INVESTIGATION OF TEMPORAL DISCOUNTING IN DWARF HAMSTERS (*Phodopus campbelli*) AND SPRAGUE-DAWLEY RATS (*Rattus norvegicus*) IN AN OPERANT CHOICE TASK

by

JESSICA MAIE GODIN SPIELDENNER

A.A.S., Vermont Technical College, 2000
B.A., University of Southern Maine, 2003
M.S., Kansas State University, 2007

AN ABSTRACT OF A DISSERTATION

submitted in partial fulfillment of the requirements for the degree

DOCTOR OF PHILOSOPHY

Department of Psychology
College of Arts and Sciences

KANSAS STATE UNIVERSITY
Manhattan, Kansas

2012

Abstract

The present experiment investigated whether dwarf hamsters (*Phodopus campbelli*) demonstrate temporal discounting. This was investigated by comparing the behavior of dwarf hamsters and Sprague-Dawley rats (*Rattus norvegicus*) in an adjusting delay procedure and applying the theory of behavioral economics to explain the resulting behavior. Dwarf hamsters demonstrated temporal discounting and tolerated longer delays than did the more impulsive rats. There was not a statistically significant difference between these species concerning indifference points. There was a statistically significant difference in the slopes of their discounting functions and the delay at which the end criterion was met. Neither species exhibited sex differences with respect to these measures nor with storage of food. There were a number of differences between the species. Rats started responding quickly, whereas dwarf hamsters waited significantly longer. When faced with increasing delays, rats increased the number of pellets earned while dwarf hamsters earned the same amount. Finally, rats lost weight throughout the experiment while dwarf hamsters gained weight. There were also a number of similarities. When faced with an increasing delay, both rats and dwarf hamsters increased the number of responses made, and increased the number of times they timed out on Larger Later trials. Some of these findings disagree with previous research and predictions of the behavioral economic theory of demand, creating a need for further research.

INVESTIGATION OF TEMPORAL DISCOUNTING IN DWARF HAMSTERS (*Phodopus campbelli*) AND SPRAGUE-DAWLEY RATS (*Rattus norvegicus*) IN AN OPERANT CHOICE TASK

by

JESSICA MAIE GODIN SPIELDENNER

A.A.S., Vermont Technical College, 2000
B.A., University of Southern Maine, 2003
M.S., Kansas State University, 2007

A DISSERTATION

submitted in partial fulfillment of the requirements for the degree

DOCTOR OF PHILOSOPHY

Department of Psychology
College of Arts and Sciences

KANSAS STATE UNIVERSITY
Manhattan, Kansas

2012

Approved by:

Major Professor
Dr. Jerome Frieman

Abstract

The present experiment investigated whether dwarf hamsters (*Phodopus campbelli*) demonstrate temporal discounting. This was investigated by comparing the behavior of dwarf hamsters and Sprague-Dawley rats (*Rattus norvegicus*) in an adjusting delay procedure and applying the theory of behavioral economics to explain the resulting behavior. Dwarf hamsters demonstrated temporal discounting and tolerated longer delays than did the more impulsive rats. There was not a statistically significant difference between these species concerning indifference points. There was a statistically significant difference in the slopes of their discounting functions and the delay at which the end criterion was met. Neither species exhibited sex differences with respect to these measures nor with storage of food. There were a number of differences between the species. Rats started responding quickly, whereas dwarf hamsters waited significantly longer. When faced with increasing delays, rats increased the number of pellets earned while dwarf hamsters earned the same amount. Finally, rats lost weight throughout the experiment while dwarf hamsters gained weight. There were also a number of similarities. When faced with an increasing delay, both rats and dwarf hamsters increased the number of responses made, and increased the number of times they timed out on Larger Later trials. Some of these findings disagree with previous research and predictions of the behavioral economic theory of demand, creating a need for further research.

Table of Contents

List of Figures

List of Tables

Acknowledgements

Thank-you to my advisor Dr. Jerome Frieman for his guidance and instruction over the years. I would like to thank Dr. Palmatier for his assistance and aid in the lab. I would also like to thank my entire committee Dr. Horne, Dr. Brase, and Dr. Palmatier for helping me to build this project.

Finally, I would like to thank my family for their support, encouragement, and love. Whether I needed support in terms of pursuing my dreams, finishing my degree, or making it through life’s ups and downs, I always know that they are there for me and will do anything that they can do to help.

Dedication

I would like to dedicate this dissertation to my family. First my parents and my brother, who have always believed in me, especially when others did not. Their faith and encouragement in my endeavors have definitely made the time and effort a little more bearable. I cannot thank them enough for all they have bestowed upon me.

I would like to also dedicate this dissertation to my husband, for staying by my side through the hard work and early morning laboratory sessions. His support and love helped me to make all this possible.

Finally, I would like to dedicate this dissertation to my daughter. This work was carried out to help secure her future and prepare for our lives together.

Chapter 1 - Introduction

Temporal Discounting

Operant choice tasks allow researchers to investigate choices between alternatives while controlling and systematically adjusting the variables affecting that choice. Two variables known to affect responding in such choice situations are the probability of reinforcement and the temporal delay to reinforcement (Mazur, 1991). When two alternatives of equal value are presented simultaneously, the selection of one alternative will become less likely if the probability of reinforcement for that alternative decreases or the delay to receive that alternative increases. Individuals sensitive to both the amount of food and the amount of delay to receive that food should also be sensitive to the correlation between the two (McNamara, & Houston, 1987), and should choose the more probable or more immediate alternative (Mazur, 1991). In operant tasks that focus on delayed rewards, the probability of reinforcement is typically set or else is adjusted in a systematic way. This type of task is referred to as intertemporal choice (Lea, 1978) and results in a phenomenon known as temporal discounting.

