42$, $d = 0.28$).

Interim Discussion

We hypothesized that social stimuli carry more affective salience than nonsocial stimuli. Consequently, we predicted that, when given the choice between a social and nonsocial stimulus, the rats would interact with the social stimulus more. Contrary to our prediction, we found there appeared to be no preference for either of the stimuli. However, BLA inhibition did appear to slightly increase interest in the nonsocial stimuli. One potential issue with this experiment is that the subjects may demonstrate high interest in the nonsocial odors because they have little to no ecological relevance to them. Both odors were explored for a high duration but possibly for different reasons. To more accurately observe the effects of BLA inhibition on stimuli that carry affective salience, we exposed our subjects to two types of stimuli that we hypothesized carried affective salience but varied greatly in their biological relevance to the subjects: male urine and

female urine.

Experiment 4

Method

To assess the role of the BLA in the female subjects' preferences in male versus female donors, the rats performed a preference test. Two blocks, one scented with Long Evans male urine and the other with Long Evans female urine, were placed on opposite sides of a rectangular polycarbonate cage. The infusion protocol for muscimol and saline was the same as outlined in the previous experiments. The rats were allowed to explore the blocks for a total of 2 minutes. One-sample t-tests and paired-samples t-tests were conducted using IBM SPSS Statistics 24.

Results

To assess the role of the BLA in male vs. female preference, a discrimination index (DI) was used. DI = ((male-female)/total exploration time)*100. A DI of 0 would represent no preference for either type of odor. A more positive DI would represent greater male social preference, while a more negative DI would represent greater female social preference. Figure 5 shows the mean DI preference scores for male social and female social odors. In the control condition, subjects demonstrated a strong preference for male odors (mean DI ± SEM = 41.63 ± 9.53, one-sample t-test versus chance (DI = 0 ± 0): $t(8) = 4.37$, $p = 0.002$, $d = 1.46$). In the muscimol condition, subjects showed even higher male preference (mean DI ± SEM = 63.55 ± 6.90, one-sample t-test versus chance (DI = 0 ± 0): $t(8) = 9.21$, $p < 0.0001$, $d = 3.07$). There was a significant difference between performances in both conditions (paired-samples t-test versus chance: $t(8) = 2.49$, $p = 0.04$, $d = 0.83$).

Interim Discussion

We hypothesized that the BLA modulated attention to more salient stimuli, in this case, male social odors. Therefore, we predicted that by inhibiting the BLA we would see a decreased interest in male social odors. Instead, we found the opposite result. BLA inhibition resulted in increased interest in male social odors. Analysis of the raw exploration times showed that interest in female social odors, by contrast, was unaffected.

General Discussion

In Experiment 1, we predicted that BLA inhibition would impair social recognition memory. Contrary to our hypothesis, subjects in the muscimol condition demonstrated what appeared to be impaired recognition memory performance for nonsocial odors as soon as 5 minutes after the initial presentation. We also did not observe evidence of recognition memory for social odors for subjects in the control condition at both the immediate and 5-minute tests, and BLA inhibition did not appear to alter that result. Because of the absence of the subjects' abilities to discriminate between novel and familiar odors even in the control condition, we hypothesized that the rats may have required more time to habituate to social odors. The results of Experiment 2 demonstrate that there were indeed differences in habituation that depended on the type of stimulus (social or nonsocial) presented. Experiment 2 also showed that, regardless of treatment, the rats explored the nonsocial odors more than the social odors on the first trial of the habituation-dishabituation test, suggesting a difference in initial interest in the two stimuli. Therefore, we conducted Experiment 3 to directly assess their preferences for the two odors. We predicted that the rats would explore the social odors more than the nonsocial odors and BLA inhibition would decrease their social interest. Interestingly, Experiment 3 showed the subjects in

the control condition demonstrated equal preference for social odors and nonsocial odors that was only slightly biased towards nonsocial odors upon BLA inhibition. To directly compare preferences for two social odors that we knew differed in biological relevance and, consequently, affective salience to the subjects, we conducted Experiment 4 in which we observed the rats' preferences for male versus female odors. We predicted that the subjects would show more interest in male odors and that BLA inhibition would decrease that interest. In fact, we found that subjects in the control condition indeed had a high preference for male odors over female odors. However, contrary to our hypothesis, BLA inhibition only increased that preference. In general, the results of each of these experiments did not support most of our a priori hypotheses.

