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THE UNIVERSITY OF VERMONT

DEPARTMENT OF PSYCHOLOGICAL SCIENCE

UNDERGRADUATE HONORS THESIS



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THE EFFECT OF REPRODUCTIVE  
EXPERIENCE ON HABIT FORMATION

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April 27, 2020

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# 1 Abstract

Habits are formed by repetitive stimulus-response (S-R) associations that induce changes in the brain's memory and learning systems, shifting from a hippocampal-based cognitive system to a striatal-based stimulus-response system. It is believed that hormones present throughout pregnancy may play a role in their modulation, and recent literature suggests that females display habitual behavior earlier in training than males and that pregnancy induces cognitive enhancements to these regions of the brain. Therefore, the focus of this project was to examine if the reproductive experience (RE) enhances, delays, or does not affect habit formation in females, and it was predicted that primiparous (one maternal experience) females will undergo habit formation *earlier* than nulliparous (virgin) rats. This was accomplished using operant training and reward devaluation methods followed by a test of habit. A 2 (RE) x 2 (devaluation) factorial ANOVA revealed a lack of significant main effects for both groups. However, *a priori* planned comparisons between devalued and non-devalued groups within each RE group showed a marginally significant difference within the primiparous condition. Given the low statistical power of this pilot study, these results suggest that primiparous rats are *more goal-directed* than virgin females at 120 reinforcers, which we speculate may be due to the new metabolic set point caused by the energy demands of pregnancy and lactation (Numan & Woodside, 2010). Altogether, this study contributes a foundational understanding of parity's effect on habit formation and metabolism in female animals, and in the future, this may help elucidate how pregnancy modulates regions of the brain associated with psychopathologies.

## 2 Introduction

It is known that the mammalian brain does not contain a single memory center or brain structure that underlies all learning processes. Instead, the brain is organized into multiple systems that interact given a certain set of environmental and biological influences. Neuroscientists theorize that there are two major memory systems: a hippocampal-based cognitive memory system and a non-hippocampal based stimulus-response system that ultimately processes habitual behavior (Packard, 2009). It has been found that hippocampal-dependent learning is acquired quicker than striatal-dependent response learning, and that there is a shift in the control of learned behavior from the cognitive system to the stimulus-response system in well trained animals. In other words, learning begins in the hippocampus but progresses towards the dorsolateral striatum (DLS) throughout training. These findings provide substantial evidence for the independence of these two memory systems, and this idea is referred to as the “multiple memory perspective” (Packard, 2009).

Habitual behavior is displayed as a result of changes in the brain, and there are a variety of ways that these changes can be measured. It is known that behaviors are goal directed at the onset of instrumental training, or in other words, the behavior is initially sensitive to the outcome of the response. Furthermore, it has been found that there is flexibility in the performance of a goal directed behavior, as these behaviors are sensitive to the value of the outcome (Adams & Dickinson, 1981). That is to say if an outcome is favorable, the animal will display appetitive goal directed behavior to earn that outcome. However, if the outcome becomes unfavorable, the animal has the flexibility to change their response and may display avoidant behavior as a result of less motivation to seek the reward. As such, this stage of instrumental learning can be referred to as reward-outcome (R-O) learning.

As an animal progresses further into training, the value of the outcome becomes less substantial in driving the behavior, and this is referred to as associative stimulus-response (S-R) learning (A. Dickinson, 1985). Under repetitive S-R training, the behavioral response is not determined by

the value of the outcome but by the presence of stimuli associated with the performance of the response, such as external contextual cues. Therefore, at this stage of training, the animal is insensitive to changes in the value of the outcome and will produce the behavior in the presence of the associated stimuli. Following instrumental training and reward devaluation, the automaticity of these responses allows for these behaviors to be classified as habits, and these methods have been widely shown to measure habitual behavior. Based on what we know about learning and memory systems, the paradigm employed in this study closely aligns with the executive shift that occurs in the hippocampus and striatum from goal-directed (R-O) to habitual behavior (S-R) in order for accurately assess habit formation.

In our lab, we have previously investigated one of these memory systems, the stimulus response system, by examining sex differences in the development of habitual behavior. We found that cycling, nulliparous female rats show habitual behavior *earlier in training* than intact male rats (Schoenberg, Sola, Seyller, Kelberman, & Toufexis, 2019). Given these findings and the significant changes that occur in the brain throughout pregnancy, we predict that there may be differences within female rats based on their reproductive experience.