Temporal discounting is demonstrated in a choice task when an individual chooses a smaller, more immediate reward over a larger, delayed reward (Estle, Green, Myerson, & Holt, 2006; Green, Myerson, Holt, Slevin, & Estle, 2004; Green, Myerson, Shah, Estle, & Holt, 2007; Henly, Ostdiek, Blackwell, Knutie, Dunlap, & Stephens, 2008; Mazur, 1987; Ong & White, 2004). This occurs because the present value of a future reward is perceived to be less than the actual value of that reward (Ostaszewski, Karzel, & Szafrańska, 2003) based on the subjective assessment of the relationship between the reinforcer's value and the delay between response and reinforcement (Estle et al., 2006; Shapiro, Schuck-Paim, & Kacelnik, 2012). As the delay to receive a reinforcer increases, the subjective assessment of the delayed reinforcer's effectiveness decreases systematically (Ainslie, 1975; Mazur, 1995). Temporal discounting, therefore, is the phenomenon which results from differing temporal relationships between responses and their corresponding delivery of reinforcements. There are a number of mathematical equations used to describe and predict behavior related to temporal discounting, most notably the simple hyperbola (see, for example, Mazur, 1987). However, such theories and calculations are more complex than is necessary for the current research.

Although simultaneous choices are to a large extent laboratory constructs (Shapiro, Siller, & Kacelnik, 2008; Stevens & Stephens, 2009), temporal discounting is a biological process with an adaptive value (resulting in increased fitness; Ostaszewski et al., 2003; Stevens & Stephens, 2009). In the field, animals seeking food have to decide between two alternatives: reward obtained from a present source of food, and the amount of food available in the surrounding environment if the present source is ignored (Shapiro et al., 2008). A delay in this situation could result in the ultimate loss of the initial food source (Ostaszewski et al., 2003).

Behavioral ecologists have proposed many hypotheses about how temporal discounting might be advantageous in making a decision in this situation. For the present experiment, the two most relevant hypotheses involve the cost imposed by collection risk and the cost imposed by investment risk (Stevens & Stephens, 2009).

When deciding to collect an item, the forager needs to decide between committing to pursuing/consuming a given food item and the values of alternative foraging opportunities lost during that period of time commitment (Bateson & Kacelnik, 1996). A delay in collecting an immediate potential reward might lead to it becoming inaccessible in the future, either by consumption by another animal, relocation (such as mobile prey), destruction by environmental occurrences (such as weather), or by an increased risk of predation.

Investment risk occurs when an individual loses out on the potential gains that could be had by investing an immediate reward. This risk is best seen with species that have high energy requirements (opportunity risk). Since digestion is a lengthy process animals with high energy requirements might benefit from eating a less favorable food item and starting the digestive processes, rather than passing over the present food item to wait for a more favorable one (Tobin & Logue, 1994). For the forager, temporal discounting is an adaptive, cognitive process which results in the present food source becoming a greater priority than that same item would be in the future, compensating for the risks associated with waiting for a delayed reward and decreasing the likelihood of loss by lessening the value of the delayed food source.

When an individual exhibits a preference for a larger, delayed reward, when faced with a temporal discounting task, it is said to be exhibiting self-control (Ito & Asaki, 1982). Conversely, when an individual demonstrates temporal discounting by choosing a smaller, more immediate reward over a larger, delayed reward, it is said to be behaving more impulsively (Henly et al., 2008; Ito & Asaki, 1982). Impulsive behavior results in a small, short-term gain at the expense of a large, long-term loss (Ainslie, 1975). Because models for foraging decision-making assume that animals make adaptive decisions in order to maximize long-term gains (expected fitness; Bateson & Kacelnik, 1996; Rosati, Stevens, & Hauser, 2006; Shapiro et al., 2012; Stevens, & Stephens, 2009), impulsive behavior is considered to be maladaptive.

A number of factors have been researched to assess their impact on temporal discounting. These investigations have demonstrated that gains are discounted more than losses (Estle et al., 2006), that temporal discounting is not observed when water is used for the reinforcer (Richards, Mitchell, de Wit, & Seiden, 1997), and that food deprivation does not seem to affect the rate of discounting (Battalio, Kagel, & MacDonald, 1985; Ostaszewski et al., 2003; Richards et al., 1997).

Other research has demonstrated that reinforcer magnitude may also affect rates of discounting, with small primary reinforcers being discounted more than large primary reinforcers (Estle et al., 2006; Farrar, Kieres, Hausknecht, de Wit, & Richards, 2003; Green et al., 2004; Ito & Asaki, 1982; Killeen, 1985; Ong & White, 2004). Increasing the magnitude of an incentive increases its ability to bridge delays (Killeen, 1985). In other words, making a choice more valuable influences how the delay for that choice will be tolerated. However, the amount of reinforcement and delay to reinforcement are not linearly equivalent in their effects on choice behavior (Ito & Asaki, 1982).

Research also suggests that there are differences among species concerning the discounting of delayed rewards (Green et al., 2004; Rosati et al., 2006; Stephens & Stevens, 2009; Tobin & Logue, 1994). For example, pigeons have steeper discounting rates than rats, suggesting more impulsive decision making (Green et al., 2004; Tobin & Logue, 1994). Tobin and Logue (1994) attributed this difference in impulsivity to the difference in metabolic rates between the species. They also noted that birds are more likely to survive (increase fitness) by acting impulsively and taking the most immediate alternative (even if less favorable). The authors suggested that this species cannot afford to <u>not</u> be impulsive. It might be beneficial to consider their finding in terms of the natural foraging behaviors of each species.

Both pigeons and rats discount more steeply than humans (Green et al., 2004). Humans may differ from other species in their rate of discounting due to the ability to use and understand language or because of the human tendency to create and follow abstract rules (Green et al., 2004). These observed differences might also be due to procedural variations: Studies with nonhumans use primary reinforcers, whereas studies with humans typically use conditioned reinforcers (Ainslie, 1975; Farrar et al., 2003; Tobin & Logue, 1994). Evolutionarily, these differences in the steepness of the rate of discounting may reflect adaptations to different niches (Green et al., 2004; Tobin & Logue, 1994).

Research investigating temporal discounting typically has employed an operant concurrent-chains procedure. In this procedure, two schedules are linked together, an initial link followed by a terminal link (Ong & White, 2004). Each initial link corresponds to a specific option (lever or key) in an operant task, and each provides access to a mutually exclusive terminal link and serves as the choice phase. The contingency is often the same for both initial links; however, these contingencies will vary for the terminal links associated with them. Choice between the similar initial links is a measure of preference for their different terminal links (Grace, 1999). Typically, the subject will match its rate of responding on the initial link to the rate of reinforcement that is possible on the terminal link it is associated with (Fantino, 1969). In relation to temporal discounting, impulsive behavior is demonstrated in a concurrent-chains task when there is a higher response rate for the initial link preceding the terminal link that delivers a smaller, more immediate reinforcer (Grace, 1999).