It is possible that the phenomena observed were not specific to memory per se. While memory enhancement is one of the functions of the BLA, it is only one of the many. Inactivation of this region prevents that memory benefit but also disrupts its other physiological roles. One of these other roles includes decision-making. The decision to explore an object is an active one motivated by a goal. Several studies demonstrate that the BLA encodes the incentive value or motivational significance of a stimulus (Schoenbaum et al., 1999; Winstanley et al., 2004). Indeed, the BLA has been found to play a role in reward-seeking behavior. Via projections to the nucleus accumbens, excitation of the BLA promotes reward-seeking behavior (Ambroggi et al., 2008). Consequently, inhibition of the BLA may result in dysregulation of affective salience attribution. Each of the previously described experiments required the rats to demonstrate preferential interest in the different stimuli presented. Higher exploration of a stimulus suggests that that stimulus has more affective salience or motivational significance to the rat exploring it. In a typical NOR, rats prefer to explore novel objects more than previously presented ones. However, if inhibition of the BLA disrupts the attribution of salience to that novel stimulus, one

would not expect to see the rats discriminate between familiar and novel odors, which is what we observed for nonsocial odors in Experiment 1. Additionally, there do appear to be differences between affective salience attribution for social and nonsocial odors. Indeed, Figure 3 suggests that, on trial 1, the animals found the nonsocial odors more salient than the social odors. Figure 3 also shows that the rats demonstrated more gradual habituation to social odors than nonsocial odors in Experiment 2, suggesting that these social odors retained some affective salience to the rats after the first few presentations, unlike the nonsocial odors to which the rats rapidly habituated. What is most striking is the increased preference for male odors due to BLA inhibition that we observed in Experiment 4. Rather than decreasing in affective salience as we had predicted, the male odors appeared to become even more interesting to the female subjects. This suggests that BLA inhibition does not result in the complete abolition of affective salience attribution per se, but rather a more complex dysregulation.

Because both male social and nonsocial odors appear to carry initially high affective salience for the rats, another study to be conducted in the lab is being planned to assess the role of the BLA in the preferences of these subjects for the two types of odors as we did in Experiment 3. Additionally, because of the high exploration times the female subjects spent on male social odors, it would be useful to repeat the habituation-dishabituation task in Experiment 2 with male social odors and new nonsocial odors that are more ecologically relevant to the rats. We did not observe any effects of BLA inhibition on performance on these tasks, but that could be attributed to the very low exploration times the females spent exploring social odors in this task. A replication of this experiment with two possibly equally salient but biologically distinct stimuli could demonstrate the role of the BLA in social processing specifically.

Because these studies will be conducted in the lab using the same subjects, the locations

of the infusion guide cannula have not yet been histologically confirmed, which is a limitation of the project. Another limitation is that the subjects have had much greater exposure to female social odors (via their own home cages or cubicles) than to the male social odors and wide variety of nonsocial odors used. Therefore, the results of each of these experiments may be very different if male social odors were used instead of female social odors.

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Figure Captions

Figure 1. BLA inhibition in novel odor recognition memory task with immediate test. The graph shows the discrimination index (DI) for novelty across social and nonsocial trials. A higher DI indicates better ability to discriminate between familiar and novel odors. White bars indicate control conditions and hatched bars indicate muscimol conditions. Asterisks indicate statistical significance relative to chance ($p < 0.05$). Subjects did not discriminate between novel and familiar odors in all conditions except in the muscimol condition in the nonsocial trial. Error bars show SEM.

Figure 2. BLA inhibition in novel odor recognition memory task with 5-minute test. The graph shows the discrimination index (DI) for novelty across social and nonsocial trials. A higher DI indicates better recognition memory for previously presented odors. White bars indicate control conditions and hatched bars indicate muscimol conditions. Asterisks indicate statistical significance relative to chance ($p < 0.05$). Pound signs indicate trends ($0.05 < p < 0.1$). Subjects did not discriminate between novel and familiar odors under all conditions except for in the control condition in the nonsocial trial. Error bars show SEM.

