Honors Projects

Psychology

2008

Behavioral Responses to Predictable and Unpredictable Competitors and c-Fos Expression in the Amygdala and Nucleus Accumbens

Jennifer Schnupp '08
Illinois Wesleyan University

Recommended Citation

Running Head: PREDICTABLE AND UNPREDICTABLE COMPETITORS

Behavioral Responses to Predictable and Unpredictable Competitors and c-Fos

Expression in the Amygdala and Nucleus Accumbens

Jennifer Schnupp

Illinois Wesleyan University

Abstract

The present study examined the effects of the presence of a competitor on the behavior of individual rats in a foraging paradigm as was done in Farmer-Dougan, Dougan, Knight, Toelle, and Chandrashekar (2007). Rats foraged for food in a large open field, with pellets delivered in one patch on a Variable Interval schedule (VI). During *alone* conditions, each rat foraged by itself. During the *unpredictable competitor* condition, a competitor rat was introduced on an unpredictable basis on the last day of foraging. In this condition, the rats displayed avoidance behavior and were significantly undermatching as was observed in Farmer-Dougan et al. (2007). During the *predictable competitor* condition, the competitor rat was always present. These rats were significantly overmatching and engaged in a competitive wrestling behavior that was casually observed in Farmer-Dougan et al. (2007). The behavioral topographies were coded after behavioral testing was complete to examine the occurrence of avoidance behaviors and competitive wrestling behaviors in each condition. After the last session of foraging, the rats were sacrificed and c-Fos analysis was completed on the amygdala and nucleus accumbens. The results showed that the rats engaged in the expected behavioral responses with rats in the predictable competitor condition of spending more time at the feeder, and they also had higher c-Fos expression in the nucleus accumbens. Rats in the unpredictable competitor condition spent more time away from the feeder, more time grooming, and more time engaging in other social avoidance behaviors; they also had significantly higher levels of c-Fos expression in the amygdala. The present data expand the literature comparing the matching law to the idea free distribution by examining the differences in behavioral responses and the neural correlates.

Behavioral Responses to Predictable and Unpredictable Competitors and c-Fos

Expression in the Amygdala and Nucleus Accumbens

The Generalized Matching Law and the ideal free distribution have long been used to study animal behavior and describe choice behaviorally (Shettleworth, 1998). For behaviorists, choice is based on reinforcement distribution between different sources of reinforcement rather than the traditional cognitive descriptions used. These laws both seek to predict the distribution of an individual or a group of individuals, respectively, in relation to alternate sources of reinforcement. The Generalized Matching Law predicts the behavior of one animal presented with two alternate sources of reinforcement while the ideal free distribution examines the number of animals in a patch of resources in relation to the density of the resources in those patches. While these concepts have several similarities, the vital difference is that the ideal free distribution takes competition into account while the Generalized Matching Law only predicts the behavior of one animal.

Although the Generalized Matching Law and the ideal free distribution have been studied independently and compared, new behavioral paradigms combine elements of both into one experiment. The present study introduced an element of competition, which is unique to the ideal free distribution, into a matching law situation as was done in Farmer-Dougan, Dougan, Knight, Toelle, and Chandrashekar (2007). The competitor was either predictable, present throughout all behavioral testing, or unpredictable, present only for the last session of behavioral testing. The parameters of the matching law, bias and sensitivity, were measured to see how they change in the presence of either a

predictable or unpredictable competitor. In addition, Farmer-Dougan et al. (2007) casually observed behavioral responses that differed whether the competitor was predictable or unpredictable. The present study explicitly examined the differences in behavior between competitor conditions that were only previously observed before.

The present study also built upon the available literature on competition in a matching law situation by examining the neural correlates to the measured matching parameters and observed behavioral responses. After behavioral testing is complete, the rats were sacrificed and c-Fos immunocytochemistry analysis was performed on the nucleus accumbens and the amygdala. The nucleus accumbens has been associated with reward behavior, such as sensitivity to reward, and the amygdala has been associated with aggressive and fear behavior, perhaps such as the behavioral responses observed due to the presence of either a predictable or unpredictable competitor.

Generalized Matching Law and Ideal Free Distribution

The Generalized Matching Law has long been used to describe operant choice on concurrent schedules and to predict the behavior of the subjects in these situations. The Generalized Matching Law expresses the relative rate of operant responding to alternate sources of reinforcement as a function of the relative rate of reinforcement provided by those sources (Herrnstein, 1961, 1970). The Generalized Matching Law says,

$$\log (P1/P2) = a \log (R1/R2) + \log b \qquad \text{(Equation 1)}$$

where P1 and P2 are the absolute rates of responding to alternative sources 1 and 2 and R1 and R2 are the absolute rates of reinforcement for these alternative sources. 1 and 2 are alternate sources of the same reinforcer on a concurrent schedule of delivery. "a" is the "sensitivity" parameter and represents the sensitivity of the response ratio to changes

in the reinforcer ratio. The value of "a" is a measure of the matching behavior occurring. An "a" value of 1 indicates perfect matching and a maximization of reinforcers received. A value below 1 indicates undermatching and less sensitivity to reward and a value of over 1 indicates overmatching and increased sensitivity to reward. "b" is known as the "bias" parameter and represents a preference for one alternative not related to the rate of reinforcement. "a" and "b" are identified for each animal in each study.

The Generalized Matching Law has been shown to provide a strong prediction of one animal's choice behavior in simple foraging situations, but does not perform as well in more complex situations. Baum (1979) has shown that the matching law can account for over 95% of the variance when animals are responding on concurrent schedules of reinforcement that provide the same reinforcer in each component. For example, pigeons in Herrnstein's original experiment (1961) were exposed to two feeders on different variable interval schedules delivering the same reinforcer. Herrnstein observed that the amount of time each animal spent at each feeder was proportionate to the frequency of reinforcement. However, if the components of the concurrent schedule are providing different reinforcers, the matching law does not predict behavior as well (Hursh, 1980). Also, the Generalized Matching Law does not take more than one animal into account in a foraging situation.

While the Generalized Matching Law describes the operant choice of one animal foraging, the ideal free distribution model was developed and has long been used to describe the distribution of foraging animals between patches differing in resource density (Fretwell & Lucas, 1970). The ideal free distribution says,

$$\log (N1/N2) = a \log (A1/A2) + \log b \text{ (Equation 2)}$$

where N1 and N2 represent the relative number of animals in each of the two patches and A1 and A2 represent the relative resource density of the two patches. "a" represents the sensitivity of the group behavior to differences in resource distribution. "b" represents a greater or lesser distribution of animals than expected in a patch for reasons unrelated to resource distribution. For example, a dominant animal in one of the patches might produce a bias to the other patch (Farmer-Dougan et al., 2007).

The equations for the matching law and the ideal free distribution have obvious similarities, but they also have several important distinctions. Perhaps the most important difference is that the ideal free distribution factors in competition by examining more than one animal in a foraging situation. Competition is a crucial difference between the models and drives predictions of the ideal free distribution (Shettleworth, 1998). When a single animal is foraging, foraging at the patch producing more reinforcers is the better strategy. This is not necessarily the case if more than one animal is present, however. When more animals are present, competition for the resources available increases and thus decreases the rate that individual animals acquire resources (Farmer-Dougan et al., 2007). In this situation, foraging in the patch with fewer resources but also fewer competitors may lead to a higher amount of reinforcers for an individual animal.

Competition is an important difference between the matching law and the ideal free distribution, but there is little research that has examined these differences in depth. Competition has been widely studied in relation to the ideal free distribution, but competition has rarely been studied in relation to the matching law. Farmer-Dougan and colleagues (2007) studied competition in relation to the matching law by introducing an element of competition into a matching situation. They examined how the introduction of

a competitor impacts the bias and sensitivity parameters of the matching law. They examined these parameters in relation to whether the presence of a competitor was predictable (present through all testing sessions) or unpredictable (only present for one session of testing).

The results of this study showed that sensitivity was affected by a competitor depending on whether the competitor was predictable or unpredictable (Farmer-Dougan et al., 2007). During the alone phase of the experiment where the animal forages alone for all testing sessions, the value of the "a" parameter was 0.99 which indicates nearly perfect matching. During the unpredicted competitor condition (UC), however, this value drops to a value of 0.59 which indicates significant undermatching and therefore lower sensitivity to reward. In contrast, during the predictable competitor condition (PC) the value jumps to 1.39 which indicates significant overmatching and increased sensitivity to reward.

