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Inequity aversion: Do rats get jealous?

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HONORS PROJECT

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Abstract

It is well known that humans have the capacity to prefer certain rewards over others. This idea has been studied in animals and is considered the relative reward processing theory. Research conducted on primates and rodents have found that they form an opinion on, and behave according to the relative magnitude of a reward compared to others (Cromwell, Hasani, & Schultz, 2005; Onge, Chiu, & Floresco, 2010). It is also accepted experience the emotion of jealousy in response to many different situations including uneven reward payoff. It has been theorized that some nonhuman animals including primates and domestic dogs are able to distinguish differences reward magnitude and modify their behaviors accordingly (Brosnan, 2006; Range, Horn, Viranyi, & Huber, 2009). This present study examines both theories by exposing experimental rats to high tones that cue high magnitude (3 pellets) rewards and low tones that cue low magnitude (1 pellet) rewards. They are also exposed to a control rat receiving only high rewards. The results show a pattern towards relative reward processing as well as significance towards inequity aversion when entering the food cup for the reward.

Introduction

An individual's motivation to complete a task in order to receive a reward is known to be driven by biological influences, selfish gain, and altruistic prosocial behavior (Zacki, Schirmer, & Mitchell, 2011; Raihani, McAuliffe, Brosnan, & Bshary, 2012). In social settings it has been shown that humans respond negatively to unfair rewards through jealousy and anger (Vecchie, 2005). Research has also shown that nonhuman primates and canines will also respond adversely to inequity (Brosnan, 2006; Brosnan, Schiff, & De Waal, 2005; Range, Horn, Viranyi, & Huber, 2009). While selfish drive can cause negative consequences to unfair rewards, human studies have also shown that one will act altruistically and receive a smaller reward if it results in one's peers receiving an equal reward (Shaw & Olson, 2012). It is believed that altruism as a social construct has evolved over time in many animals that frequently interact with other nonkin animals in order to maintain a balanced social structure as well as to ensure the beneficial cooperation of partners in the future (Brosnan, 2006; Zacki et al., 2011; Horowitz, 2012). The idea that humans and other animals have a sense of unfairness and respond adversely to unequal reward distribution is called inequity aversion (Brosnan et al., 2005). It is suggested that there are three steps towards the evolution of inequity aversion. The first step says that an organism must be able to recognize the rewards of others and then compare that to their own reward magnitude. Then, an organism must develop the ability to respond to unequal rewards. Finally, an organism must be able to develop specific responses to uneven reward payoffs in order to achieve the most favorable social gain (Raihani et al., 2012).

In order for an organism to understand the inequity of others' rewards, it must first learn to favor some rewards over others. Relative reward processing allows one to understand the incentive value of a reward and favor it to a less preferred reward, or consider it as a lesser

reward compared to a more favored reward (Cromwell & Schultz, 2003; Cromwell, Hasani, & Schulz, 2005). By exposing nonhuman primates to three juices that hold reward values of differing magnitudes it has been found that there is higher neural activity in the striatum when the animals receive a higher reward compared to the lower rewards (Cromwell et al., 2005). Research has also shown that human participants actively respond to relative rewards both behaviorally and through neural activation (Bijleveld, Custers, & Aarts, 2012; Bjork, Gang, Smith, & Homer, 2010; Carlson et al., 2011). A study conducted on human participants using monetary rewards ranging from 0 cents to 5 dollars showed increased activity in the medial frontal cortex (mFC) as well as the ventral striatum (VS) including the nucleus accumbens (NAcc) when a reward cue was shown compared to a loss of reward cue. This study also found that there is increased activation of the NAcc with increased reward magnitude; however, a difference in activation to reward magnitude only occurred when the amount was gained compared to when the amount was lost (Bjork et al., 2011).