Figure 3. BLA inhibition in habituation/dishabituation to social and nonsocial stimuli. The graph shows the raw exploration time of the stimulus presented in the trial. The same stimulus is presented on each of the first five trials and a new stimulus is introduced in the final trial. White markers indicate control conditions and black markers indicate muscimol conditions. Squares represent social trials and circles represent nonsocial trials. Three-way repeated measures ANOVA showed a main effect of trial on exploration time and a significant interaction between trial and odor type. There were no other statistically significant main effects or interactions. Error

bars show SEM.

Figure 4. The role of the BLA in social preference. The graph shows the discrimination index (DI) for social versus nonsocial odors. A higher DI indicates greater social preference or decreased nonsocial interest. White bars indicate control conditions and hatched bars indicate muscimol conditions. Asterisks indicate statistical significance relative to chance ($p < 0.05$). Subjects appeared to demonstrate no preference for social versus nonsocial odors. BLA inhibition slightly increased nonsocial interest, but this result was non-significant. Error bars show SEM.

Figure 5. The role of the BLA in male versus female preference. The graph shows the discrimination index (DI) for male social versus female social odors. A higher DI indicates greater male social preference. White bars indicate control conditions and hatched bars indicate muscimol conditions. Asterisks indicate statistical significance relative to chance ($p < 0.05$). Asterisks above the horizontal lines indicate statistical significance between conditions ($p < 0.05$). Under both conditions, subjects demonstrated a strong interest in male odors. BLA inhibition appeared to increase that interest ($p = 0.0412$). Error bars show SEM.

Figures

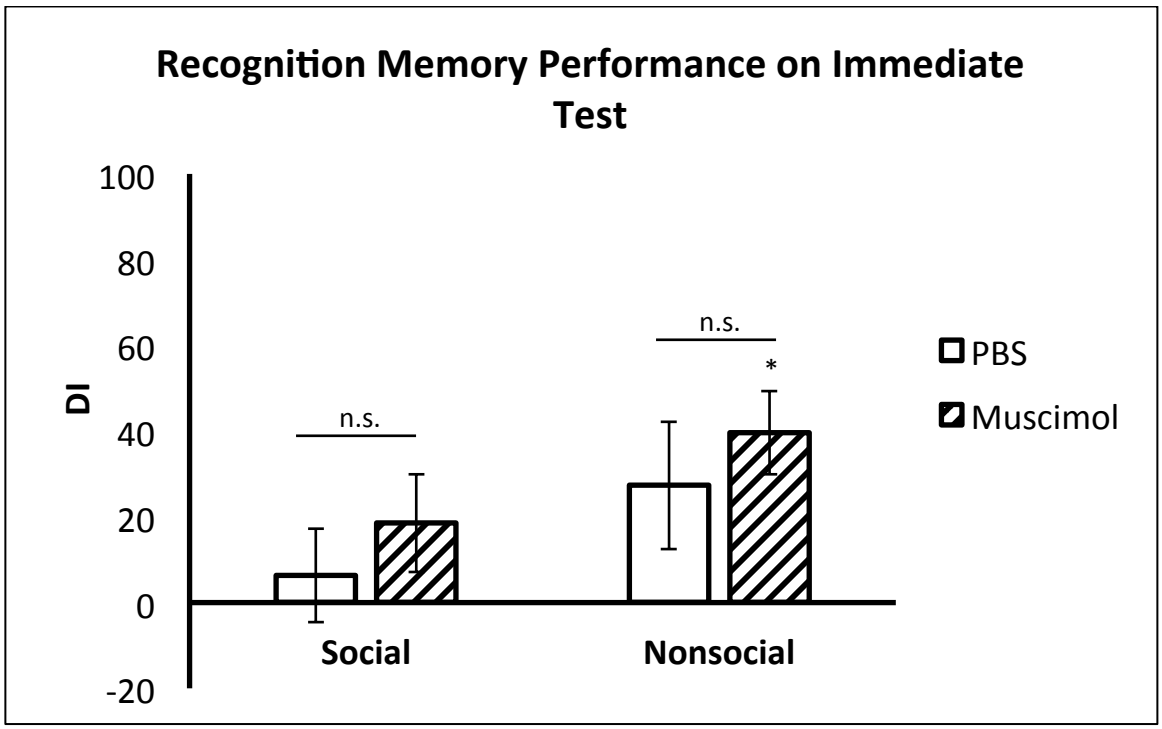

Figure 1. BLA inhibition in novel odor recognition memory task with immediate test.