In addition to the results that Farmer-Dougan and colleagues (2007) were explicitly testing for, casual observation suggested different behavior topography when the competitor was present on a predictable basis. Rats exposed to an unpredictable competitor tended to avoid each other. "Social avoidance" is consistent with undermatching since the avoidance behavior could potentially interfere with foraging efficiency. Rats exposed to predictable competitors engaged in "competitive wrestling" behavior near the opening of the feeder. This behavior was an apparent attempt to position themselves in front of the feeder when the pellet was delivered to ensure getting the reward and may account for the overmatching behavior and thus increased sensitivity to reward (Farmer-Dougan et al., 2007).

The present study explicitly measured the behavior topography that was previously, but casually, observed by Farmer-Dougan and colleagues (2007). Since these behaviors had not been systematically observed before, the present study was designed to quantify and code them. The same behavioral paradigm used by Farmer-Dougan et al. (2007) was used in the present study and was simplified to put the focus on the behavioral responses rather than matching behavior; only one feeder was used. It was predicted that similar behaviors among conditions would occur as was observed in the original study with rats in UC showing avoidance behavior, and those in PC would show competitive wrestling. A no competitor condition was also added as a control group since the present experiment used a between subjects design. The original study used the same subjects to measure both the predictable and unpredictable competitor conditions while the present study had different subjects in each condition which necessitated a control group for comparison.

c-Fos Immunocytochemistry Analysis

The nucleus accumbens and the amygdala have been demonstrated to be correlated to components of Farmer-Dougan et al.'s findings (2007) such as reward sensitivity and aggression. Aggressive behavior and competitive behavior have often been linked to activity in the amygdala (Blanchard, McKittrick, & Blanchard, 2001; Roseboom, Nanda, Bakshi, Trentani, Newman, & Kalin, 2007; Vazdarjanova, Cahill, & McGaugh, 2001; Veneema & Neumann, 2007) while reward has been linked to activity in specific brain regions such as the nucleus accumbens (Schultz, 2002; Stefani & Moghaddam, 2006). In order to gain a complete picture of the behavioral responses,

neural regions were examined and correlated with the observed behavioral responses and calculated matching parameters.

Thus the present study used c-Fos immunocytochemistry in an attempt to analyze the amygdala and the nucleus accumbens in order to correlate the behavioral observations with hypothesized activation of these regions after behavioral testing was complete. c-Fos is a product of the immediate early gene *c-fos* and expression of the Fos protein is an accepted marker of increased neural activity (Zhu, McCabe, Aggleton, & Brown, 1997; Vann, Brown, Erichsen, & Aggelton, 2000). c-Fos analysis can therefore be used to examine differential activation in specific regions of the brain by looking at levels of c-Fos expression.

Neurological Substrates of Reward Sensitivity: Sensitivity to reward was significantly different between predictable competitor and unpredictable competitor conditions, and reward and sensitivity to reward have been linked to specific neurotransmitters and brain regions (Farmer-Dougan et al., 2007). A large body of research has shown that dopamine is the neurotransmitter involved with reward and the use of reward information for learning and consummatory behavior (Schultz, 2002). More specifically, dopamine signals encode the value of probability and value of a reward (Stefani & Moghaddam, 2006). Cell bodies of dopamine neurons are primarily located in the ventroanterior midbrain in regions such as the substantia nigra and ventral tegmental area (Schultz, 2002). The axons of these neurons project to the straitum and ventral striatum which includes the nucleus accumbens.

The nucleus accumbens has been shown by multiple studies to be involved in reward sensitivity. Dopamine has been named as a signal that encodes the value and

probability of a reward (Stefani & Moghaddam, 2006). Because the nucleus accumbens receives high levels of dopaminergic projections, it has been implicated in aspects of learning and motivated behavior involving reward (Stefani & Moghaddam, 2006). Dopamine neurons in the midbrain regions, including the nucleus accumbens, show similar activations following rewards or stimuli that predict reward (Schultz, 2002). The nucleus accumbens has also been shown to be involved in appetite motivated instrumental learning and responding.

Schultz (2002) describes the relationship of dopamine and reward more specifically. When an animal encounters a morsel of food in the absence of other stimuli that would trigger dopamine firing, about 75% of dopamine neurons in the brain are activated. In contrast to this, only 14% of dopamine neurons are activated when the animal is presented with an aversive stimulus. This suggests that fewer dopamine neurons would be activated when an animal is exposed to an aversive stimulus. The presence of an unpredictable competitor, such as in the present study, is considered an aversive stimulus and may result in lower dopamine levels in the nucleus accumbens.

Stefani and Moghaddam (2006) also showed that dopamine release in the nucleus accumbens differs if the task is predictable or unpredictable. Predictable reward that was not contingent on behavior was associated with increased dopamine levels in the nucleus accumbens. The reward situation in Farmer-Dougan et al. (2007) uses a predictable, noncontingent reward situation which suggests that dopamine levels would be increased over a rat exposed to a reward schedule contingent on its behavior. All conditions in the experiment are exposed to a predictable reward schedule suggesting that all three conditions would have increases in nucleus accumbens activity. However, this increase in

activity may be more in PC and no competitor conditions since rats in these conditions were more sensitive to this noncontingent reward than those rats exposed to the UC condition.

The findings of these previous studies along with the research design and results of Farmer-Dougan and colleagues (2007) suggest that differences in nucleus accumbens cell activation may be present among the competitor conditions in the current experiment. First, the results of the previous study showed that the rats in UC were less sensitive to reward which suggests that fewer dopamine neurons would be activated in the nucleus accumbens. Also, UC rats are also exposed to an aversive, disruptive stimulus which could lead to a further decrease in dopamine neuron activation. In contrast, rats in PC are more sensitive to reward, lack an aversive stimulus, and are exposed to a noncontingent reward schedule and would be predicted to have higher levels of dopamine activation in the nucleus accumbens than those rats exposed to an UC. Rats in the no competitor condition could be predicted to have activation levels between the other two conditions since they lack the aversive stimulus of the UC and have lower sensitivity to reward than rats in the PC, but higher sensitivity to reward than those exposed to an UC.

Neurological Substrates of Competition: Rats in the PC and UC conditions displayed aggressive, competitive, and avoidance behaviors which have been widely studied outside of a matching paradigm. Aggression, competition, and stress have been previously studied in relation to social stressors, competition, and aggression and the underlying neurological responses. While physical stressors are most frequently used to induce stress responses, social stress situations like the one used by Farmer-Dougan and colleagues (2007) are the most relevant to humans and induce the same stress responses

(Roseboom et al., 2007). For example, exposure of a rodent to a natural competitor or predator will induce similar physiological responses as physical stressors. This social stress can be the presence of a competitor for a sudden or short period of time or for a longer period of time (Blanchard et al., 2001). This is applicable to the present study as both of these types of social stress are represented by the UC condition and the PC condition respectively and result in different behavioral responses.

The amygdala has been repeatedly shown to be related to aggressive behavior, competitive behavior, and social stressors. The amygdala is a medial temporal structure that is important in identifying and interpreting cues associated with threatening stimuli and unconditioned fear responses (Roseboom et al., 2007). Numerous studies in rodents, primates, and even humans have demonstrated the amygdala's role in mediating the emotional, behavioral, and physiological responses associated with fear and anxiety (Kalin, Shelton, & Davidson, 2004). Increases in c-Fos expression have been demonstrated in the amygdala in response to social and physical stress (Bubser & Deutch, 1999; Herringa, Nanda, Hsu, Roseboom, & Kalin, 2004) and in response to aggressive encounters (Davis & Marler, 2004). More specifically, the basolateral amygdala has been implicated in relation to fear and aggressive responses (Vazdarjanova et al., 2001).