There have been many studies conducted on rat behavior and their responses to relative rewards as well as risky choice behavior. Because most of these studies center on dopamine levels in the medial prefrontal cortex (mPFC) and nACC with regards to risky choice behavior, they have implications to human impulsivity and substance abuse disorder (Onge, Chiu, & Floresco, 2010; Ostlund & Maidment, 2012). However, the results of these studies are also important in understanding the relative reward process in the rat model. A study using rats to compare the relative reward of a high pellet magnitude but risky outcome choice compared to a low pellet magnitude but certain outcome choice found that the rats will press a lever for the risky choice but high reward outcome more often than the certain low reward outcome (Onge et

al., 2010). These findings have been duplicated in multiple other studies (Ostlund & Maidment, 2012; Izquierdo et al., 2012; Mai & Huber, 2012).

After humans and nonhuman animals are able to distinguish relative magnitudes of rewards and behave accordingly, they can view other's rewards and react according to the inequity aversion theory. Research using nonhuman primates show signs of inequity aversion. A study using capuchin monkeys showed that both reward magnitude and effort to achieve the reward have an effect on their behavior. The capuchin monkeys were less likely to exchange a token for a lesser reward when their neighbor monkey received a greater reward, and would even refuse to exchange the token when the neighbor monkey did not need to exchange anything for a reward. This suggests that primates actively view and analyze the rewards their partners get and behave accordingly. In the wild, this understanding may increase an animal's fitness by learning from the animal that is receiving a greater reward (Brosnan, 2006; Brosnan, Schiff, & De Waal 2005).

Following the findings of inequity aversion in nonhuman primates, several studies of inequity aversion have been conducted on domestic dogs. One such study investigated the willingness of a dog to give a paw to the experimenter in order to receive a reward that was either of lower quality or lesser magnitude than the control dog received. The results of this study show that, when they expect to receive a lower magnitude reward, they will give the experimenter their paw significantly less than when they expect an equal reward as the control dog. However, there were no significant behavioral changes when the experimental dog would receive a lower quality food reward (Range et al., 2009). Research has also shown that domestic dogs will prefer a higher rewarding trainer compared to a fair trainer. In this experiment, the experimental dog was put into an inequity aversive situation by exposing them to a trainer who

gives the control dog a higher reward and a trainer who rewards the two dogs evenly. While the dog preferred the trainer who gave uneven rewards, the experimental dog did not show signs of aversion towards the trainer or the control dog when presented with the lower magnitude reward (Horowitz, 2012).

In human participants, it was also found that children as young as six show signs of inequity aversion when they are told to distribute resources among their peers. They would often rather throw a resource away than distribute it unequally amongst a group. According to Shaw and Olsen (2012), the researchers of this study, the concern with equity may have evolved to signal to others that they are interested in social welfare. This would increase fitness in social animals because it would encourage others to also offer their resources to that individual. As well as showing sensitivity to inequity aversion, human gambling studies have shown that the striatum, and mPFC are involved in decision making in a social situation. An fMRI study found that there is increased activity in the striatum when participants won more than the confederate in a gambling task compared to when they won alone. Activity in the striatum was also less when the confederate won and the participant lost compared to when the participant lost by themselves. The mPFC also showed higher activity when a participant won in the social setting comparatively (Bault, Joffily, Rustichini, & Coricelli, 2011).

While rat research has been conducted studying the relative reward processing theory as a model for human addiction, to date there has been no testing done to examine the inequity aversion theory. It is known that rats are playful and social animals (Panksepp & Burgdorf, 2003; Siviý & Panksepp, 2011). Since rats do interact with nonkin animals within their species they should react similarly to how canines, nonhuman primates, and human participants react to inequity aversive situations. This present study tests the reward processing theory and inequity

aversion in the rat by exposing the subjects to unequal reward amounts for the same amount of work as well as exposing them to these unequal rewards in a social situation. It is hypothesized that rats will respond more quickly to a lever press and subsequent food cup entry when they predict a higher reward due to the relative reward processing theory. It is also predicted that a rat, when presented with a lower reward value than a neighboring subject, will respond less quickly to a lever press and food cup entry due to inequity aversion.