In the context of reproductive behavior, there is a substantial body of research that suggests that maternal experience enhances cognitive function. Additionally, the efficiency to which these tasks are consigned to habit may prove to be highly adaptive. Specifically, studies have shown that in female rats, reproductive experience enhances certain types of cognitive performance, such as hippocampal spatial learning and object-in-place learning (Macbeth & Luine, 2010; Paris & Frye, 2008). These types of cognitive enhancements, especially spatial learning, may be adaptive in that they would augment foraging behavior to ultimately increase offspring survival. Some studies have noted increases in behavioral flexibility, particularly in the postpartum period, in which set shifting, a task dependent on the prefrontal cortex, is greatly enhanced (Albin-Brooks, Nealer, Sabihi, Haim, & Leuner, 2017). While these changes are most likely *initiated* by the extensive hormonal changes throughout pregnancy and the postpartum period, other studies have demonstrated that these

cognitive enhancements are *sustained* after parity (post-weaning) and once female rats have returned to their normal estrous cycle (Macbeth & Luine, 2010). Therefore, these cognitive enhancements resulting from parity appear to be preserved throughout the rest of a female's life.

Enhanced cognitive ability is not the only adaptive benefit triggered by parity in rats. In order to assure successful mother-offspring interactions, maternal behavior must be rapidly initiated at birth (Olazábal et al., 2013). This entails the activation of reward pathways in the brain that stimulate appetitive motor responses toward the pup stimuli. These behaviors include, but are not limited to, approaching pups, nest-building, licking and grooming, and crouching to mediate suckling. These behaviors are mediated by certain neural mechanisms and hormones that work to motivate maternal behavior (For extensive reviews of the mechanisms underlying maternal behavior, see (Numan & Young, 2016)). Similar to how cognitive enhancements are sustained post-parity, these maternal responses towards pup stimuli are sustained throughout the life of the mother, regardless of if she gives birth again (Olazábal et al., 2013). Our previous work has established differences in habit formation between males and females, however the effect of reproductive experience on habit formation has yet to be investigated.

Since appetitive maternal motor behavior is rapidly initiated after giving birth and retained throughout the life of the mother, and because cognitive enhancements are maintained in female rats following reproductive experience, we hypothesize that the changes that occur over the course of pregnancy (and possibly the lactational period) include systems that control habit formation, such as those within the striatum. Altogether, this would result in persistently altered habit formation **in general**. Therefore, we predict that habit formation in primiparous rats will occur *earlier in training* than nulliparous rats at 120 reinforcers.

Lastly, it is important to note that this project is a pilot study designed to provide preliminary data. Therefore, because this study is the first of its kind, results of this experiment will serve as a foundation for future projects regarding parity's impact on habit formation. In order to test this hypothesis, the following experimental approach was employed.

## 3 Methods

### 3.1 Subjects

8 timed-pregnant (primiparous) and 8 adult virgin (nulliparous) Long-Evans were housed in a climate-controlled colony room maintained at 23°C. The colony room had a 12-hr light-on-light-off cycle, and all testing was completed during the light phase. Primiparous females were housed singly after day 15 of pregnancy and gave birth on day 21. They were left to rear their offspring to weaning (21 days) and were then rehoused in pairs. To ensure that each primiparous animal had equal metabolic demands given that males require more maternal attention, the litters were numbered and sex balanced. Nulliparous females were also housed in pairs, and experimental procedures began 21 days post-weaning for both primiparous and nulliparous groups. Prior to operant training, subjects were food restricted to maintain a target weight of 85% of their *ad libitum* weights for the duration of the experiment, and vaginal swabs were taken daily at approximately 12 pm in order to monitor the estrous cycle.

### 3.2 Apparatus

The training apparatus consisted of six standard rat operant chambers (Med Associates, St. Albans, VT). On the right-facing chamber wall was a port into which a hopper delivered a 45-mg sucrose pellet. At the right of the head entry was a nose-poke device that emitted an infrared beam which detected the animal's nose-poke by disruption of the beam. This then signaled the delivery of a sucrose pellet to the operant chamber.