The basolateral nucleus of the amygdala has been implicated in being involved in avoidance and freezing responses to unconditioned stimuli such as the presentation of a natural predator or competitor. Vazdarjanova et al. (2001) demonstrated that the basolateral nucleus of the amygdala is a critical brain region in expressing the avoidance response and freezing response to an unconditioned fear-eliciting stimulus. Freezing behavior occurs when the rat lacks all movement besides movement associated with

respiration in the presence of the stimulus. On the other hand, avoidance behavior is when the rat continues to move, but does not make contact with the stimulus. If the rat does make contact with the stimulus, it will quickly withdraw to another area.

Avoidance and fear behavior to an unconditioned fear-eliciting stimulus was observed in the unpredictable competitor condition of Farmer-Dougan and colleague's study (2007) and implies that differences in amygdala function may be present among competitor conditions. Rats in the UC condition were attempting to avoid the competitor and appeared to be distracted (Farmer-Dougan et al., 2007). This avoidance behavior is likely a reason why the rat was less sensitive to reward and was significantly undermatching. It was more concerned with avoiding the competitor than receiving a reward. Since PC condition rats do not display this avoidance behavior to their competitor, it can be predicted that there is a difference between amygdala activation in UC conditions in relation to the PC and no competitor conditions such that rats in the UC condition would have higher amygdala activity.

The amygdala also seems to be involved in aggressive responses such as the competitive wrestling that was observed in the PC condition. For example, the amygdala is involved in mediating aggressive behavior in response to fear-eliciting stimuli and competitive threats (Veneema & Neumann, 2007; Roseboom et al., 2007). The competitive wrestling observed is a type of aggressive behavior that is known to increase c-Fos expression (Bubser & Deutch, 1999; Herringa et al., 2004). Aggressive behavior between members of the same species is an efficient means of competition for resources, including food. This aggression between same-species members has dangers for both animals involved, though, and can become ritualized to decrease physical aggression and

avoid serious injury (Veneema & Neumann, 2007). The aggressive wrestling observed from rats exposed to a PC appears to have become ritualized in this way as the rats were not harming each other and demonstrated increased sensitivity to reward, which indicates more efficient means of competition for food. This may lead to less amygdala activity than other aggressive encounters since the behavior is altered to decrease aggression and avoid injury.

Summary

The present study seeks to systematically observe behavioral responses to predictable and unpredictable competitors in a matching situation that had previously only been causally observed. The research of Farmer-Dougan et al. (2007) was replicated in order to explicitly observe the behavioral responses in a matching paradigm to a predictable competitor, an unpredictable competitor, or no competitor. It was predicted that similar changes in the matching law parameters would be observed with rats in the PC condition demonstrating an increased sensitivity parameter and rats in the UC condition demonstrating a decreased sensitivity parameter compared to no competitor rats; this variable was not measured in the present study since only one feeder is being used, but it was predicted that the parameters would change in the same direction. It was also predicted that similar patterns of behavior would be observed in this study as were observed in the original experiment. It was predicted that rats in the PC condition would exhibit competitive wrestling behavior that was not present in the other conditions and that rats in the UC condition would exhibit significantly more avoidance and fear behavior than those with PC. Refer to Table 1 for clarification of these behavioral hypotheses.

The present study also examined c-Fos expression in relation to the behavioral responses observed. c-Fos immunocytochemistry was performed in the basolateral amygdala and the nucleus accumbens to examine differences in c-Fos expression in these regions among competitor conditions. It was predicted that significant differences in c-Fos expression would be observed among conditions with the PC condition having significantly higher expression in the nucleus accumbens and with the UC condition having significantly higher expression in the amygdala. The examination of the neural activity associated with the behavioral responses will help expand this new area of research on competition in a matching paradigm by understanding the underlying neural correlates.

While it could be predicted that rats in the no competitor condition will have less amygdala activity due to the lack of an aggressive encounter, it is difficult to accurately predict what differences would exist in cell counts between the PC and UC conditions since rats in both of these conditions engaged in a form of aggressive or competitive behavior as a result of a social stressor. The rats foraging alone could be predicted to have lower levels of amygdala activity since they are not exposed to a competitor or social stressor during behavioral testing. It could also tentatively be predicted that rats in the UC condition will have higher levels of amygdala activation since the competitor will be introduced immediately before c-Fos immunocytochemistry is performed. The rats in the PC condition were exposed to the competitor for 15 sessions before and may have less amygdala activation as the competitive behavior became ritualized to reduce aggression. Refer to Table 1 for clarification of the c-Fos expression hypotheses.

Table 1

Hypotheses

Behavioral Testing

1. Rats in the predictable competitor condition will demonstrate higher occurrences of competitive wrestling behavior than the other conditions.

2. Rats in the unpredictable competitor condition will demonstrate higher occurrences of avoidance and fear behavior than the other conditions.

c-Fos Analysis in the Amygdala

1. Rats in the unpredictable competitor condition will have significantly higher levels of c-Fos expression than rats in the other conditions.

2. The levels of c-Fos expression in the amygdala will be positively correlated to the frequency of the social avoidance and fear behaviors observed among conditions.

c-Fos Analysis in the Nucleus Accumbens

1. Rats in the predictable competitor condition will have significantly higher levels of c-Fos expression in the nucleus accumbens core and shell than the other conditions.

2. The levels of c-Fos expression in the nucleus accumbens will be positively correlated to the competitive wrestling behaviors observed and negatively correlated to behaviors associated with aggression and fear.

Methods

Subjects

Twenty-four Sprague-Dawley rats, approximately 6 months old, served as subjects. All rats were housed individually on a 12-hour light/dark cycle with free access to water. Rats were maintained at a minimum of 80% *ad libitum* body weight throughout the experiment. Animal care followed the guidelines advised by the Guide for the Care and Use of Laboratory Animals, and the project was approved by the Institutional Animal Care and Use Committee of Illinois Wesleyan University.

Apparatus

A rectangular open field of approximately 1.25M by .75M with 30 cm walls was used for all testing. One feeder was mounted inside the box at the north corner. One stainless steel "foraging" pan was located directly below and in front of the feeder. The pan was positioned such that food pellets dropped from the feeder fell directly into the foraging pan. This apparatus was similar to that used by Farmer-Dougan et al. (2007), but only included one feeder to simplify behavioral observations. All experimental events were controlled via a Windows PC running Med Associated Med-State software connected to a Med Associated interface. Data was recorded by a video recorder placed above the apparatus and scored for behavior as described below.

Procedure

All rats were acclimated to the foraging box prior to the start of the experiment. The experiment proper began after all rats were reliably approaching the feeders when a pellet was delivered. This experiment consisted of two distinct phases- behavioral testing

followed by immunocytochemistry analysis. The rats were randomly divided into three groups labeled *predictable competitor subjects, unpredictable competitor subjects*, and *no competitor subjects* with n=8 in the predictable and unpredictable conditions and n=7 in the control no competitor condition due to one rat becoming ill and not being able to serve as a subject.

Predictable Competitor Condition: All sessions in this condition were conducted with two rats in the foraging apparatus. At the start of each session, the primary subject rat and the competitor rat were placed in the center of the apparatus simultaneously. The session began immediately after the rats were placed in the chamber and continued for 20 minutes. The feeder delivered food pellets on a variable interval 30 second schedule independent of the rat's behavior. The rats were removed from the apparatus immediately at the end of the session. These sessions were called predicted competitor sessions because the competitor will be present on a regular basis. Data was collected from both subjects, one of which was marked with blue nontoxic paint so the primary subject could be differentiated from the predictable competitor.

No Competitor Condition: These rats foraged alone for all 10 days of testing. At the start of each session in this condition, the primary subject rat was placed in the center of the apparatus. The methodology for this condition was identical to the predictable competitor condition described above except only one rat was used.

Unpredictable Competitor Condition: This condition consisted of two different phases. For the first 9 days of the experiment, each of the rats foraged by itself. These sessions were identical to the no competitor condition described above. On day 10, a second competitor rat was introduced. These sessions were identical to the predictable

competitor sessions described above. These pairings were considered unpredictable because they were done very infrequently (Farmer-Dougan et al., 2007). Data was only collected from the primary subject who was marked blue with nontoxic paint so the two rats could be easily differentiated. The primary subject rat was exposed to several more sessions in the foraging box than the competitor rats. This was an intentional part of the methodology to keep the competitor rats naïve to the foraging schedules and the apparatus (Farmer-Dougan et al., 2007). During the alone sessions, competitor rats remained on food deprivation but will not removed from their home cages.