An alternative to the concurrent-chains procedure, which also provides information about delayed reinforcement and can be used to profitably study choice between two reinforcers, is an adjusting procedure with a titration schedule (Mazur, 1987; Rodriguez & Logue, 1988). The discrete-trial adjusting delay procedure was introduced by Mazur (1984). In this design, subjects are given a choice between a standard alternative and an adjusting alternative. For the standard alternative, the scheduled contingency remains constant within a condition such that the subject can come to expect a specific reward after a specific delay (typically < 1 second). For the adjusting alternative, the scheduled contingency changes depending on the subject's choice on the previous trial or average of previous trials. If the subject shows a preference for (chooses) the adjusting alternative, the delay for that choice will increase on subsequent trials. Conversely, if the subject shows a preference for (chooses) the standard alternative, the delay for the adjusting alternative will decrease. If the subject shows no preference (chooses each alternative equally across a number of trials) then the delay for the adjusting alternative remains the same on the next trials.

There is also an adjusting amount procedure where the amount of reinforcer for each alternative is varied rather than the delay to its delivery. Researchers comparing the adjusting delay and adjusting amount procedures have found no systematic differences between them, as both have the same underlying mechanism; however, data associated with the adjusting delay procedure was more orderly (Green et al., 2007).

The main benefit of an adjusting delay procedure in comparison to the concurrent-chains procedure is that it allows for the calculation of an indifference point. The delay of the adjusting alternative will continue to be adjusted according to the choices made by the subject until it eventually fluctuates between a narrow range where the subject chooses each alternative about fifty percent of the time. The middle of this range is the indifference point, a quantitatively derived point at which the effectiveness or subjective value of a small reinforcer presented after a short delay is assumed to be equivalent to a larger reinforcer presented after a longer delay (Green et al., 2004; Mazur, 1987, 1991, 1995; Richards et al., 1997; Rodriguez & Logue, 1988).

By obtaining indifference points for different species, discounting functions can be developed that allow for comparison of the choice of delayed reinforcers between species (Green et al., 2004). In the experiment reported here, the rates of temporal discounting in dwarf hamsters (*Phodopus campbelli*) and Sprague-Dawley rats (*Rattus norvegicus*) were compared by examining their performance in an adjusting delay procedure. Indifference points and discounting functions, as well as temporal discounting, have not been studied in the dwarf hamster until now, although they have been studied extensively in rats (e.g. Farrar et al., 2003; Richards et al., 1997), making rats excellent subjects to compare with dwarf hamsters.

Although dwarf hamsters and rats are similar in some ways (e.g. both are social), it is their differences that make them interesting. First, hamsters and rats differ both in response to food deprivation as well as in their willingness to work for food in an operant task. Second, hamsters and rats differ in their behavioral strategies for dealing with food.

In a typical operant task that studies the impact of deprivation on the rate of responding, a baseline rate is measured while the animal has ample access to food. The subject is then deprived of food for a period of time, anywhere from mild deprivation (e.g. only fed for a period of 2 hours per day; Rowland, 1982) to severe deprivation (e.g. deprived food for 72 hours; Rowland, 1982; only fed every other day; Silverman & Zucker, 1976). The subject is then given access to ample food again, and the rate of responding is re-assessed. This second assessment is compared to the baseline rate of responding to see what kind of impact deprivation has on the rate of responding.

Rats exposed to this type of task increase their rate of response in proportion to the severity of the deprivation (Phillips, Robinson, & Davey, 1989; Silverman & Zucker, 1976). This increase in responding means that a rat exposed to a period without food will respond by eating more when food becomes available again, an ecologically sound response (Phillips et al., 1989; Silverman & Zucker, 1976).

This finding is closely related to the finding that rats exposed to an increased Fixed-Ratio (FR) schedule will increase their number of responses per session (Tarte & Vernon, 1974). In an FR schedule, the delivery of reinforcement is contingent upon performing a fixed number of responses (Killeen, Posadas-Sanchez, Johansen, & Thrailkill, 2009). As the FR schedule requirement increases, the animal needs to work harder by emitting a greater number of responses to receive the same amount of reward. For example, a subject may start on a FR-5 schedule, receiving a reinforcer after five responses and then be increased to a FR-8 schedule now only receiving that reinforcer after emitting eight responses, thus working harder for the same reward. Typically, the subject is placed on some kind of deprivation schedule for this task. This simple task measures a subject's willingness to work for its food as well as the impact of deprivation on this willingness. As food becomes harder to earn, rats will work harder in order to earn the same amount of food, suggesting that the demand for food in rats is inelastic.

Inelastic demand is a concept from the behavioral economic theory of demand (Lea, 1978). Although economists use demand theory to predict the effects of price on the quantity of commodities purchased, the fundamentals of the theory carry over into operant conditioning, especially when considering choices of varying value. Behavioral economists acknowledge that the demand for a commodity is a function not only of its own price but also of the price of other available commodities and consumer income. In terms of an operant task, the economic commodity is the reinforcer, the price of that commodity is a function of the schedule contingency of the experiment, and income refers to the amount of energy an animal will/can expend to obtain a reinforcer (commodity). If the commodity is essential (cannot be lived without), the economic prediction is that as the price goes up the amount of that commodity that consumers are willing to buy will remain the same. In more psychological terms, the behavior is relatively insensitive to the schedule, and continues at a steady rate considering the total amount of reinforcer obtained despite changes to the schedule. Economists describe this as inelastic demand: the expenditure of energy for a commodity is unaffected by its price (Lea, 1978). Inelastic demand is representative of rat behavior when faced with an increasing FR schedule. As the FR schedule increases, rats work harder to maintain the same total number of food reinforcers earned over the course of the session; therefore, the FR schedule did not affect the total number of reinforcers earned.