### **3.3 Instrumental Training**

All subjects were assigned an operant chamber where they were trained and tested for the duration of the experiment. At the beginning of each session, the house light in the chambers was turned on and was subsequently turned off at the end of each session.

#### **3.3.1 Magazine Training**

All subjects received two 30-minute magazine training sessions, during which the nose poke devices were physically removed from the operant chambers, but the sucrose pellet reinforcers were delivered on a variable time 60 second (VT 60-s) schedule. The purpose of these sessions was to allow the animals to become familiar with the operant chambers and to learn the positive value of the sucrose reinforcer, in addition to the sound of the sucrose pellet being delivered to the magazine.

#### **3.3.2 Nose-Poke Acquisition**

All rats received two sessions of training with a continuous schedule of reinforcement following magazine training, in which every nose-poke was reinforced, with a total of 25 reinforcers earned in each session. The purpose of these sessions was to allow rats to learn the association between the nose-poke response and the receipt of sucrose pellet reinforcement. Following these sessions, animals underwent 3 daily sessions of nose-poke acquisition training on a variable-interval (VI-30-s) schedule. This schedule of reinforcement was chosen because variable interval schedules of reinforcement have been shown to facilitate habit formation (Dickinson, Nicholas, & Adams, 1983). Each VI-30 sessions terminated when each rat had earned 40 sucrose pellets, for a total of 120 response-reinforcer pairings over the course of the acquisition training. We have previously shown this amount of limited training supports goal-directed responding in intact female rats (Schoenberg et al., 2019).

### 3.3.3 Reinforcer Devaluation (RD)

Following acquisition, half of the animals were randomly assigned to a devalued group, and half were assigned to a non-devalued group. During each RD session, nose-pokes were prohibited by the physical removal of the holes from the chambers.

On odd-numbered days in this paradigm, all rats were placed in the operant chambers. However, only the devalued group received sucrose pellets (beginning with a total of 40 pellets on Day 1). Rats in the non-devalued group were only given exposure to the operant chambers; on these days they received no sucrose and sessions were terminated simultaneous to their devalued counterparts. At the end of these sessions, all rats were immediately removed from the chamber and injected intraperitoneally (i.p.) with a 10 ml/kg dose of 0.15 M lithium chloride (LiCl) to induce nausea and were subsequently returned to their home cage.

A similar procedure was conducted on even-numbered day, however only the non-devalued group received sucrose reinforcers, while the devalued animals were only placed in the operant chambers. Immediately following the session's termination, all rats received an i.p. injection of 0.9% physiological saline of equivalent size to the LiCl injections. In this way, exposure to the operant chamber, the sucrose reinforcer, and the injections of both LiCl and saline was controlled for such that the only difference between the devalued and non-devalued group was the pairing of nausea with the sucrose reinforcer in the devalued group. Thereby the conditioned taste aversion to the sucrose only occurred in the devalued group.

The reinforcer devaluation paradigm continued in 2-day cycles until all animals in the devalued group ceased all consumption of sucrose pellets. The zero-consumption criterion in the devalued group is considered evidence of a successful taste aversion to the sucrose reinforcer, which allows for the interpretation of responding during a later test session to be evidence of habitual behavior (as opposed to any remaining operant motivation for the reinforcer).

## **3.4 Testing Habit & Confirming Devaluation**

### **3.4.1 Extinction Test**

Following the final day of RD, habitual behavior was assessed during a 12-minute session under specific extinction conditions: the nose poke holes were present in the chambers, which allowed for a response, although no reinforcers were delivered during the session. Nose-pokes per minute were recorded and the data was collected using computer software. The critical comparison to assess habitual behavior is between response rates during this test session between devalued and non-devalued groups within each parity group. If animals were habitual, it was expected that the devalued groups would respond at the same rate as the non-devalued groups. Conversely, it was expected that the devalued groups would respond significantly less than the non-devalued groups if habit was not present and subjects remained goal-directed.