Data Collection and Coding: The data was collected over 10 sessions of testing that lasted 20 minutes each. The sessions from the last day of testing from the UC condition and the PC condition were video recorded to be coded for behavior at a later time by two raters, one of whom was kept blind to the competitor condition. Data from the alone condition will not be coded since the rats were not engaging in any unique behavior and were matching at the predicted rate (Farmer-Dougan et al., 2007). The video tapes of the data collection sessions were initially watched to examine what behaviors occurred and determine how the behavior will be coded. The coding system was developed after the behavioral testing was complete to ensure that the behaviors of interest occurred and so the coding could be developed around the behaviors that did occur. Once the coding system was established, the video tapes were watched again and coded for the behaviors of interest. The time was measured in seconds from when the activity began and ceased and totaled together for the session. The behaviors examined were time grouped into three main categories: competitive wrestling behavior (number of jumps over the competitor rat and number of times pushing the other rat with their paw),

social avoidance or fear behaviors (time spent away from the feeder, time on back feet

away and at feeder, number of jumps out of the apparatus), and other behaviors (time

spent grooming away and at feeder and time sniffing the other rat away and at feeder).

After each session was coded, the mean duration of these behaviors across rats within

each condition were calculated. See Table 2 for reliability rates between the two raters for

each behavior.

Immunocytochemistry: After behavioral testing was complete, the rats were

sacrificed within an hour of their final session as described by Colombo, Brightwell, and

Countryman (2003). Subjects were deeply anesthetized with a Ketamine (100

mg/ml)/Xylazine (20 mg/ml) solution (1.65 mg/kg) and placed in a dark room until

perfusion. Once the rats were unresponsive to painful stimuli, they were perfused

transcardially with 2% sodium nitrate in saline followed by 4% paraformaldehyde in 0.1

M PBS. The brains were removed, post-fixed in 4% paraformaldehyde, and transferred to

a 20% sucrose/phosphate cryoprotectant overnight at 4 degrees Celsius.

Using a cryostat, 50 micrometer coronal sections were cut and tissue will be

placed into a sucrose solution and stored at 4 degrees Celsius for immunocytochemistry.

For each subject, two sections will be selected from the basolateral amygdala (Bregma

-3.24 mm), the core of the nucleus accumbens (Bregma 1.20 mm), and the shell of the

nucleus accumbens (Bregma 1.20 mm) and immunostained as described by Colombo et

al. (2003). Twelve-2mL trays were used to wash the tissue sections multiple times in .05

M PBS and then one time in 1% normal goat serum (NGS), 0.02% Triton X-100 (TX),

and 1% H_2O_2 in PBS for 10 minutes to inhibit endogenous peroxidase. Sections were

blocked for 15 minutes in a 2% NGS and 0.4% TX in PBS followed by incubation in 1%

NGS and .4% TX in PBS containing c-Fos rabbit polyclonal antibody (1:1000; Santa

Cruz Biotechnology, Santa Cruz, CA) for 48 hours at room temperature. Sections were

washed four times with 0.05 M PBS for 15 minutes each before a one hour incubation in

biotinylated goat anti-rabbit secondary antibody (1:400 in 1% NGS and 0.2% TX PBS;

Santa Cruz Biotechnology). Sections were washed in 0.05 M PBS three times for 5

minutes each and then processed with avidin-biotinylated horseradish peroxidase

complex in PBS (Elite Kit; Vector Laboratories, Burlingame, CA) for 45 minutes at room

temperature. Sections were washed four times for 15 minutes each in PBS and the

reaction was visualized with diaminobenzidine (DAB, Sigma). The reaction was then

stopped by washing three times for 10 minutes each in cold 0.01 PBS. Sections were

mounted on slides and dried overnight. They will then be plated under cover slips.

Quantification of c-Fos Positive Nuclei: Sections were imaged using a Nikon Y-

FL Eclipse E600 light microscope and Nikon Digital Sight DS-SM camera interfaced

with an Intel Penticom 4-PC computer. Scion Image software was used to count cells.

Cell counts were taken within the outlined regions using a defined particle size depending

on brain region. A 4x objective was used to capture all images.

Statistical Analyses

Data was analyzed using SPSS 15.0 software. Behavioral data was analyzed using

independent t-tests to examine behavioral differences between rats in the unpredictable

and predictable competitor conditions. The *p*-value was set at .01 due to a large number

of related measures in order to reduce Type I error. c-Fos data was analyzed using one-

way ANOVA's and Bonferonni post hoc tests. The independent variable was competitor

condition (PC, UC, or no competitor) and the dependent variables were the number of

cells stained in the basolateral amygdala and nucleus accumbens core and shell. Two

sections were counted from each brain region. The two counts were averaged within each

region for use in statistical analyses. Pearson's correlation coefficients were also

computed between the behaviors associated with social avoidance, competitive wrestling,

and reward sensitivity in the UC and PC conditions and the number of c-Fos positive

cells in the nucleus accumbens core, nucleus accumbens shell, and the amygdala. These

behaviors included time away from the feeder, time spent on feet, time spent grooming,

number of jumps over the other rat, and number of times hitting the other rat with its

paw.

Table 2

Correlations Between the Two Raters' Coding by Behavior

Behavior	Pearson's r
Time Away	.99*
Feet	.93*
Feet Feeder	.89*
Feet Away	.98*
Grooming	.98*
Grooming Feeder	.98*
Grooming Away	.77*
Sniffing	.97*
Sniffing Feeder	.95*
Sniffing Away	.96*
Leaps Over	.95*
Paws	.98*
Jumps Out	1.00*

* p<.01

Results

Behavioral results

The behavioral data from the last day of testing was coded for three main

categories of behavior: competitive wrestling behavior (number of jumps over the

competitor rat and number of times pushing the other rat with their paw), social

avoidance or fear behaviors (time spent away from the feeder, time on back feet away

and at feeder, number of jumps out of the apparatus), and other behaviors (time spent

grooming away and at feeder and time sniffing the other rat away and at feeder).

Independent two-tailed *t*-tests were use to examine differences between the UC and PC

groups. Due to a high number of related measures, the minimum *p* value for significance

was set at .01. See Table 3 for a summary of the mean durations, *t* values, and *p* values.

As seen in Table 3, rats exposed to an UC engaged in a number of the behaviors

more frequently than rats exposed to a PC. Rats in the UC condition spent significantly

more time away from the feeder [$t(14)=-5.84$], more time on their feet [$t(14)=-5.62$], and

more time grooming than rats in the PC condition [$t(14)=-3.46$]. They also spent

significantly more time sniffing the other rat than rats in the predictable condition, [$t(14)=$

-4.28]. These behaviors were also analyzed for significant differences in the amount of

time the behaviors occurred at the feeder or away from the feeder. Rats in the UC

condition spent significantly more time on their feet away from the feeder than rats in the

PC condition [$t(14)=-4.78$] and more time sniffing away from the feeder than rats in the

PC [$t(14)=-3.63$].

Table 3 also shows that rats in the PC condition engaged in some behaviors

significantly more than rats in the UC. The PC rats jumped over the other rat at the feeder

significantly more than the other condition [$t(14)$=3.60] and also pushed the other rat out

of the way with its paw more at the feeder than the other condition [$t(14)$=6.53].

There were no significant differences between conditions on time spent grooming

away from the feeder, [$t(14)$=-.33, p=.75], on time spent sniffing the other rat at the

feeder, [$t(14)$=-1.70, p=.11], time spent grooming at the feeder, [$t(14)$=-2.50, p=.03], or in

number of jumps out of the apparatus, [$t(14)$=2.41, p=.03]. Rats in the UC condition did

not attempt to jump out of the feeder significantly more times than rats in the PC, [$t(14)$=

-2.41, p=.03], or spend significantly more time on their feet at the feeder than rats in the

PC condition, [$t(14)$=-2.66, p=.02].

c-Fos immunocytochemistry results

A one-way ANOVA showed significant differences between the three competitor

conditions in c-Fos positive cells in the nucleus accumbens core, $F(2, 20)$=21.18, p<.01.