The behavioral economic theory of demand for food has not been researched in dwarf hamsters (*Phodopus campbelli*); however, research with golden hamsters (*Mesocricetus auratus*) suggests that in contrast to the inelastic demand for food in rats, the behavior of golden hamsters toward food can be described as elastic (Lea & Tarpy, 1986). Elastic demand is observed when the quantity of a commodity that consumers are willing to buy decreases as the price of that commodity increases (Lea, 1978; Madden, Dake, Mauel, & Rowe, 2005). In an operant task, this results in the amount of reinforcer obtained decreasing at a proportionally greater rate compared to the rate of price increase.

Golden hamsters seem unable, or at least unwilling, to increase their rate of responding following a period of deprivation (Lea & Tarpy, 1986; Phillips et al., 1989; Rowland, 1982; Silverman & Zucker, 1976; Wong & Jones, 1985). Representative of elastic demand their behavior is sensitive to the price imposed by changes in schedule contingency, and therefore responding decreases more dramatically in relation to the increase in price (Madden et al., 2005). Elasticity of demand is further supported by research which shows that golden hamsters will not increase their rate of responding in response to an increasing FR schedule, and as such do not maintain the same amount of food earned. Golden hamsters are sensitive to the schedule contingencies. This finding is related to other research in which golden hamsters do not increase food intake following periods without food (Rowland, 1982). These behaviors in golden hamsters, combined with the economic theory that elastic demand is usually related to nonessential commodities, seem to be ecologically disadvantageous.

One plausible explanation for the difference between rats and golden hamsters in this situation is their behavioral strategies for dealing with food, specifically the presence or absence of hoarding. Hoarding is loosely defined as food storing activity (Morgan, 1947). More formally, hoarding is regarded as the deliberate storing of food materials in greater quantities than is immediately eaten, which is then available for consumption in the future (Marx, 1950). The demand for food may be elastic in hamsters because they maintain a hoard that they can feed from in times of need (Lea & Tarpy, 1986).

Hamsters are one of the most, if not the most, prodigious hoarders of food (Etienne, Matathia, Emmanuelli, Zinder, & Crapon de Caprona, 1982; Lea & Tarpy, 1986; Morgan, 1947; Silverman & Zucker, 1976; Waddell, 1951). In German, "hamster" means "hoarder" (Silverman & Zucker, 1976). The extensively researched golden hamster is highly specialized for hoarding food, storing it in a particular location in the burrow (the granary; Etienne et al., 1982). An interesting example of this prodigiousness is the European hamster (scientific name not provided). It is known to hoard such vast amounts of food that in times of famine in Europe its hoards have been raided to supply human food stocks (Morgan, 1947). Hamsters have also evolved cheek pouches, an anatomical adaptation that improves their ability to hoard although it is not known whether the anatomical adaptation preceded hoarding or resulted from it (Lea & Tarpy, 1986).

In natural settings, hamsters are relatively inactive during the day, emerging from their burrows at night to feed and drink. However, because hamsters have a high metabolic rates they need to eat small amounts at regular 2-hour intervals. According to the ‘metabolic hypothesis’ (Tobin and Logue, 1994) hamsters should respond impulsively in order to maintain enough food reserves to survive. Hamsters typically forage at night carrying food back to their burrows in their cheek pouches and adding to a hoard over the course of the night, thereby able to eat from their hoard during the day (Toates, 1978). The hoard is also believed to sustain an individual over more long-term scales, such as periods of surface food shortage that may last days or even weeks (Silverman & Zucker, 1976).

The anatomical adaptation of cheek pouches permits the hamster with a way to stave off the immediate need for food, required by a high metabolism. Having a hoard that a hamster can continue to eat from at regular intervals provides a source of security, allowing the hamster to demonstrate more self-control despite increased metabolic need. Hamsters might be less concerned about delay, or more specifically about the delays associated with obtaining food because the security offered by a hoard allows for greater ability to take risks (Stevens & Stephens, 2009). These behavioral observations are also supported by experimental evidence. As mentioned earlier, golden hamsters do not increase their rate of responding when faced with an increased FR schedule. Although not increasing their behavioral responding results in less food earned over time, their rate of food intake remains relatively stable. This is because as work demand increases the golden hamster becomes more likely to feed from its hoard. These observations would seem to suggest that although the demand for earning food is elastic for golden hamsters, hoard consumption may be representative of an inelastic demand (Lea & Tarpy, 1986).

Adding to the hoard is so vital to the golden hamster that, in some research they have died of starvation following periods of deprivation because their priority when food becomes available again is to replenish the hoard rather than to eat (Rowland, 1982). Lea and Tarpy (1986) demonstrated that following periods of deprivation, golden hamsters will respond by creating a larger hoard than they maintained pre-deprivation, which parallels rats' increase in meal size following deprivation, again suggesting that hoarding is a primary drive for the hamster.

Hoarding in the rat, on the other hand, is debatable. Miller (1945) and Morgan (1947) claim that the common laboratory rat hoards. Beach (1950) and Marx (1950) claim that rats may learn to hoard in certain situations. Calhoun (1963) contends that what is considered hoarding in rats is no more than observations of the tendency to carry items. However, most literature agrees that rats rarely hoard under natural conditions (Beach, 1950; Miller, 1945; Waddell, 1951).

The differences in primary motivation for food might impact how dwarf hamsters and rats would respond in a temporal discounting task. More specifically, since dwarf hamsters' primary motivation is the maintenance of future food availability, it would be more likely that they would tolerate longer delays in order to maximize the amount of food earned. On the other hand, since rats' primary motivation is present satiety, it would be more likely that they would prefer the choice that would satisfy that motivation more quickly, not tolerating delay.

In the experiment reported here, the performance of dwarf hamsters (*Phodopus campbelli*) and Sprague-Dawley rats (*Rattus norvegicus*) in a temporal discounting task is explored by determining and comparing their indifference points and discounting functions using a delay procedure. To date, operant choice research in hamsters has focused on the golden hamster (*Mesocricetus auratus*). Dwarf hamsters have only participated in one published operant conditioning task involving rate of reinforcement and flavor variety (Lupfer-Johnson, Murphy, Blackwell, LaCasse, & Drummond, 2010), as well as one unpublished study investigating the effect of increasing FR schedule on performance in an operant task (Wertz, 2007). Temporal discounting has not been investigated for this species.