### **3.4.2 Consumption Test**

On the day following the extinction test, successful devaluation of the sucrose reinforcer was evaluated using 20 free presentations of the sucrose pellets on a VT-30-s schedule. During the consumption test, nose-pokes were physically removed, but the consumption of sucrose pellets in each group was recorded. Devalued animals were expected to consume none of the delivered pellets during this session because it was expected that devalued animals would recall the memory of the LiCl induced nausea paired with sucrose during reinforcer devaluation, which would cause them to reject the reinforcer. This would indicate successful devaluation of the devalued group. The non-devalued animals were expected to consume all of the pellets presented because the pellets remained value reinforced, as LiCl induced nausea was not paired with sucrose in this group.

### **3.4.3 Reacquisition Test**

On the day following the consumption test, successful devaluation was evaluated again during a 30-minute reacquisition test. The animals were placed in the operant boxes and were allowed to nose-poke for the reinforcer, delivered on a VI 30-s schedule. During the session, it was expected that devalued animals would integrate the memory of conditioned taste aversion to sucrose and the memory that the nose-poking response earns reinforcers. Therefore, the devalued groups were expected to demonstrate decreased nose-poking for the sucrose pellets over the course of the session. In contrast, the non-devalued animals were expected to reacquire nose-poking for the sucrose pellets during this session.

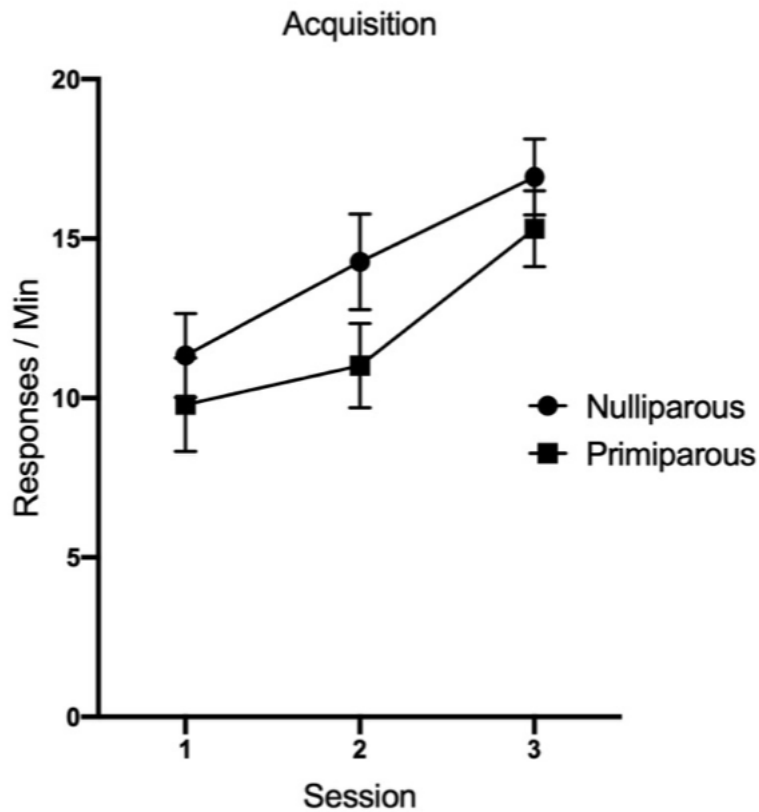
## **3.5 Statistical Analysis**

Data analysis was completed using ANOVA with repeated measures for acquisition and reacquisition. A 2 (reproductive experience group) x 2 (devaluation group) factorial ANOVA was completed for the extinction test.