Bonferonni post hoc tests showed that rats in the PC condition had significantly higher

cell counts than both the UC and the controls in this region, but that the UC condition and

controls did not significantly differ. Correlations showed that time away from the feeder

and time spent on feet were significantly negatively associated (r= -.81) and that number

of hits to the other rat with a paw was positively associated with the number of c-Fos

positive cells in the nucleus accumbens core (r=.63). Correlations to other observed

behaviors were not significant. A one-way ANOVA also showed significant differences

among the three conditions in c-Fos positive cells in the nucleus accumbens shell,

$F(2,20)$=18.13, p<.01. Post hoc tests showed that rats in the PC condition had a

significantly higher number of c-Fos positive cells than both of the other conditions, but

that the UC and control condition did not differ. Pearson's correlations showed that time

away from the feeder (r=-.76) and time on feet (r=-.70) were negatively correlated to the number of c-Fos positive cells in the nucleus accumbens shell. Other behaviors were not significantly correlated to the number of c-Fos positive cells in these regions.

A one-way ANOVA also showed significant differences among the three conditions in the amygdala, $F(2, 20)$=29.48, p<.01. Bonferronni post hoc tests revealed that rats in the UC condition had significantly higher numbers of c-Fos positive cells than rats in the PC condition and controls which did not differ significantly from each other. Pearson's correlation coefficients showed that time away (r=.64), time spent on feet (r=.70), and time spent sniffing (r=.66) were positively correlated to the number of c-Fos positive cells in the amygdala; the number of leaps over the other rat (r=-.63) and number of times hitting the other rat with a paw (r=-.71) were negatively correlated. Other behaviors were not significantly correlated. See Figure 1 for a summary of mean c-Fos positive cell counts by brain region and condition and Figure 2 for representative photographs of each brain region in the three conditions. See Table 4 for correlation coefficients among the three brain regions and behaviors of interest.

Table 3

Mean Time in Seconds (Standard Error) for Behavioral Data

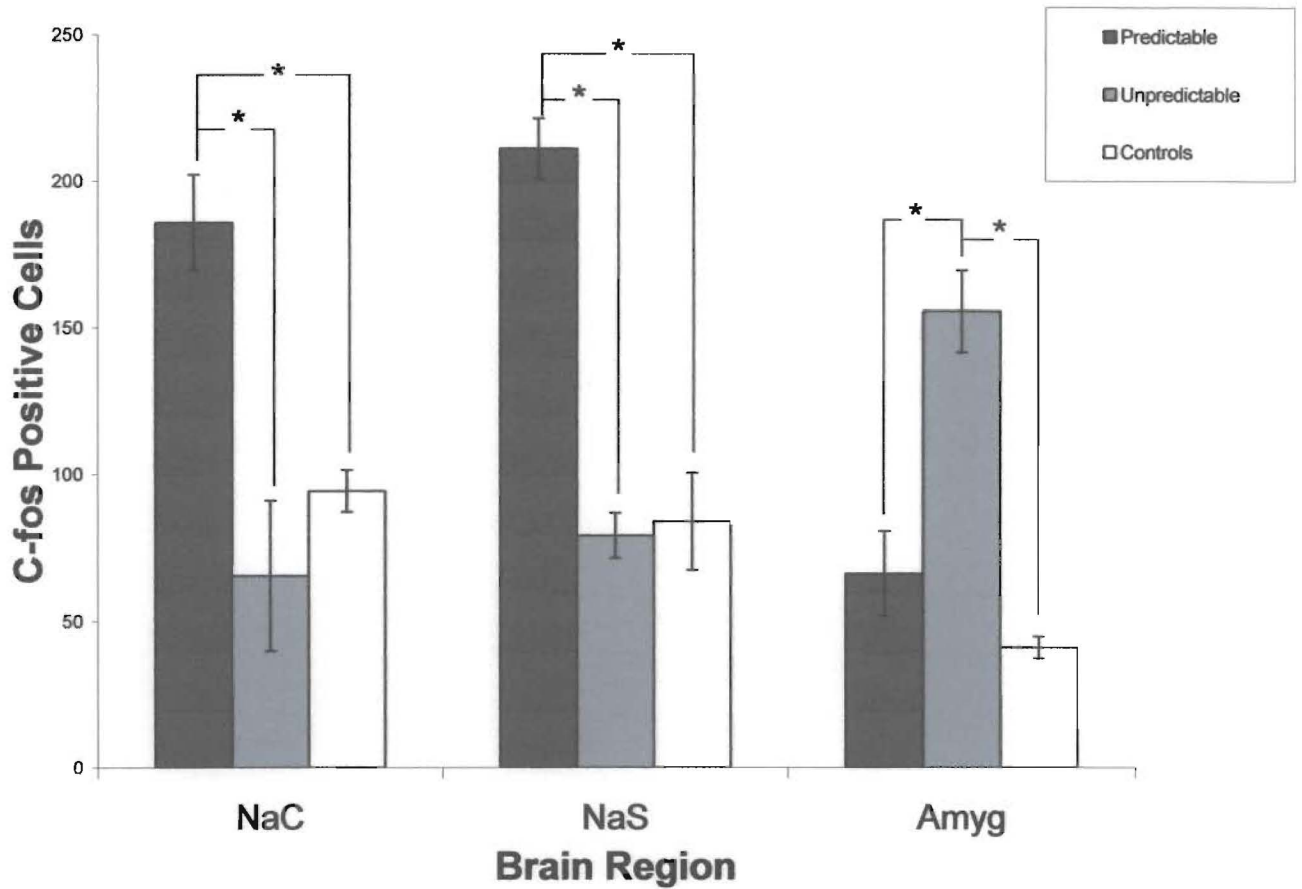|	Mean (SE)			
	Predictable Competitor	Unpredictable Competitor	$t(14)$	p-value
Jumps over other rat	8.6 (1.6)	2.0 (.84)	3.598	.003*
Paws to the other rat	33.0 (4.7)	2.0 (.57)	6.53	.000*
Time away from feeder	159.8 (36.6)	490.6 (43.1)	5.846	.000*
Time on feet	28.2 (7.8)	91.3 (8.0)	5.624	.000*
At feeder	14.6 (4.6)	32.9 (5.1)	2.657	.019
Away	14.8 (6.4)	58.4 (6.5)	4.784	.000*
Jumps out of apparatus	0 (0)	3.4 (1.4)	2.414	.030
Grooming	3.8 (2.6)	22.1 (4.6)	3.463	.004
At feeder	3.1 (2.6)	18.5 (5.6)	2.500	.025
Away	.62 (.62)	.88 (.44)	.327	.749
Sniffing	15.0 (6.3)	46.3 (3.7)	4.278	.001*
At feeder	12.5 (5.7)	25.8 (15.2)	1.697	.112
Away	2.5 (1.5)	21.8 (5.1)	3.629	.003*