The procedure for the current experiment is based on Mazur's (1984) discrete-trial adjusting delay procedure. Mazur's design assumes that subjects are able to perceive and compare the lengths of delays associated with each lever in as few as two free choice trials. Since operant choice tasks have never been investigated in dwarf hamsters, it was unclear whether this small amount of time would be enough to produce dependable choices. Due to this uncertainty, Mazur's experimental design was changed to create greater control by the experimenter and more time for subjects to get acquainted with each lever's contingency.

Hypotheses

The main hypothesis of the present experiment is that dwarf hamsters, like rats, will exhibit temporal discounting. This would be demonstrated by dwarf hamsters decreasing the number of responses to the Larger Later alternative as the delay associated with it increased. This hypothesis is supported by an unpublished study investigating operant responding in dwarf hamsters which found a non-significant trend for dwarf hamsters to decrease responding when faced with an increasing FR schedule (Wertz, 2007), mirroring the results found in golden hamsters (Lea & Tarpy, 1986; Phillips et al., 1989; Rowland, 1982; Silverman & Zucker, 1976; Wong & Jones, 1985) and rats (Tarte & Vernon, 1974).

In addition to the hypothesis that dwarf hamsters will demonstrate temporal discounting when faced with an increased demand, it is also hypothesized that dwarf hamsters will have a greater indifference point than rats, demonstrated by a greater preference for the Larger Later alternative in an adjusting delay procedure over a longer range of delays (Mazur, 1995). The indifference point represents how willing a subject is to wait for food before switching strategies to a more immediate alternative. Because golden hamsters demonstrate an elastic demand for food, eating from their hoard when the schedule demand becomes more severe, it is expected that dwarf hamsters will tolerate longer delays compared to rats, resulting in a greater indifference point. Since the rat's primary motivation is to eat, their behavior should be more inelastic and therefore should result in less tolerance for delay.

Finally it is hypothesized that there will be a sex bias in responding, with females of both species earning more pellets overall than males. Both female golden hamsters (Etienne et al., 1982; Wong & Jones, 1985) and female rats (Calhoun, 1963) store more food than males, suggesting that they will most likely work more to earn food. For the present experiment this would be demonstrated by a greater number of responses made per experimental session by females of both species.

Chapter 2 - Method

Subjects

Thirteen (six male and seven female) dwarf hamsters (*Phodopus campbelli*) and 10 (five male and five female) Sprague-Dawley rats (*Rattus norvegicus*) were used for this experiment. Five dwarf hamsters were removed from the experiment; one for inappropriate shaping and four for having a lever bias that prevented them from learning the schedules, resulting in a decrease in weight below the cutoff criteria for this study. One rat was dropped from the study due to health reasons that were unrelated to the experimental design. Therefore data were collected and analyzed for eight dwarf hamsters (four male and four female) and nine Sprague-Dawley rats (five male and four female).

All subjects were experimentally naive and sexually mature at the start of testing. Dwarf hamsters were from KSU stock bred in-house and were between 7 and 10 months old at the start of experimentation. Sprague-Dawley rats were obtained from Charles Rivers and varied in age at the start of experimentation (four were 4 months old, two were 7 months old, two were 11 months old and one was 14 months old). All subjects were maintained, on a closed economy, on the same standard rodent diet. In a closed economy, the experimenter does not artificially cap daily consumption and does not provide supplemental, extra-session feedings (Madden et al., 2005). In other words, the subject can only get as much food as it earns during the experimental session.

Due to restrictions in the number of operant chambers available, subjects were run in different groups. Eight subjects were run per group (except for the third group), with four subjects (one male and one female of each species) running in the morning (AM group: approximately 7:00 a.m. – 6:30 p.m.), and four more (one male and one female of each species) running in the evening (PM group: approximately 7:00 p.m. – 6:30 a.m.). The second group was started as chambers became available from the first group finishing. A ninth rat (third group) was run following the first open chamber after the second group of rats (in the PM group).

Apparatus

Housing. Dwarf hamsters were housed individually in standard shoebox cages (27 cm x 47 cm x 20 cm) topped with mouse wire bar lids. CareFRESH recycled paper bedding (Absorption Corp., Washington), and a single paper towel were the only items present in the home cage. Water was provided ad lib. Rats were housed in similar shoebox cages but with rat lids. All other housing conditions were the same.

All subjects were maintained on a 12:12 Light:Dark cycle. All subjects were run during the dark phase of their Light:Dark cycle necessitating that they be housed in four separate rooms. There were two rooms for the AM group (lights on at approximately 6:00 p.m.), one for each species. These subjects were run during the dark phase of their cycle (starting at approximately 7:00 a.m.). There were two other rooms for the PM group (lights on at approximately 6:00 a.m.), one for each species. These subjects were also run during the dark phase of their cycle (starting at approximately 7:00 p.m.).

Testing. Two standard rat operant test chambers (54 cm x 25 cm x 29 cm, Med. Associates) surrounded by sound isolation cubicles (94 cm x 63 cm x 60 cm) were used. The isolation cubicles had two ventilation holes each with a ventilation fan. These fans also provided white noise in addition to ventilation. The operant chambers were equally bisected into two smaller chambers (each 26 cm x 25 cm x 29 cm) by the insertion of a partition.

Two subjects per operant chamber were run simultaneously, with one male running in one half of the chamber and one female in the other (chamber selection was counterbalanced across all subjects by sex), for a total of four subjects running at a time. Dwarf hamsters and rats were not run in the same operant chamber concurrently. Because dwarf hamsters are so much smaller than rats, the metal rod flooring of a chamber in which dwarf hamsters were run was covered with hardware cloth to help prevent injury.

Since liquid would spill easily and presented a threat to the equipment, HydroGel, (ClearH_2O, Maine) a non-wetting, sterile water gel, was placed in each subject's chamber. A disinfected tea light container was filled with the gelatinous water and secured to the metal flooring by way of a metal washer (glued to the bottom of the tea light container) and magnets. The same container was used for both AM and PM subjects; however, containers were not shared between species.