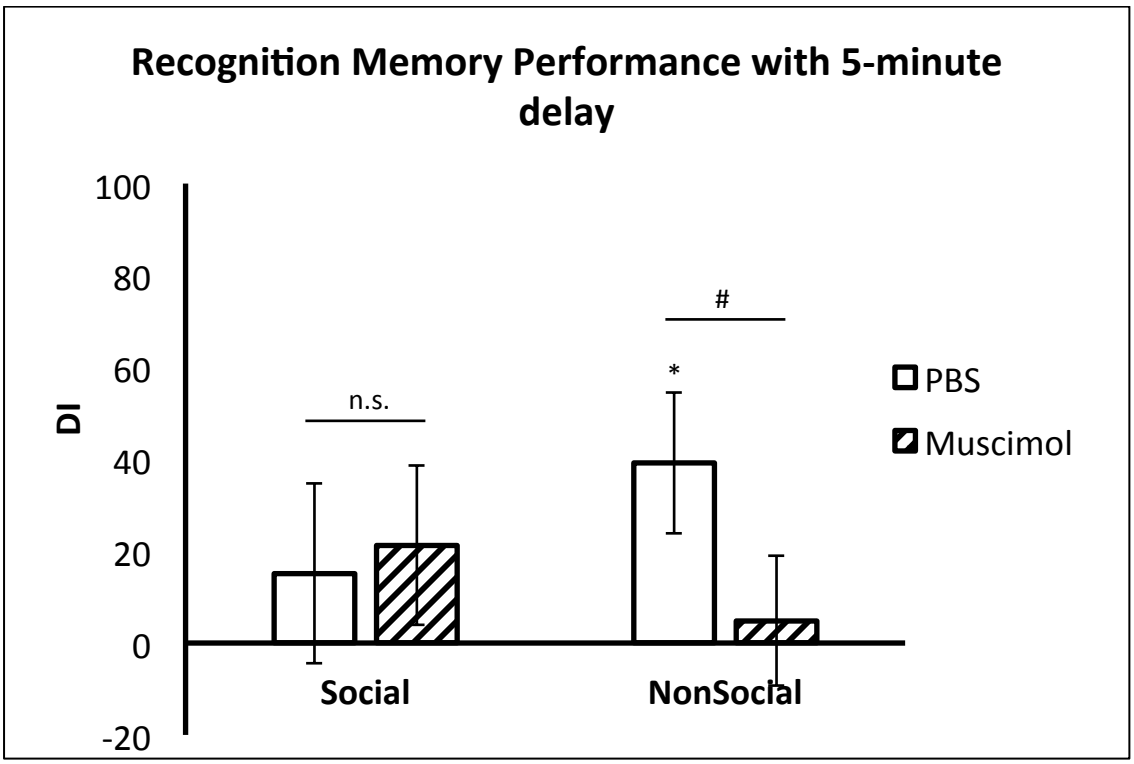

Figure 2. BLA inhibition in novel odor recognition memory task with 5-minute test.