The results of this study could suggest implications to the human theories of jealousy. We may also be able to better understand workplace envy as well as efficiency as a result of uneven rewards and incentives.

Materials and Methods

Animals

N=12 male Sprague-Dawley rats (Charles Rivers) housed in a temperature (75° F) and humidity (20%) controlled room on a 12/12 hour light dark schedule were used. The rats were housed in separate home cages and allowed water ad libitum throughout the training and experimental procedures. They were food deprived to 85%-90% of their free feeding weights during training and experimental sessions. N=10 rats were used as the experimental rats and n=2 rats were used as controls.

Lever Training

In order to lever train the rats, they were placed in an operant chamber with a food cup and a retractable lever in a dark room as can be seen in figure A1 of the appendix. Each training session began with the house light off and the lever retracted, this is considered the intertribal state. After a variable interval time period (15 seconds, 20 seconds, 25 seconds, 30 seconds, 35 seconds, 40 seconds, and 45 seconds) randomized by the Medstate program, the light will house

light turned on. Two seconds after the light turned on the lever would protract. When the rat pressed the lever the rat received a food pellet reward, the light turned off, and the lever retracted and that trial ended. The lever remained protracted until the rat pressed it or until the session timer was up. Following each trial the chamber returned to the intertrial period until the interval time schedule was up and the light turned on cueing the protraction of the lever. In order to move on to the tone training sessions the rat must have completed 20 trials in a one hour time period for two days in a row.

Tone Training

After each rat has completed lever training they were then exposed to three days of tone training. Each rat was exposed to the low tone (70 dB, 2000 Hz) and a low reward (1 pellet) on a Tuesday, a high tone (70 dB, 6000 Hz) and a high reward (3 pellets) on Wednesday, and again a low tone for the low reward on Thursday. The rat had to complete 20 trials in an hour for all three sessions. The trials during the tone training sessions were similar to those in the lever training sessions with the same variable interval time period between each trial. Each trial began when the house light turned on, two seconds after the light turned on the tone played from the audio generator for five seconds. Following the five second tone the lever protracted. After the rat pressed the lever it received a food reward dependent on which tone was played, the lever retracted, and the box returned to the intertrial state, this process can be seen in figure A2. Both the experimental rats and control rats completed the same tone training sessions.

Experimental Session

The week following tone training both the experimental and control rats were exposed to one session a day for four consecutive days (Monday-Thursday). The control and experimental rats were placed in boxes next to each other and could see the other rat and hear the different

tones. As in the tone training sessions, a house light turned on to cue the tone. After the tone played for five seconds the lever protracted for the respective rat. Each session would start with the house lights off for both boxes and. After the variable time period, the light would turn on in the control rat's box cueing the high tone and, following the lever press, the subsequent high reward. After the control rat completes one trial a trial will then begin for the experimental rat. After a variable interval intertrial period the house on the experimental rat's chamber turned on cueing the tone, lever, and return to intertrial phase following the lever press. This process continued back and forth until each rat completed twenty trials, as shown in figure A3. This continued until each rat completed twenty trials. The first week of the experimental session lasted four days with the control rat exposed to only high tones for all twenty trials while the control rat received a combination of both high and low rewards. The four conditions that the experimental rats were exposed to are 1.) 5 consecutive high tones for a high reward followed by 15 low tones for a low reward, 2.) 10 high tones followed by 10 low tones, 3.) 5 consecutive high tones and 5 consecutive low tones until the rat has completed 20 trials, and 4.) 2 high tones followed by 2 low tones until 20 trials have been completed. Each experimental rat was exposed to these situations in a random order.

Following the four days in the chamber with the control rat next to it receiving the high reward, the rat then underwent four days with the same series of conditions; however, this time there was no control rat in the chamber next to it. During this final week of testing the rats were exposed to the four conditions in the same order as the previous week. In this situation there is no neighboring rat as well as no cues coming from the neighboring box.