## 4 Results

### 4.1 Acquisition

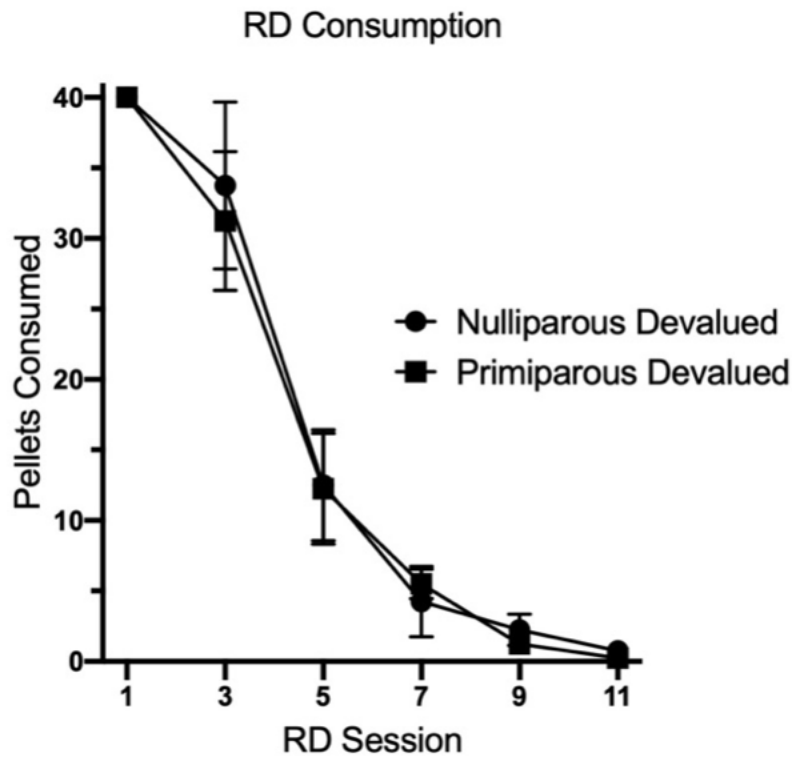
All animals significantly acquired nose poking for sucrose pellets, as confirmed by a significant main effect of the session in the repeated measures ANOVA, ( $F(2, 24) = 31.44, p < .001$ ). Therefore, regardless of what test group animals were in, they statistically increased their nose-poking across all three sessions. Furthermore, comparison between nulliparous and primiparous groups revealed that both groups acquired at an equivalent rate (non-significant effect of reproductive experience), ( $F(1, 12) = 1.32, p = .257$ ; see Figure 1), as did anticipated devalued and non-devalued groups (non-significant effect of anticipated devaluation group), ( $F(1, 12) = 0.07, p = .797$ ).



**Figure 1:** Mean responses per minute across VI-30-s acquisition training for both nulliparous and primiparous groups, collapsed across anticipated devaluation groups.

## 4.2 Reward Devaluation

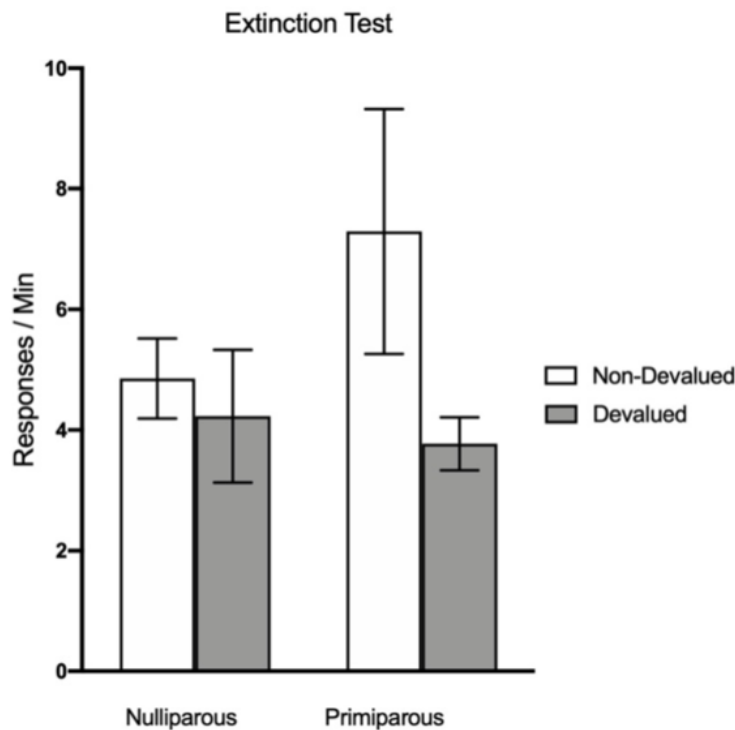
In reward devaluation, all devalued animals successfully acquired the condition taste aversion to sucrose, reaching criteria of zero consumption of sucrose pellets at the end of the 11th day of RD; see Figure 2. As anticipated, all non-devalued animals consumed all delivered pellets on even-numbered days of RD.



**Figure 2:** Mean number of pellets consumed by devalued females in both reproductive experience groups across 11 sessions of RD.