Reinforcers consisted of 45 mg LabDiet#5001 rodent diet pellets (PMI, Indiana), a pelleted form of the standard rodent chow that was fed ad lib prior to experimentation. No other food or enrichment was available within the testing chamber.

Recording. Data collection was carried out by the Med Associates software designed for these operant chambers. A cumulative record of performance was generated from the data. Data recording equipment was housed in the same room as the testing chambers. Also housed in this room were additional operant chambers in which other experiments were run concurrently.

Procedure

Shaping. Shaping occurred during an 11.5-hour period that corresponded with the time the subject was run for the experiment (approximately 7:00 a.m. - 6:30 p.m. or 7:00 p.m.- 6:30 a.m.). Each subject was introduced to the experimental chamber and allowed to explore and perform freely. Two levers were present and active during shaping. Shaping was conducted over 2 consecutive days.

In each shaping session there was non-contingent pellet delivery for the first 6 hours. Ten magazine pellets were randomly introduced in the first hour and was reduced to five pellets delivered per hour for the following 5 hours (for a total of 35 non-contingent pellets delivered over the course of 6 hours). Non-contingent pellet delivery was discontinued for the remaining 5.5 hours of the session. Any lever presses during the 11.5-hour period (including the time when non-contingent reinforcements were presented) were also reinforced with subjects able to earn a maximum of 999 pellets in a session.

Subjects were maintained on a closed economy starting with the first day of shaping and continuing throughout testing such that food was only received as reinforcement in the operant chamber. At the end of each daily session, any hoarded food was removed, counted, and discarded. Subjects were also weighed at the start of each testing session. Any subject falling below 85% of their initial free feed body weight was removed permanently from the experiment.

Operant Testing. At the start of each session, each subject was introduced to the experimental chamber with both levers retracted. Prior to the testing phase was an initial warm-up phase. For this warm-up phase, a fixed-delay of one second was in effect on both levers such that one reinforcer was presented one second following a response made to either lever. After the subject obtained the maximum of three reinforcers on a lever that lever was retracted. Once the second lever was retracted (a total of six reinforcers dispensed), both levers remained retracted for a period of 30 seconds. After this period, the levers were then presented again signaling the start of the experimental phase.

During the experimental phase, the left lever served as the Smaller Sooner (SS) alternative (Mazur's standard alternative). This lever remained on a fixed-delay of one second such that after a response to it the lever was retracted and the subject would receive one pellet after 1 second followed by a 20 second inter-trial interval (ITI). The other lever served as the Larger Later (LL) alternative (Mazur's adjusting alternative). Following a response on this lever, it remained inserted into the chamber for the duration of the delay associated with it. The delays and the order they were presented on the Larger Later alternative were; 2, 3, 4, 6, 7, 10, 13, 16, 21, 28, 36, 47, 61, 79, 102, 133, and 173 seconds (although not all subjects experienced all delays listed, see the explanation for the end criterion below). Following the specified delay, the lever was retracted, three pellets were delivered, and the 20 second ITI started. Due to limitations of the operating program, lever placement could not be counterbalanced across chambers and therefore remained the same for all subjects.

Testing consisted of serial, ten-trial blocks, with an ITI of 20 seconds between each trial and block. Each block consisted of two forced-choice trials followed by eight free-choice trials. On a forced-choice trial only one lever was inserted into the chamber followed by the insertion of the other lever on the following forced-choice trial. Order of lever presentation for the forced-choice trials was randomly assigned throughout the session so that both levers had an equal probability of being presented first. The forced-choice trials are designed to ensure that the subject was aware of the existing contingencies on each lever by requiring frequent sampling of each. On free-choice trials, both levers were presented, and the subject was allowed to choose either one. Choice of a lever resulted in both levers being retracted (according to the delay specifications above), presentation of the appropriate reinforcement after the scheduled delay of reinforcement, and the start of the 20-second ITI.

Each session ran for 11.5-hours. At any point during a session, if a subject did not respond on either lever for 15 minutes, any levers extended were retracted and remained retracted for an additional 15 minutes (resulting in a 30-minute timeout period).

The first five delays associated with the Larger Later lever (2, 3, 4, 6, and 7 seconds) were controlled by the experimenter with each delay being present for 2 consecutive days (for a total of 10 days). Subsequent delays increased by 30% and remained in effect until the subject reached stability at that delay (at least 4 days). The stability criterion for a given delay was averaged over the 4 most recent days of responding at that delay. (This average was based on the responses to the lever chosen most often over each session, either the SS lever or the LL lever.) Thirty percent of this average was added and subtracted to this average and were considered the upper and lower limits of stability. If each of the four most recent responses individually fell within this upper and lower limit, the subject was considered stable at that delay. The delay was then lengthened by 30% until the subject again reached stability.

The delays continued to increase by 30% until the end criterion was reached. The experiment ended when a subject selected the Shorter Sooner level on 90% of free choice trials for 4 consecutive days. These 4 days did not all have to be at the same delay. Because of this open-ended design not all subjects experienced every delay, nor did they spend the same number of days at each delay.

Data Analysis

Since this is the first time dwarf hamsters have been researched in an operant choice task, every event that occurred was time stamped allowing for the development of cumulative records for both species and providing information on when and how often events occurred throughout the experimental session. These records were observed for interesting patterns, and repeated measures ANOVA were conducted when appropriate. Parametric testing was not always appropriate because the experimental design was self-limiting: Each subject controlled both the number of trials experienced by their activity each session, as well as the number of delays that they experienced by their performance on each lever during the previous delay. Because these factors were controlled by an individual's performance not all subjects experienced the same number of trials per session nor the same number of delays. In such instances, non-parametric tests were used.

Indifference points, linear slopes of discounting functions, and the delays at which the end criterion were achieved were evaluated using an Exact Randomization Test (Siegel & Castellan, 1988). Because all subjects did not experience each delay, and because of outliers in the data (see Figure 1) classical statistical analyses were inappropriate. Unless otherwise stated, all values presented for a given delay are an average across the 4 days that constituted stability at that delay. The alpha level was set at .05 for parametric and non-parametric tests. Because the hypotheses were directional, randomization tests were based on one-tail tests of significance.