*$p<.01$

Figure 1. Mean +/- standard error number of c-Fos positive cells in each brain region by condition. In the nucleus accumbens core and the nucleus accumbens shell, rats in the predictable competitor condition had significantly higher amounts of c-Fos positive cells. In the amygdala, rats in the unpredictable competitor condition had significantly higher c-Fos positive cells than the other two conditions. *$p<.01$
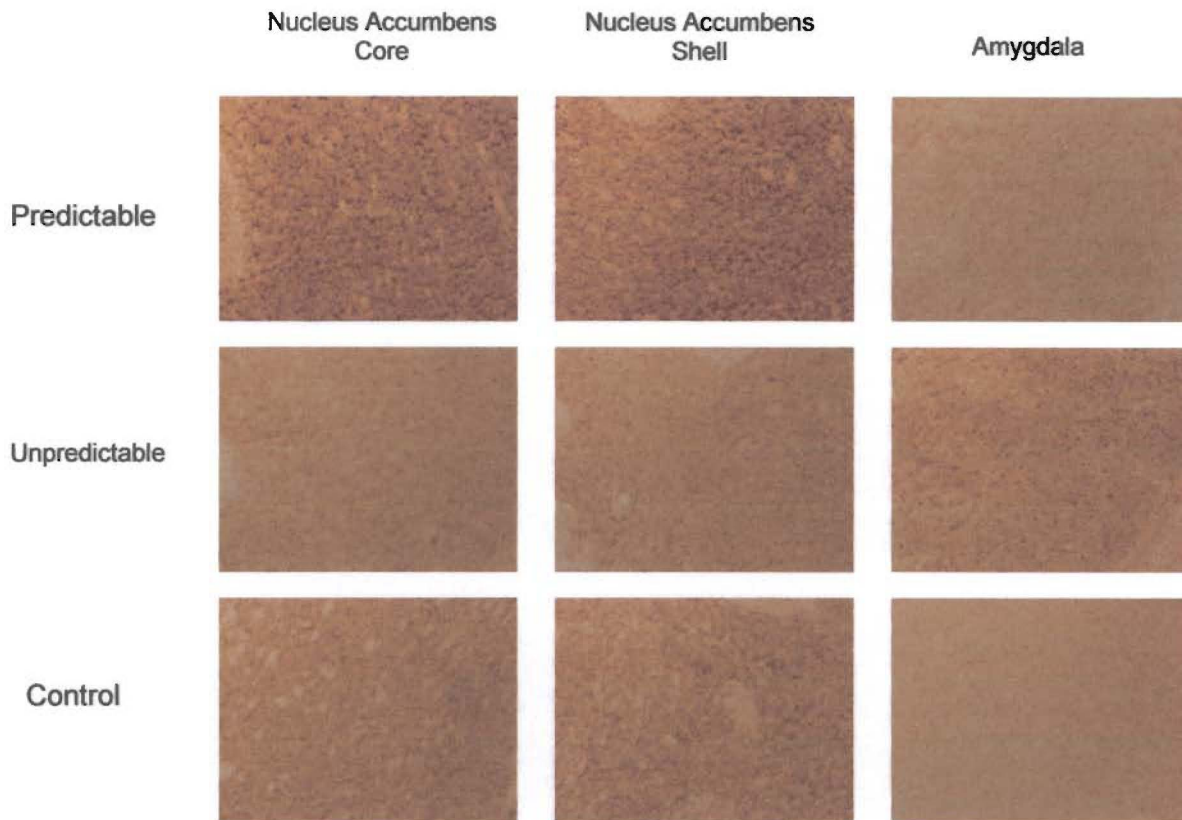
Figure 2. Representative sections of c-Fos staining by condition from the core of the nucleus accumbens, shell of the nucleus accumbens, and the amygdala.

Table 4

Pearson's Correlation Coefficients Between c-Fos Positive Cells and Behaviors

	Time Away	Time on Feet	Grooming	Sniffing	Leaps Over	Paws
Nucleus Accumbens Core	-.806*	-.764*	-.533	-.599	.400	.634*
Nucleus Accumbens Shell	-.764*	-.701*	-.563	-.438	.330	.537
Amygdala	.643*	.699*	.515	.657*	-.630*	-.705*

*p<.01

Discussion

The generalized matching law and the ideal free distribution have frequently been used to predict the behavior of an animal or a group of animals in relation to a source of reinforcement. These equations have several similarities, but perhaps the most important difference is that the ideal free distribution takes competition into account. The generalized matching law and the ideal free distribution have been studied extensively by themselves, but despite their commonalities, have rarely been combined empirically. In order to combine these laws into one foraging situation, Farmer-Dougan et al. (2007) introduced a competitor into a matching law foraging situation in order to examine how an element of competition impacted the matching law. It was found that the presence of an UC led to decreased sensitivity to reward while the presence of a PC led to increased sensitivity to reward compared to controls. Behavioral differences were also casually observed with rats in the UC condition demonstrating social avoidance and fear responses and rats in the PC condition engaging in competitive wrestling behavior.

The present study sought to replicate and expand previous findings by Farmer-Dougan and colleagues (2007) by examining the responses of rats to a PC or an UC. The rats were tested with another rat for all ten days of testing (the PC condition) or were tested alone for the first nine days and were introduced to a competitor rat on the final day UC condition). The results of the current study support observations from the previous study with the two groups of rats behaving very differently; rats in the UC condition demonstrated social avoidance behaviors (more time away from the feeder and more time on their feet) and more sniffing and grooming which rats in the PC condition

demonstrated more competitive wrestling behaviors (more jumps over the other rat, more hits to the other rat, and less time away from the feeder).

The present study also sought to examine the underlying neurological correlates of the observed behaviors by looking at difference in c-Fos expression among conditions in the amygdala and the nucleus accumbens and correlated the observed behaviors to the number of c-Fos positive cells. The previous behavioral observations by Farmer-Dougan et al. (2007) indicated that rats in the PC condition demonstrated increased sensitivity in reward compared to controls which would lead to significantly higher cell counts in the nucleus accumbens and that rats in the UC condition demonstrated avoidance responses which would lead to significantly higher cell counts in the amygdala compared to controls. The results of the present study supported these hypotheses; rats in the PC condition had higher numbers of active cells in both the nucleus accumbens core and shell compared to the other conditions and rats in the UC condition had higher numbers of Fos-positive cells in the amygdala compared to the other conditions. The behaviors associated with social avoidance or competitive wrestling were correlated to the number of c-Fos positive cells in each brain regions with both significant and non-significant associations found.

As described previously and as supported by the present study, rats in the UC condition showed a "social avoidance" response and displayed behaviors that interfered with collecting a reinforcer. They would remain away from each other and the feeder in the foraging box and would not interact. They also spent more time sniffing the other rat which would be expected since they were not familiar with each other. The rats in this condition also spent more time on their feet, more time grooming, and rarely jumped over

their competitor or pushed it with their paw. This set of behaviors together supports

Farmer-Dougan and colleagues' (2007) previous conclusion that the rats were engaging

in avoidance behavior and that these behaviors seemed to interfere with collecting

reinforcement and tended to occur away from the feeder.

Rats in the UC condition also spent more time grooming which is a behavior that

has previously been associated with avoidance behavior and stress exposure. Rats

engaging in avoidance behavior display more grooming behavior than other rats (Ferric,

Fernandez-Teruel, Escorihuei, Driscoll, Corda, Giorgi, & Tobena, 1995). The finding that

rats in the UC condition spend significantly more time grooming supports previous

findings that these rats are engaging in avoidance behaviors while rats in the PC

condition displayed significantly less grooming behavior. Also, grooming has been

shown to be stressed induced in a fear-eliciting situation (Katz & Roth, 1979). The rats

with an UC can be assumed to be stressed by the presence of the competitor more so than

the rats in the PC condition. Also, rats in the UC group spent significantly more time

grooming at the feeder which may indicate the presence of a competitor stressed them

more at the feeder due to new competitor for reinforcers.

The observed social avoidance and fear behavior was reflected by the higher

number of c-Fos-positive cells in the amygdala of UC condition rats compared to the PC

condition and controls and the associations between cell counts and the observed

behaviors. The higher number of c-Fos positive cells may indicate that they engaged in a

more aggressive or fear-eliciting situation. The amygdala has previously been shown to

be involved with aggressive responses and fear responses including social avoidance

behaviors such as the ones observed in the present study (Blanchard et al., 2001;

Vazdarjanova et al., 2007). Increases in c-Fos expression have previously been demonstrated in response to a social stressor, such as the introduction of a competitor (Bubser & Deutch, 1999; Herringa et al., 2004). The results of the present study showed that rats in the UC condition had significantly higher levels of activation in the amygdala compared to the predictable competitor condition and controls which supports these previous findings. Corrleational data also showed that the social avoidance behaviors of time away from the feeder, time spent on feet, and time spent sniffing were positively associated with the number of c-Fos positive cells in the amygdala. This association indicates a relationship between engaging in this set of social avoidance responses and a larger number of c-Fos positive cells present in the amygdale which indicates a greater fear-induced response. However, the amount of time spent grooming was not significantly correlated to the number of c-Fos positive cells in the amygdala ($r=.515$), nucleus accumbens core ($r=-.533$), or the nucleus accumbens shell ($r=-.563$), but the coefficients suggest strong trends in the expected direction that may be significant with a less stringent p value or a greater number of subjects. These rats were engaging in a seemingly more fearful response as was predicted by the previous findings and is now supported by c-Fos cell counts.