### 4.3 Extinction

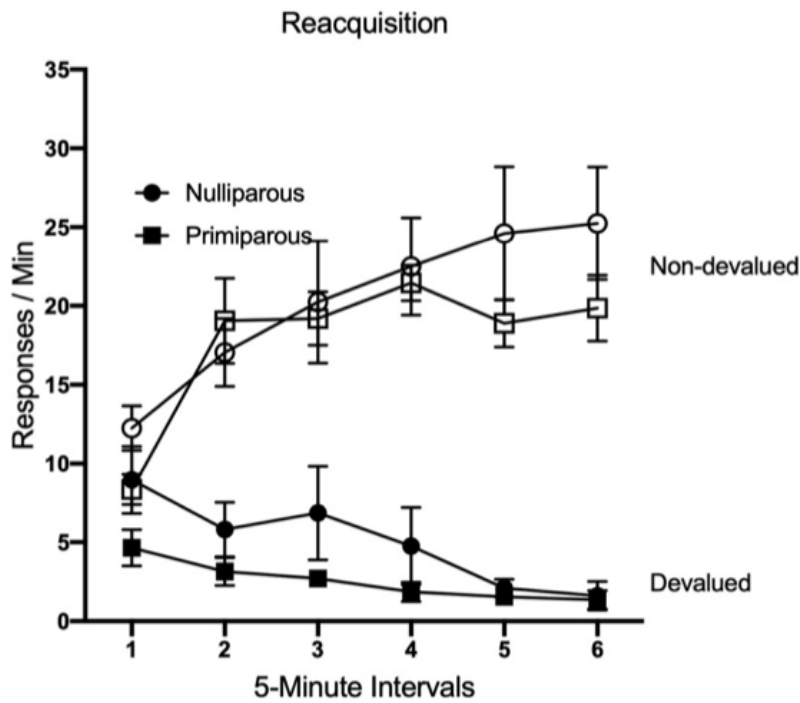
To assess sensitivity to devaluation in the extinction test, a 2 (RE group) x 2 (devaluation group) factorial ANOVA was conducted, which revealed a lack of significant main effects for RE group ( $F(1, 12) = 0.66, p = .434$ ), or devaluation group ( $F(1, 12) = 2.88, p = .116$ ). However, *a priori* planned comparisons between devalued and non-devalued groups within each RE group did show a marginally significant difference within the primiparous condition ( $F(1, 12) = 4.15, p = .064$ ), with primiparous devalued animals exhibiting lower average response rates ( $M = 3.77, SD = 0.88$ ) than primiparous non-devalued animals ( $M = 7.29, SD = 4.07$ ; see Figure 3).



**Figure 3:** Mean responses per minute by devalued and non-devalued females in each reproductive experience group during the extinction test.

## 4.4 Consumption & Reacquisition

In the consumption test, all animals behaved as anticipated. On average, devalued animals consumed zero pellets whereas non-devalued animals consumed all presented pellets. For the reacquisition test, a 6 (5 time bins) x 2 (RE group) x 2 (devaluation group) repeated measures ANOVA was conducted. There was a significant main effect of time ( $F(5, 60) = 4.37, p = .002$ ). There was no significant main effect of RE group ( $F(1, 12) = 2.20, p = .164$ ). There was a significant main effect of devaluation group ( $F(1, 12) = 82.61, p < .001$ ). Additionally, there was a significant time by devaluation group interaction ( $F(5, 60) = 20.86, p < 0.001$ ), indicating that as the session progressed the devalued and non-devalued animals continued to significantly differ; see Figure 4.



**Figure 4:** Mean nose pokes per minute during reacquisition by devalued and non-devalued females in each reproductive experience group, binned by 5 minute intervals.



## 5 Discussion

As anticipated, the results indicate that all animals successfully acquired nose-poking for sucrose pellets and that devalued animals successfully acquired conditioned taste aversion to sucrose (Figures 1 and 2). The extinction test revealed a lack of significant main effects for RE group (nulliparous vs. primiparous) or devaluation group (non-devalued vs. devalued), meaning that overall, there was no difference in the level of responding within either RE or devaluation groups. However, *a priori* planned comparisons between devalued and non-devalued groups within each RE group did show a marginally significant difference within the primiparous condition, with devalued animals responding less on average than non-devalued (Figure 3). All animals behaved as anticipated in consumption and reacquisition (Figure 4), which confirmed successful devaluation.