Data Analysis

The data were collected for all trials during the training and experimental sessions. The

rat's latency to press the lever as well as the latency to enter the food cup after the lever was pressed was recorded using the Medstate program. Paired samples t tests were run to compare the means between the latencies after hearing the high tone and the low tone for both lever pressing and entering the food cup, this data was analyzed during the final week of experimentation. In order to look at the inequity aversion theory in rats, paired samples t-tests were run using the means for all low tone lever press latencies and food cup latencies when the experimental rat was paired with a control rat and compared those with the data collected when the rats completed the sessions on their own. The data were also analyzed for each session by running a paired samples t-test to compare the means for lever press latency and food cup entry latency for sessions 1, 2, 3, and 4 between the sessions with the experimental rats paired with a control rat and the experimental rats on their own. Finally, to show individual variability in the rats, paired samples t-tests were run to compare the means from each session 1-4 when the rats were paired with a control and when they completed the session by themselves. For all data analyzed to examine the inequity aversion theory, only the low tone data were used.

In order to remove any extreme outliers from the data, all trials that had latencies more than two standard deviations above the mean were removed from analysis. N=1 rat did not complete session two when coupled with the control rat. Therefore, data for session two for both paired and alone sessions for that rat were excluded from all data analysis.

Results

Relative Reward

A repeated measures t test did not show any significant difference between the lever press latency and the food cup latency between the high and low tones. However, the results of the t test did show that the food cup latency between the high reward ($M = 2.46$, $SD = 4.19$) and the

low reward ($M = 3.65$, $SD = 12.08$) is reaching significance, $t(337) = -1.71$, $p = .09$. This can be seen in figure B1.

Inequity Aversion

The results of a repeated measures t test show that there is a significant difference for the food cup entry latency generalized between all four conditions where the experimental rats were paired with the control rats ($M = 7.61$, $SD = 27.37$) and when the control rats were by themselves ($M=3.48$, $SD = 10.86$) for the low reward only, $t(429) = 3.045$, $p < .05$. A repeated measures t test comparing the food cup entry latency between the alone and paired sessions also showed significance for all four conditions individually; condition one paired ($M = 13.92$, $SD = 42.8$) and alone ($M = 2.29$, $SD = 2.75$) is significant, $t(140) = 3.22$, $p < .05$, condition two paired ($M = 2.37$, $SD = 3.0$) and alone ($M = 1.5$, $SD = .72$) shows significance, $t(81) = 2.7$, $p < .05$, condition three paired ($M = 7.45$, $SD = 20.01$) and alone ($M = 2.57$, $SD = 5.95$) is significant, $t(95) = 2.42$, $p < .05$, lastly, condition four paired ($M = 8.97$, $SD = 22.01$) and alone ($M = 1.46$, $SD = .71$) is also significant, $t(93) = 3.34$, $p < .05$, which can be seen in figure B2.

Of the ten experimental rats, $n=8$ of them showed a significant difference for at least one of the conditions (1, 2, 3, or 4) for either the lever press latency or food cup latency after the low tone. The first rat showed a significant difference between food cup entry paired ($M = 1.44$, $SD = 1.03$) and alone ($M = .026$, $SD = .02$), $t(14) = 5.32$, $p < .05$, for the first condition. The second rat showed a significant difference between lever press latency paired ($M=.34$, $SD=.10$) and alone ($M=.27$, $SD=.07$), $t(9) = 2.04$, $p < .05$ during the fourth condition. The third rat showed a significant difference between food cup entry paired ($M=1.33$, $SD=.10$) and alone ($M=1.26$, $SD=.04$), $t(14) = 2.12$, $p < .05$ during the first condition. The fourth rat showed a significant difference between food cup entry paired ($M=1.37$, $SD=.34$) and alone ($M=1.04$, $SD=.23$), $t(9) =$