Chapter 3 - Results

Performance of an operant task

The percentage of Larger Later choices made on free choice trials at each delay is presented in Table 1. Both dwarf hamsters and rats successfully switched responding from the Larger Later alternative to the Smaller Sooner alternative as the delay associated with the Larger Later alternative increased. This successful switch between the alternatives suggests that subjects understood and adequately accomplished the task demands and demonstrated temporal discounting as expected.

Comparison of indifference points, slopes and end delays

The primary data from the choice task (indifference points, slopes of discounting functions, and the delays at which the end criterion were met) are presented in Table 2. Because subjects were run in different groups, boxplots were plotted for the indifference points, slopes of discounting functions and the delays at which the end criterion were met (delay at which the subject was selecting the Smaller Sooner option at least 90% of the time) for the data in Table 2 (Figures 2 and 3 respectively). Descriptive statistics for these measures by species are presented for Sex in Table 3 and for Group in Table 4 (the ninth rat was included in the data for Group 2). Because there were no meaningful differences, as indicated by significant overlap and large variances, the data were collapsed within species. Graphical representations of the discounting functions for each subject are presented in Appendix A.

An exact randomization test (Siegel & Castellan, 1988) was conducted on the indifference points, the slopes of discounting functions and the delay at which the end criterion was met. Because all subjects did not experience each delay, and because of outliers in the data (see Figure 1) classical statistical analyses were inappropriate.

For indifference points, the effect of species was not statistically significant, *p* = .06. (Two female rats were excluded from this analysis because they never reached an indifference point.)

The slopes of the discounting functions, for the present experiment, were used to describe and predict behavior as well as to compare and contrast rates of discounting. These slopes were derived by graphing the average percentage of the number of times each subject selected the Larger Later alternative at each delay (see Appendix A). These graphs were then fit with a line of best fit. The linear slope of this line was used as a measure of each subject's rate of discounting. (Exponential slopes provided a better fit for the data, but could not be calculated for all functions.) Also, the delay at which a subject reached the end criterion was used as an additional measure of the subject's tolerance of delay.

There was a statistically significant effect of species for both the slopes of the discounting functions, *p* = .03, and the end criteria, *p* = .01. These findings supported the hypothesis that dwarf hamsters would be more tolerant of longer delays than the rats.

Sex differences

The effect of sex on choices made on free choice trials, $F(1,7) = 0.12$, $p = .75$, $\eta^2=0.20$ and pellets earned, $F(1,7) = 0.02$, $p = .89$, $\eta^2=.003$ were not statistically significant for dwarf hamsters. Nor was the effect of sex on choices made on free choice trials, $F(1,7) = 0.37$, $p = .57$, $\eta^2= .06$ and pellets earned, $F(1,7) = 0.44$, $p = .53$, $\eta^2= .07$ statistically significant for rats.

Possible sex differences were investigated further considering food storage. Food storage was operationalized as the number of uneaten pellets remaining in the food hopper tray at the end of a session and although it was not directly manipulated in the present experiment, it was recorded informally. The average number of pellets stored by each subject at every delay encountered is presented in Table 5. There was not a reliable pattern for food storage as defined here. When food was left in the food hopper at the end of the session it was only a couple of pellets, and occurred infrequently and seemingly at random by both species and by both sexes. These findings do not support the hypothesis that females of both species would earn more food than males.

Additional Findings

The main purpose of the present research was to compare the performance of rats and dwarf hamsters in a temporal discounting task. Because operant choice tasks have not been previously researched in dwarf hamsters, the data were investigated beyond these hypotheses to both compare the rat and dwarf hamsters on the performance of different aspects of this task as well as discover other possible patterns and interesting findings.

Appendix B presents the response distributions and timeout occurrence distributions for each individual at the indifference point, the 10 second delay, and the delay at which end criterion was met[1]. Because of missing data points resulting from the open ended procedural design, not every subject faced each delay, making statistical analysis inappropriate (see Table 6).

Response distributions. Although there was considerable individual variation visual inspection of the graphs in Appendix B revealed that rats distributed their choices more often throughout the experimental session, whereas dwarf hamster choice distributions were more consolidated within the session. When the cumulative records for individual lever choice were investigated, the majority of choices dwarf hamsters made seemed contained within a time span of one half to one hour, with additional periods of activity only containing one or two choices. There also did not appear to be any dependable pattern to the choice distributions. Subjects distributed choices fairly consistently throughout the 11.5-hour session. Subjects also seemed to distribute their choices to both levers fairly evenly throughout the course of the session.

Timeout distributions. The average number of timeouts experienced are presented in Table 7. Rats on average had 15 timeouts (range: 12-19), spending at least 7.5 hours without a response and only 4 hours actively responding for reinforcement over the 11.5-hour session. Dwarf hamsters averaged 18 timeouts (range: 16-21), spending on average 9 hours without a response and only 2.5 hours of active responding.

In addition to the number of timeouts per session, average latency to start the experimental session was investigated and is presented in Table 8. For rats, the first response for the warm-up phase occurred on average 5 seconds (range: 1-19 seconds) from the start of the session, and the first response for the experimental phase started on average 57 seconds (range: 44-79 seconds) from the start of the session (including the warm-up phase). Dwarf hamsters, on the other hand, made their first response for the warm-up phase on average 401 seconds (7 minutes; range: 61-1147 seconds) after the start of the session, and the first response for the experimental phase on average 3592 seconds (60 minutes; range: 1462-7016 seconds) after the start of the session.

There was a statistically significant effect of species on both the latency to start the warm-up phase, $F(1,15) = 31.64$, $p < .001$, $\eta^2 = .68$, as well as the latency to start the experimental phase, $F(1,15) = 136.14$, $p < .001$, $\eta^2 = .90$. This finding indicates that dwarf hamsters waited significantly longer to start both phases of the experiment compared to rats. This latency to start the experiment also means that, dwarf hamsters were only actively responding for an average of 1.5 hours of the 11.5 hour session.

Timeout by trial type. The average number of timeouts on each trial type (SS forced choice, LL forced choice, and free choice) by each subject is presented in Table 9, and represented graphically in Figure 4.