As previously stated, this investigation was designed as a pilot study aimed to collect preliminary data, and due to this constraint, only 16 animals were used ( $N=16$ ). Therefore, the statistical analyses performed were relatively underpowered. There appeared to be a lack of significant main effects for RE group ( $p = .434$ ) and devaluation group ( $p = .116$ ), suggesting that both RE groups were in habit, as both devalued groups within each RE group appeared insensitive to devaluation (Figure 3). However, we have previously shown that at 120 reinforcers, nulliparous intact females are generally goal-directed (Schoenberg et al., 2019), and therefore, we speculate that the lack of statistical difference between devaluation groups, specifically within the nulliparous condition, was a result of low statistical power and *not* a true display of habit. We are confident that adding more test subjects to increase statistical power would reveal a difference between devaluation groups, showing clear goal-directed behavior in nulliparous rats.

Furthermore, *a priori* planned comparisons revealed a marginally significant difference between devalued and non-devalued groups within the primiparous condition ( $p = .064$ ; see Figure 3). Given the statistical constraint, marginal significance suggests that primiparous females may have displayed stronger goal-directed behavior compared to nulliparous females, as the devalued group

responded less on average than the non-devalued ( $M = 3.77$  and  $M = 7.29$ , respectively; see Figure 3). We originally hypothesized that primiparous females would exhibit habitual behavior earlier in training due to the rapid enhancements of hippocampal- and frontal- based cognition that are triggered by parity, however these early results suggest the opposite. In the context of the multiple memory perspective (Packard, 2009), pregnancy-induced cognitive enhancements (hippocampal) were initially thought to work in conjunction with non-hippocampal based S-R learning to strengthen the response of habitual behavior, or in other words, the enhancement of one system would apply to both. Conversely, the results suggest that hippocampal enhancements may *impair* striatal learning in the DLS, and by extension, *delay* habit formation in primiparous rats. We speculate that this delay may be revealed with higher levels of training and greater statistical power. Additionally, it is possible that parity does not impact habitual behavior altogether, but this seems very unlikely given the literature that proposes that regions of the brain associated with habit formation are permanently altered following pregnancy.

Contrary to our initial hypothesis, the data revealed that primiparous rats may remain *goal-directed* longer than nulliparous rats. However, we speculate this observed goal-directed behavior in the primiparous condition may be attributed to the high metabolic demands of pregnancy and the lactation period post-parity. The metabolic strain induced by pregnancy and lactation is extensive, as it essentially drains the mother's energy stores in order to sustain the life of her offspring. This huge depletion of energy resources is remembered by changes in metabolic markers that may alter their set point for food intake (Hyatt, Zhang, Hood, & Kavazis, 2019). Thus, when our females were food restricted to maintain a target weight of 85% of their *ad libitum* weights across training, the biological salience for the sucrose reward may have been increased. This may have been exacerbated in primiparous females because metabolism is greatly affected by sucrose consumption due to its caloric density. Therefore, the high metabolic demand in pregnancy and lactation, the subsequent food restriction before operant training, as well as the use of calorie-dense sucrose as a reward, may have caused primiparous rats to remain highly goal-directed. Future studies, in

which food restriction is not used, as well as employing a non-caloric reinforcer, such as saccharin, may help overcome the confound that increased sensitivity to metabolic resources in female rats following parity. Indeed, we hypothesize that the use of an appetitive reinforcer that does not impact metabolism would reveal a more accurate depiction of how parity influences habit formation.

An additional factor that may have acted to maintain goal-directed behavior in primiparous rats is increased taste-aversion conditioning that may have transferred to the operant task. This effect was hinted at in the reacquisition test, in which primiparous rats showed an immediate reduction and a more rapid decline in nose-poke responding than nulliparous rats. If true, this may necessitate using a different kind of reward devaluation method that avoids aversive conditioning, such as satiation.

In essence, this pilot study revealed several possible confounds that may have to be addressed in order to accurately measure changes in habit formation due to reproductive experience. This, in turn, provides a substantial basis for future investigation.

## 6 Acknowledgements

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