2.25, $p < .05$ during the fourth condition. The fifth rat showed a significant difference between lever press latency paired ($M=1.99$, $SD=1.27$) and alone ($M=.31$, $SD=.07$), $t(9) = 4.25$, $p < .05$ during the third condition. This rat also showed a significant difference between lever press latency paired ($M=1.35$, $SD=1.31$) and alone ($M=.67$, $SD=.70$), $t(9) = 2.28$, $p < .05$ during the fourth condition. Lastly, this rat also showed a significant difference between food cup entry paired ($M = 1.75$, $SD = .60$) and alone ($M = .06$, $SD = .06$), $t(9) = 8.63$, $p < .05$ during the fourth condition. The sixth rat showed a significant difference between lever press latency paired ($M = .54$, $SD = .33$) and alone ($M = .31$, $SD = .09$), $t(14) = 2.62$, $p < .05$ for the first condition. The seventh rat showed a significant difference between the food cup entry paired ($M = 23.9$, $SD = 13.8$) and alone ($M = 2.24$, $SD = .28$), $t(8) = 4.73$, $p < .05$ during the fourth condition. The last rat showed significant differences for conditions one and two. In condition one the rat showed a significant difference, $t(13) = 3.37$, $p < .05$, for lever press latency paired ($M = 1.25$, $SD = .93$) and alone ($M = .36$, $SD = .21$) in condition one, and a significant difference, $t(9) = 2.42$, $p < .05$ between the paired session ($M = 3.65$, $SD = 1.85$) and the alone session ($M = 2.56$, $SD = .87$). For all other sessions the data was not significant.

Discussion

While there was no significant difference across all rats and sessions for the high and low tone lever press latency or food cup entry latency during the third week of experimentation, figure B1 shows that the rats do show a pattern of distinguishing between the high and low tones. This suggests that certain rats use relative reward processing when deciding the value of a reward. Lovic, Saunders, Yager, and Robinson (2011) posit that some rats are considered sign trackers and will find that a cue signaling a reward is attractive and will therefore respond equally to each cue. Cue trackers, on the other hand, will find the cue itself an effective tool for

deciphering the magnitude of the reward. The present study did not use any method to distinguish if the rats were either sign trackers or cue trackers which could cause the data to be less consistent.

The results for the inequity aversive portion of the experiment, however, show that the rats do respond negatively when they would receive a lower reward than their partner. While the data is not consistently significant for all rats individually, when considered as a whole the data does show behavioral changes between the paired conditions and alone conditions. This could be because there are many more trials considered causing the standard error to be less.

The rats may have responded slower to receiving a low reward when their partner is receiving a high reward could be because the rats were feeling a sense of unfairness as a response to the unequal payoff for the same amount of work. In one situation, a rat failed to press to lever completely when exposed to the low reward in a social situation. This occurred during the twelfth trial in the second condition. The second condition has the experimental rat receiving ten consecutive high tones followed by ten consecutive low tones; after the low tone played twice the experimental rat may have stopped responding because it refused to do the work to receive a low reward compared to the control rat suggesting that inequity aversions is playing a role in their thought process. This occurred on the second day of experimental testing and did not occur any subsequent times.

The findings of this experiment are consistent with the literature that suggests inequity aversion is an evolutionary construct in nonhuman animals such primates and dogs as well as humans. While the debate surrounding the theory of inequity aversion states that these behavioral changes could be the result of a frustration effect (Silberburg, Roma, Ruggiero, & Suomi, 2005). The frustration effect occurs when the animal has no incentive to complete a task

for a reward because of their experiences with higher rewards (Gutman & Sgro, 1979). This confound was removed by adding the second experimental week. During this week the rats were exposed to the same conditions on the same day without a partner next to them receiving a high reward. If the results were due to a frustration effect then we would see the same behavior during both paired and alone sessions. This effect should also cause the results for relative reward processing to be much more dramatic.