In contrast to the UC, when the competitor was predictable, the rats spent significantly more time at the feeder and engaged in the competitive wrestling behavior that was previously casually observed. The rats would climb over each other and push the other rat out of the way with their paw while at the feeder which is what Farmer-Dougan et al. (2007) described as the competitive wrestling behavior. While rats in the UC condition occasionally used a paw or climbed over the other rat, rats in the PC condition

did these behaviors significantly more. Rats in the PC condition also spent significantly less time away from the feeder, less time on their feet, less time grooming, and less time sniffing which suggests lower levels of social avoidance. Rats in this condition were not engaging in social avoidance behavior and spent the majority of their time at the feeder engaging in competitive wrestling behavior.

The observed competitive wrestling behavior in the PC condition appears to have become ritualized and may be able to be described as an operant response as described by Farmer-Dougan and colleagues (2007) and Skinner (1938). While the rats may have interacted in a more aggressive fashion during the start of testing, this behavior became ritualized into this less aggressive competitive wrestling behavior (Veneema & Neumann, 2007). Ritualizing this aggressive response would prevent the chance of injury and increase the chance of obtaining reinforcement (Veneema & Neumann, 2007). The rats did not have to engage in this behavior to receive a reinforcer, but this contingency seemed to develop as it would be very difficult to receive a reinforcer without engaging in this response; this may have led this behavior to develop into an operant response. The rat that was in front of the feeder would likely get the pellet which may suggest this behavior developed in order to ensure they were in front of the feeder when the reward was delivered (Farmer-Dougan et al., 2007). Since there were two rats in the apparatus at all times, this behavior developed in order to increase the chance of being in front of the feeder when a pellet was delivered and to prevent the chance of injury to the other rat.

Results from c-Fos immunocytochemistry demonstrated that rats in the PC condition and the control condition both had lower levels of c-Fos positive cells in the amygdala than rats in the UC condition, but they did not differ significantly from each

other. This may suggest that the competitive wrestling behavior became ritualized to the point that it was no more aggressive than foraging alone in the apparatus. These results may also indicate the lower levels of fear compared to the UC condition. Future studies could examine how many days a rat needs to be with a competitor for activation in the amygdala to decrease to levels that do not differ significantly from controls. For example, if these rats had been examined halfway through testing, how would the cell count have differed from controls?

The number of c-Fos positive cells in the nucleus accumbens regions was correlated to come of the observed behaviors in both the UC and PC conditions. Correlational data showed that the number of leaps over the other rat was not significantly associated with the number of c-Fos positive cells in the nucleus accumbens regions, but was negatively associated with the number of c-Fos positive cells in the amygdala. This suggests that greater c-Fos positive cell levels in the nucleus accumbens regions do not associate with greater occurrences of these behaviors, but greater amounts of c-Fos positive cells in the amygdala, and thus a greater aggressive or fear response, negatively associates with these behaviors that increase the chance of reinforcement. Correlations also showed that the number of c-Fos positive cells in the nucleus accumbens regions was negatively associated with social avoidance behaviors such as the amount of time spent away from the feeder and the time spent on their back feet. Correlational data also showed that the number of times pushing the other rat with a paw was positively correlated to the number of c-Fos positive cells in the nucleus accumbens core and negatively associated to the number of c-Fos positive cells in the amygdala. The association between the number of times pushing the other rat and the number of c-Fos

positive cells in the nucleus accumbens shell was not significant, but r was equal to .537

suggesting a strong trend in this direction that may be significant with more subjects or a

less stringent minimum p value. These correlations demonstrate a relationship between a

higher number of c-Fos positive cells, a greater amount of competitive wrestling

behavior, and a lower amount of social avoidance responses.

The results of the present study can also be related to the previous finding by

Farmer-Dougan et al. (2007) of increased reward sensitivity when the competitor was

predictable and decreased sensitivity when the competitor was unpredictable. The rats in

the PC condition spent the majority of their time in front of the feeder and engaged

primarily in behaviors that would improve their chances of obtaining a reinforcer such as

climbing over the other rat and pushing them away. They spent significantly less time

than rats with an UC sniffing, grooming, or on their hind legs which all interfere with

obtaining a reinforcer. However, rats exposed to an UC spend more time away from the

feeder and engaging in other behaviors not related to obtaining a reinforcer. For example,

they spend much more time on their feet, grooming, and sniffing which would all inhibit

their ability to retrieve a reinforcer and result in a lower sensitivity to the reward. The

competitor may be a "distraction" and the primary subject rat may be less attentive to the

reward than they were previously.

Results from the present study supported that rats in the PC condition were more

sensitive to reward by observing significantly higher levels of c-Fos expression in the

nucleus accumbens than rats in the other conditions. Previous studies indicate that the

nucleus accumbens is involved with reward behavior in the brain due to the projections of

dopamine neurons being centered there; dopamine is released when a stimulus or

behavior is rewarding and leads to higher levels of c-Fos expression (Stefani &

Moghaddam, 2006). It was predicted that since rats exposed to a PC demonstrated

increased sensitivity to reward in the previous study that levels of c-Fos expression in the

nucleus accumbens would be significantly higher and the present results supported this.

Rats in this condition had significantly higher levels of c-Fos expression in both the core

and the shell of the nucleus accumbens compared to the other two conditions.

A surprising finding was that controls and the UC rats did not significantly differ

on the number of cells active in the nucleus accumbens, while rats in the PC condition

had significantly higher numbers than these conditions. The previous study by Farmer-

Dougan et al. (2007) found that rats in the UC condition demonstrated undermatching

and lower sensitivity to reward than rats foraging alone, but the present data did not

reflect this. One possible explanation is that the undermatching behavior observed in the

previous study is only a behavioral phenomenon; perhaps they are just as sensitive to the

reward, but the presence of an UC prevents them from performing the matching behavior

to reflect their sensitivity. Another explanation is that the differences in reward sensitivity

between the UC condition and controls neurologically are not as easy to differentiate

between as the behavioral observations they translate to.

The finding that rats exposed to an UC were less sensitive to reward and also

spent more time grooming than rats in the other condition can be explained by behavior

systems theory. Behavior systems theory states that behaviors are grouped into biological

functions and goals (Timberlake, 1994). These sets of behaviors include feeding, sexual,

grooming and defensive. When an animal is engaging in one of these sets, they will be

insensitive to reinforcement received for a behavior in another set; for example, when an

animal is engaging in grooming behavior, they are not sensitive to food reward that is being delivered (Timberlake & Grant, 1975). This is relevant to the present study as the rats in the UC condition engaged in a large amount of stress-induced grooming behavior which would make them insensitive to the food pellets being delivered which supports their undermatching and lower sensitivity to reward. Research has also shown that grooming is one of the very few behaviors that cannot be increased by reinforcement which also indicates that the rats in the UC condition may not have been sensitive to reinforcement while they were grooming (Shettleworth, 1975).

Limitations and Future Research

Overall, the present data expand on previous literature by examining these social avoidance and competitive wrestling responses systematically. These behaviors, while only previously casually observed, have now been replicated and coded systematically. This systematic observation helped illustrate what these response topographies consist of and allow for future studies to focus on specific behavioral elements that occur in response to these competitor conditions. For example, future studies could focus on simply the response of those in the PC or only in the UC condition. Since rats in the UC condition spend significantly more time grooming, more time away from the feeder, and more time sniffing factors influencing these behaviors could be examined. The difference between number of jumps out of the apparatus was not significantly different between conditions; however, rats in the PC condition did not attempt to jump out at all while rats in the UC condition did. One future idea would be to create an apparatus that the rats were not able to jump out of with taller walls. If the rat were not able to jump out in this condition, it could be seen if they will still attempt to jump out or engage in another

avoidance behavior more frequently. The sniffing behavior may occur simply because the rat is not familiar with the competitor; future studies could examine how the sniffing behavior and avoidance behavior in general differ based on previous exposure to the competitor. For example, if they are exposed to it outside of the foraging situation before it is introduced as a competitor, will this sniffing behavior and avoidance behavior still occur when placed in the foraging situation together?

Future studies can also focus on the competitive wrestling behavior and expand on the possibility that it is an operant response in a variety of ways. Since the present study only examined this behavior explicitly on the final day of testing, future studies could investigate how this behavior develops over the course of the ten days. This would help create a full picture of how the behavioral response changes over testing from more of an avoidance response at the start into the competitive wrestling behavior that occurs after they have been together longer. If this competitive behavior is a type of operant response, future studies could focus on this competitive wrestling and examine it as other operant responses have been tested. For example, does it respond to the same variables that other operantly shaped behaviors do? (Skinner, 1938). One possible way to test this may be to change the rate of reinforcement, type of reinforcer, or stop reinforcement to see how this competitive wrestling behavior responds to changes in reinforcement.