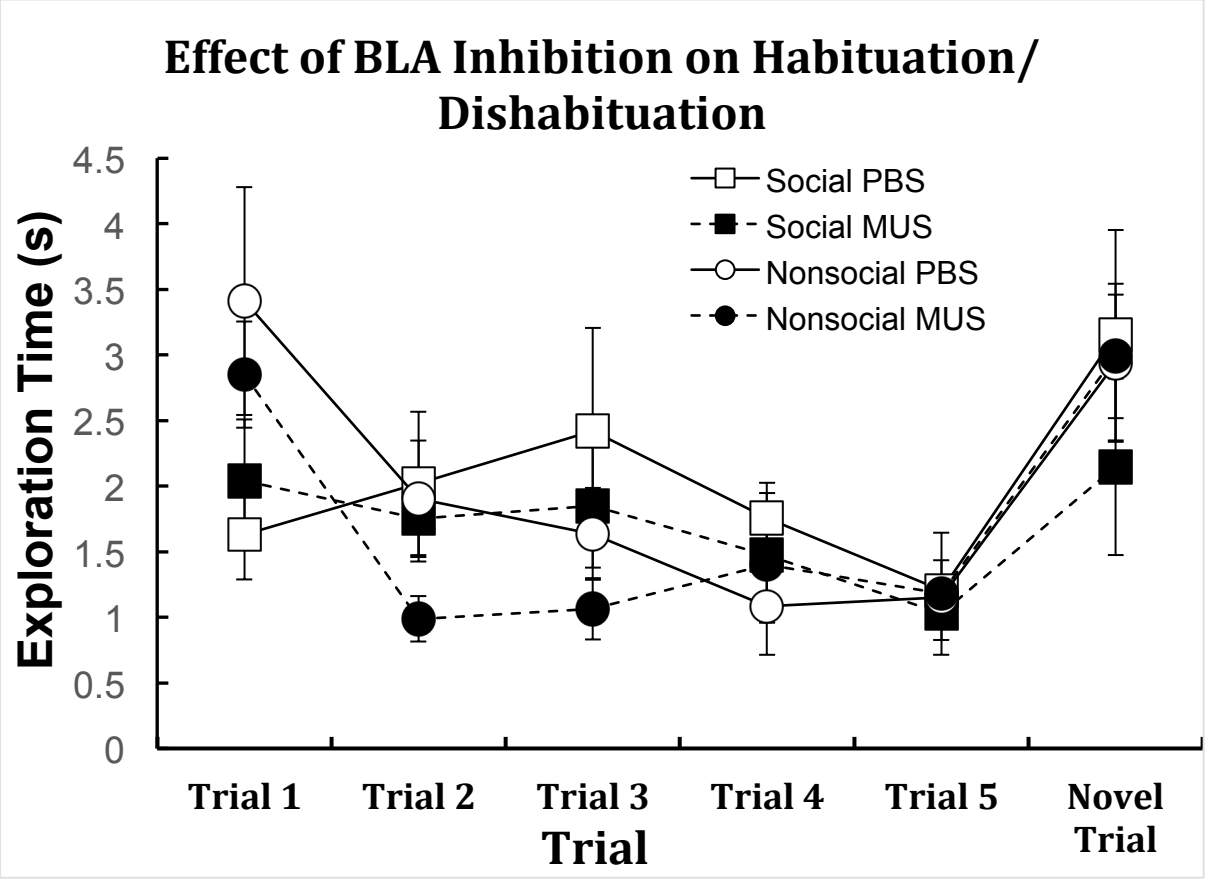

Figure 3. BLA inhibition in habituation/dishabituation to social and nonsocial stimuli.