Due to the fact that we did not distinguish between sign trackers and cue trackers there was a lot of variability within the data. In order to remove that confound future research should work to remove any rats that would be considered sign trackers from the experiment. We may also be able to look at the brain areas involved in reward processing and the differences that can be seen in sign trackers versus cue trackers. Another confound present in this study is the fact that most of the rats used were not naïve rats. They were of varying ages and some may have been involved in another study of the relative reward process using a similar setup with a tone cueing a certain reward magnitude. Lastly, because each rat completed the paired sessions first and the alone sessions the week after, there is a possibility that an order effect could be a confound within the data. This could be removed in future studies by having an equal amount of rats perform the alone sessions before the paired sessions as well the order presented in this study.

The results of this study imply that rats may be using basic inequity aversion functioning when evaluating the worth of a reward in a social setting. Studying this theory in rats is beneficial because of the possibility to manipulate certain brain structures through lesions, the ability to monitor localized neural firing, as well as psychopharmacological manipulations that can be made. By completing more extensive research on the subject we may gain a better

understanding of jealous behavior and the mechanisms behind it.

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Appendix A

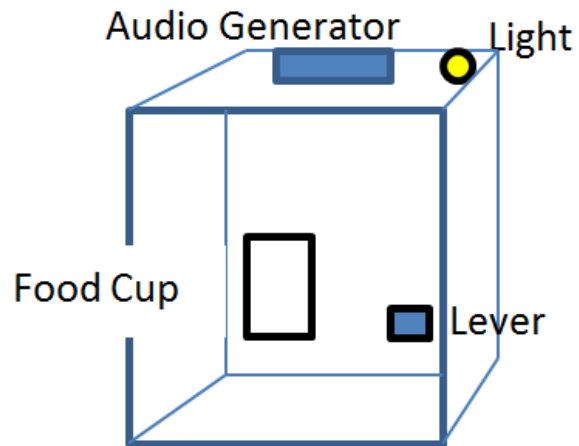


Figure A1. This is the operant box used for the experiment. For the experimental rat the light is on the right side of the box while the control chamber has a light on the left side of the chamber.

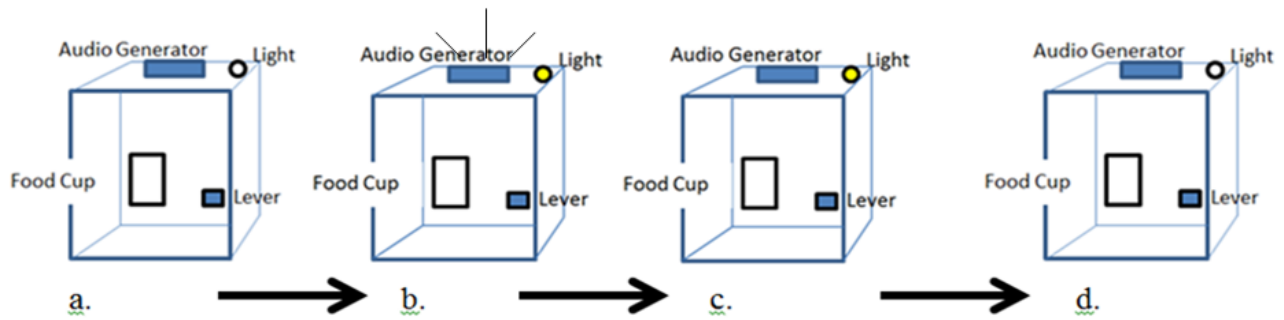


Figure A2. This shows the series for one trial during the tone training sessions. a) Shows the chamber during the intertrial phase. b) Represents the light turning on and two seconds later the tone plays. c) After the tone plays for five seconds the tone stops and the lever protracts; the light remains on. d.) After the lever has been pressed the food reward enters the food cup, the lever retracts, and the light turns off returning it to the intertrial phase.