A possible limitation of the current study is that the behavior coding system was developed by a person who was aware of the purpose and hypotheses of the study. The knowledgeable rater was aware of what behaviors were expected to occur in each condition. Even though this rater was kept blind to the condition that the rats were in, the behavior varied extensively between conditions such that it may not have been truly

blind. Due to the high rates of reliability between the coder kept blind to the hypotheses and the coder aware of the hypotheses, it seems that the criterion were coded reliably despite these limitations. However, future studies should replicate these findings using the same coding system in order to determine its validity outside of the current laboratory situation. Also, only behaviors of direct interest to the current study were coded for. This may mean that other behaviors occurred that were not examined that may have differed between conditions.

The present data also help expand the available literature on the reconciliation of the matching law and the ideal free distribution. These laws, while similar mathematically, have been studied separately in the past due to the theoretical differences between them. The present study combines these laws into one testing paradigm in order to investigate them side by side. These results show that the matching behavior of an individual rat does change in the presence of a competitor as would be predicted by the ideal free distribution. In order to determine if these two laws share an underlying common process, future research will need to expand on the complexity of the testing paradigm. The present study only used two subjects while real foraging situations would likely have more animals. In real life foraging situations, there are also social structures and issues of dominance that would need to be taken into account. For example, animals living in a group need to compete for resources, but need to balance this competition with the benefits of living in a group (Shettleworth, 1998). If a certain animal is higher in dominance, they may be entitled to a larger share of the food which also needs to be taken into account (Shettleworth, 1998). Since this experiment only used two animals, it cannot resolve the issue of an underlying common process to these laws. Future studies

can expand this concept by using more animals in a more complex social situation in order to resolve issues of determining an underlying process for both of these laws.

In summary, the present study replicated and expanded on previous findings by Farmer-Dougan et al. (2007) and demonstrated the different responses of a rat exposed to either a predictable or an unpredictable competitor. Rats exposed to a predictable competitor engaged in significantly more competitive wrestling behaviors while rats exposed to an unpredictable competitor engaged in significantly more social avoidance behaviors; these behaviors were also related to the increased reward sensitivity previously observed in rats exposed to a predictable competitor and the decreased reward sensitivity previously observed in rats exposed to an unpredictable competitor. c-Fos immunocytochemistry showed that rats in the PC condition had higher levels of c-Fos positive cells in the nucleus accumbens region and that rats in the UC condition had higher levels of c-Fos positive cells in the amygdala. These cell counts were occasionally found to significantly correlate to behaviors associated with competitive wrestling or a social avoidance response, and non-significant correlations were very strong and trending in the expected direction. While the current study expanded on previous findings by coding behavior and examining them on a neurological level, future research can expand on these findings in a number of ways in order to further understand responses to a predictable or an unpredictable competitor and in order to work towards reconciling the generalized matching law and the ideal free distribution.

References

Baum, W. M. (1974). On two types of deviation from the matching law: Bias and undermatching. *Journal of Experimental Analysis of Behavior, 22*, 137-153.

Baum, W. M. (1979). Matching, undermatching, and overmatching in studies of choice. *Journal of the Experimental Analysis of Behavior, 32*, 269-281.

Blanchard, R. J., McKittrick, C. R. & Blanchard, D. C. (2001). Animal models of social stress: Effects on behavior and brain neurochemical systems. *Physiology & Behavior, 73*, 261-271.

Bubser, M. & Deutch, A. Y. (1999). Stress induces Fos expression in neurons of the thalamic paraventricular nucleus that innervate limbic forebrain sites. *Synapse, 32*, 13-22.

Colombo, P. J., Brightwell, J. J., & Countryman, R. A. (2003). Cognitive strategy-specific increases in phosphorylated cAMP response element-binding protein and c-Fos in the hippocampus and dorsal striatum. *The Journal of Neuroscience, 23(8)*, 3547-3554.

Davis, E. S. & Marler, C. A. (2004). C-fos changes following an aggressive encounter in female California mice: A synthesis of behavior, hormone changes, and neural activity. *Neuroscience, 127*, 611-624.

Farmer-Dougan, V., Dougan, J. D., Knight, R., Toelle, M., & Chandrashekar, S. (2007). *Competition and sensitivity to reward: Effects of predictable and unpredictable competitive pairings in an open field paradigm*. Manuscript submitted for publication.

Fretwell, S. D. & Lucas, H. L. (1970). On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica, 19*, 16-36.

Herringa, R. J., Nanda, S. A., Hsu, D. T., Roseboom, P. H., & Kalin, N.H. (2004). The effects of acute stress on the regulation of central and basolateral amygdala CRF-binding protein gene expression. *Molecular Brain Research, 131*, 17–25.

Herrnstein, R. J. (1961). Relative and absolute strength of response as a function of frequency of reinforcement. *Journal of the Experimental Analysis of Behavior, 4*, 267-272.

Herrnstein, R. J. (1970). On the law of effect. *Journal of the Experimental Analysis of Behavior, 13*, 243-266.

Hursh, S. R. (1980). Economic concepts for the analysis of behavior. *Journal of the Experimental Analysis of Behavior, 34*, 219-238.

Kalin, N. H., Shelton, S. E. & Davidson, R. J. (2004). The role of the central nucleus of

the amygdala in mediating fear and anxiety in the primate. *The Journal of*

Neuroscience, 24, 5506-5515.

Katz, R. J. & Roth, K. A. (1979). Stress induced grooming in the rat: An endorphin

mediated system. *Neuroscience Letters, 13*, 209-212.

Roseboom, P. H., Nanda, S. A., Bakshi, V. P., Trentani, A., Newman, S. M., & Kalin, N.

H. (2007). Predator threat induces behavioral inhibition, pituitary-adrenal

activation and changes in amygdala CRF-binding protein gene expression.

Psychoneuroendocrinology, 32, 44-55.

Schultz, W. (2002). Getting formal with dopamine and reward. *Neuron, 36*, 241-263.

Shettleworth, S. J. (1975). Reinforcement and the organization of behavior in golden

hamsters: Hunger, environment, and food reinforcement. *Journal of Experimental*

Psychology: Animal Behavior Processes, 1, 56-87.

Shettleworth, S. (1998). Cognition, evolution, and behavior. New York: Oxford

University Press.

Stefani, M. R. & Moghaddam, B. (2006). Rule learning and reward contingency are

associated with dissociable patterns of dopamine activation in the rat prefrontal

cortex, nucleus accumbens, and dorsal striatum. *The Journal of Neuroscience, 26(34),* 8810-8818.

Timberlake, W. (1994). Behavior systems, associationism, and Pavlovian conditioning. *Psychonomic Bulletin & Review, 1,* 405-420.

Timberlake, W., & Silva, K. M. (1995). Appetitive behavior in ethology, psychology, and behavioral systems. In N. S. Thompson (Ed.), *Perspectives in ethology, Vol. 11: Behavioral design* (pp.211-253). New York: Plenus Press.

Vann, S. D., Brown, M. W., Erichsen, J. T., & Aggleton, J. P. (2000). Fos imaging reveals differential patterns of hippocampal and parahippocampal subfield activation in rats in response to differential spatial memory tasks. *The Journal of Neuroscience, 20,* 2711-2718.

Vazdarjanova, A., Cahill, L. & McGaugh, J. L. (2001). Disrupting basolateral amygdala function impairs unconditioned freezing and avoidance in rats. *European Journal of Neuroscience, 14(4),* 2001.

Veneema, A. H. & Neumann, I. D. (2007). Neurobiological mechanisms of aggression and stress coping: A comparative study in mouse and rat selection lines. *Brain, Behavior, and Evolution, 70,* 274-285.

Zhu, X. O., McCabe, B. J., Aggleton, J. P., & Brown, M. W. (1997). Differential

activation of the rat hippocampus and perihinal cortex by novel visual stimuli and

a novel environment. *Neuroscience Letters, 229*, 141-143.