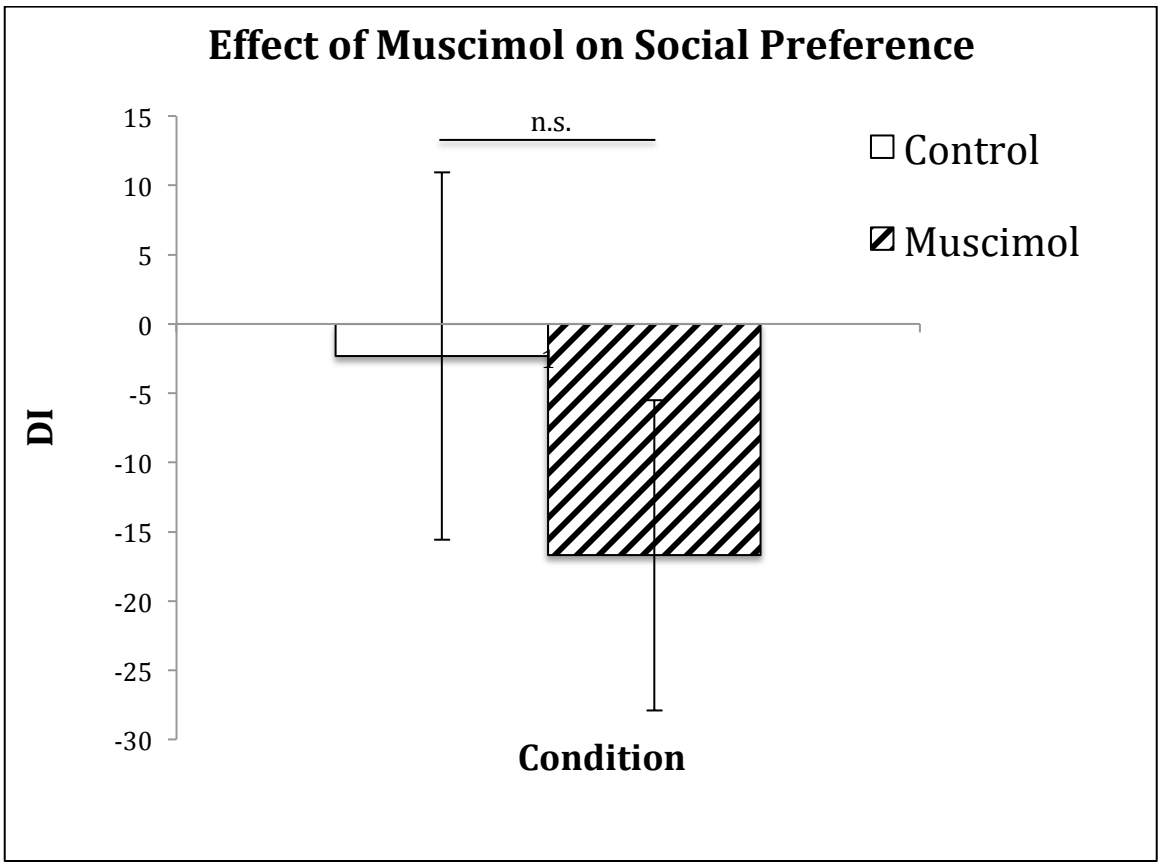

Figure 4. The role of the BLA in social preference.

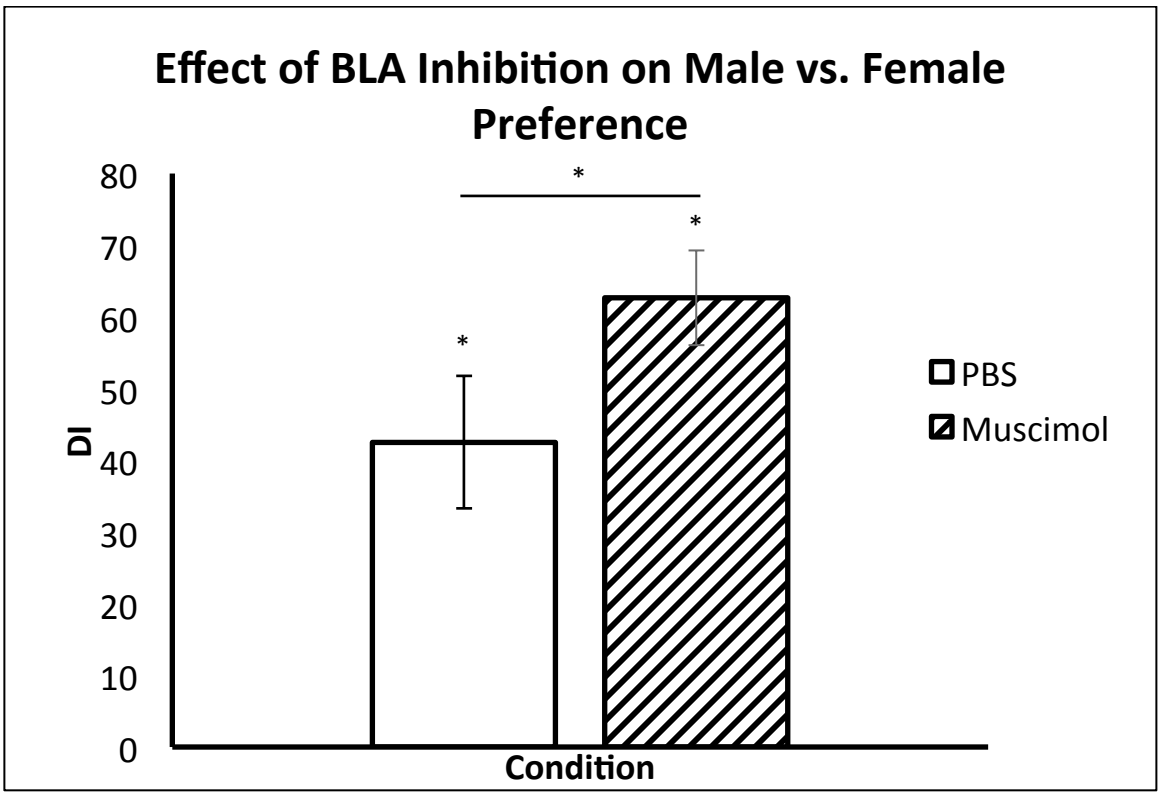

Figure 5. The role of the BLA in male versus female preference.