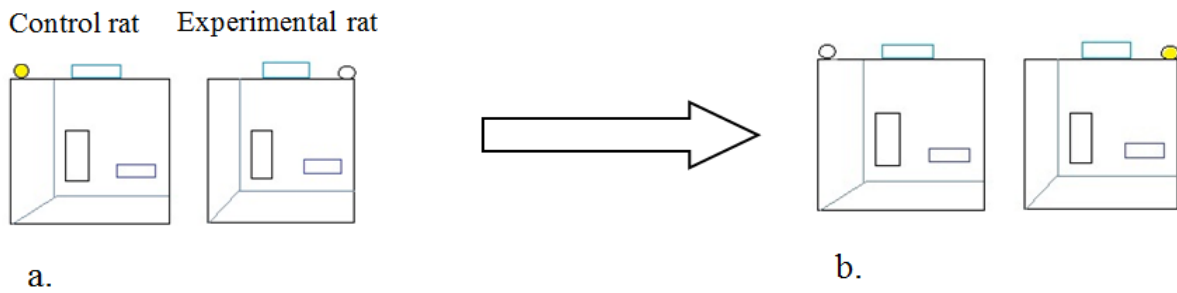


Figure A3. This figure shows one trial for the control rat and experimental rat during the experimental session. a) The light turns on first for the control rat cueing a trial. For the control rat the trials will always have a high tone followed by a high reward. During a trial for the control rat the house light for the experimental rat is off and the lever is retracted. b) When the control rat's trial has finished, the control rat's chamber returns to the intertrial phase. After a variable interval time the experimental rat's house light turns on cueing a trial. This rat will receive either a high tone or a low tone depending on the condition.

Appendix B

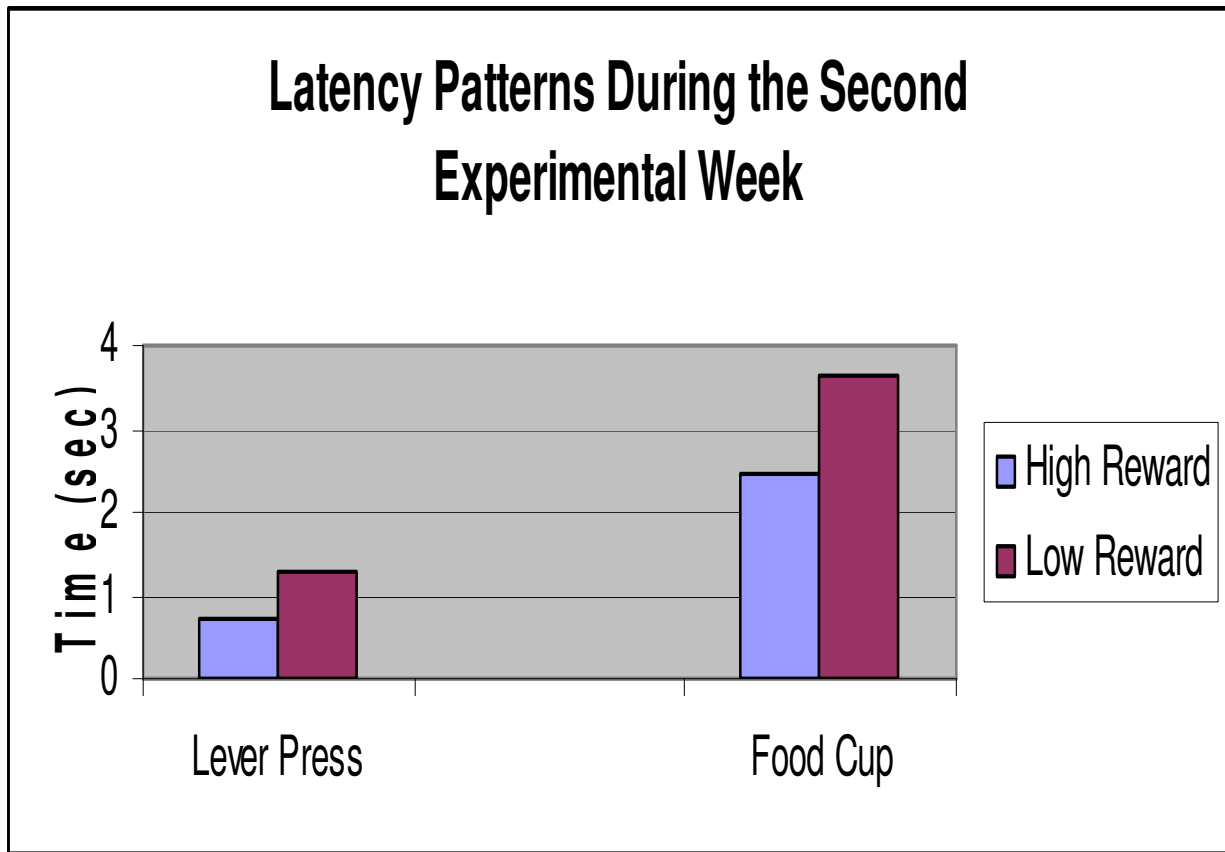


Figure B1. This graph shows the rats latency to press the lever and enter the food cup for all high and low trial during the final experimental week.

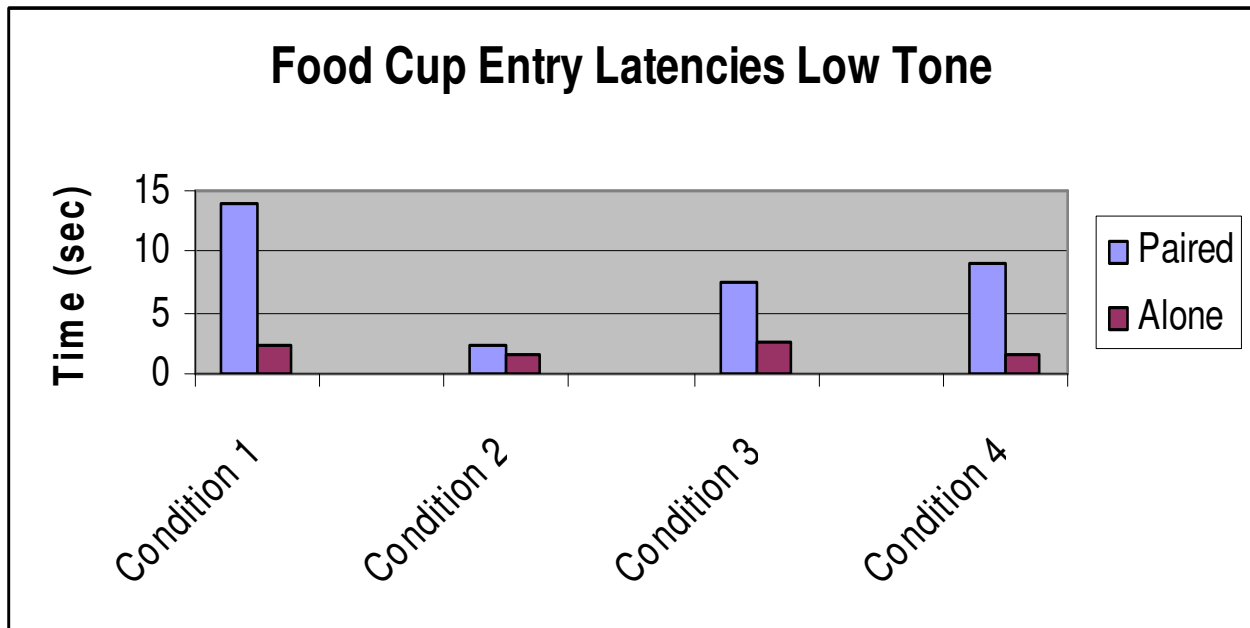


Figure B2. This graph represents the pattern of food cup entry after the low tone has played between the paired session and the alone sessions for conditions 1, 2, 3, and 4. All differences are significant.