Rats appear to timeout more often on the Larger Later forced choice trials as the schedule delay increased compared to the Smaller Sooner forced choice trials or the free choice trials. It also appears that they timed out less often on the free choice trials compared to either forced choice option throughout the experiment. It is harder to discriminate whether this was also true for dwarf hamsters; however, it does appear to have the same pattern although less dramatic.

A repeated measures ANOVA comparing the number of timeouts for the Shorter Sooner forced choice trials, the Larger Later forced choice trials, and the free choice trials was conducted. Because of missing data points resulting from the open ended procedural design, not every subject faced every delay (see Table 6), so both rats and dwarf hamsters were compared at their 10-second delay and the delay at which enough subjects were still responding to make statistical analysis meaningful. Dwarf hamsters were compared at 133 seconds (n = 6) for their final delay, and rats were compared at 47 seconds (n = 4).

Despite the difference that seems apparent in Figure 4, only dwarf hamsters showed a statistically significant effect of type of trial $F(2, 30) = 13.08$, $p = .003$, $\eta^2 = .47$. Rats did not reach statistical significance $F(2, 20) = 4.32$, $p = .07$, $\eta^2 = .30$, and no other findings reached statistical significance. It is difficult to assess if this lack of significance for rats is a reflection of the small portion of the data being tested or the possible impact of outliers. However, both the patterns suggested in Figure 4 and the significant difference found for dwarf hamsters provide interesting considerations that could benefit from further research. Timeout data was not investigated by any of the research reviewed for the present experiment.

Behavioral Economic Theory

Total choices made by delay. The average number of choices made on free choice trials per subject for each delay is presented in Table 10. Repeated-measures ANOVAs were conducted comparing the total number of choices made at the 10-second delay and the total number of choices made at the last delay each subject experienced. There was a statistically significant effect of choice for both dwarf hamsters $F(1,7) = 18.58$, $p = .004$, $\eta^2 = .73$ and rats $F(1,7) = 34.57$, $p = .001$, $\eta^2 = .83$ indicating that the total number of choices made increased significantly from the 10-second delay to the delay at which the end criterion was met. This finding suggests that as the delay associated with the Larger Later alternative increased, both rats and dwarf hamsters increased the number of choices made per session.

Pellets earned. The average number of pellets earned per subject for each delay is presented in Table 11. Repeated-measures ANOVAs were conducted for both dwarf hamsters and rats comparing the number of pellets earned at a 10-second delay to the number of pellets earned at the last delay experienced by each subject. There was not a statistically significant difference in the number of pellets earned for hamsters, $F(1,7) = 0.06$, $p = .81$, $\eta^2 = .01$, but there was a statistically significant increase in the number of pellets earned for rats, $F(1,7) = 16.15$, $p = .005$, $\eta^2 = .70$. These findings indicate that as the delay associated with the Larger Later alternative increased dwarf hamsters maintained the same number of pellets earned, whereas rats increased the number of pellets earned.

Weight change by delay. The average weight of subjects at shaping and at the end of the experiment, as well as the difference between the two is presented in Table 12. As the length of delay associated with the Larger Later alternative increased, rats lost on average 24 grams (4%) of their initial body weight. Dwarf hamsters, on the other hand, gained on average 5 grams

(17%) of their initial body weight as the length of delay associated with the Larger Later alternative increased.

Repeated-measures ANOVAs were conducted for both dwarf hamsters and rats comparing weight at the start of the experiment to weights at the final delay experienced by each subject. There was a statistically significant increase in weight for dwarf hamsters, $F(1,7) = 14.83$, $p = .006$, $\eta^2 = .68$, as well as a statistically significant decrease in weight for rats $F(1,7) = 19.27$, $p = .003$, $\eta^2 = .73$.

Chapter 4 - Discussion

Experimental Limitations

The research presented here is the first to investigate temporal discounting and indifference points in dwarf hamsters. Because of this, predictions for the present research were based on research in golden hamsters, as well as inferred from predictions of the behavioral economic theory (also based on golden hamsters). Although both served as great sources on which to build the present hypothesis, it was necessary to also make certain assumptions about the performance of dwarf hamsters (as it was unknown) and presented limitations that could not be overcome.

The most obvious limitation of the present experiment results from the size difference between rats and dwarf hamsters. Rats are about ten times larger than dwarf hamsters (based on body weight). Because of the larger size of rats, it was assumed they would have greater physical strength when pressing a lever. Due to equipment limitations, lever tension could not be adjusted differently for the species. Levers in the rat operant chambers required the same amount of force to depress as those in the dwarf hamster chambers. These physical requirements were likely to be more limiting for the dwarf hamsters than for the rats.

Whereas this size difference benefited the rat in ease of depressing the lever, they were disadvantaged in regard to the confinement of the operant chambers, and to the magnitude of the reinforcer. Reinforcement on the Larger Later alternative was three pellets compared to one pellet on the Smaller Sooner alternative. Since 45 mg pellets were used for both species, dwarf hamsters received more food per gram of body weight than the rats. For the reinforcers to be equivalent for both species (gram of reinforcer/gram of body weight), rats would need to earn approximately 6 pellets for the Smaller Sooner alternative and 18 pellets for the Larger Later alternative, or have 270 mg pellets as reinforcers if the 1:3 ratio was maintained. Neither of these options was feasible with the apparatus available for the present experiment. It would be interesting for future research to replicate this study with these pellet changes factored in.

In addition to the lack of equivalence of the absolute value of reinforcer per gram of body weight between the species; the metabolic requirements were also not equivalent. Tobin and Logue (1994) proposed that animals with higher metabolic rates were negatively correlated with self-control (pigeons vs. rats). This finding was contradicted by Campbell's and Persaud's (2008) simulation study, which found that species with higher metabolic rates and lower energy reserves benefitted from self-controlled intertemporal choice strategies. The metabolic requirements of rats and dwarf hamsters for the purpose of the present experiment are unknown, and are assumed to be equivalent.

Not only were the metabolic requirements for each species unknown, the subjective value of each reinforcer to each species is also unknown. As mentioned in the introduction, reinforcer magnitude may also affect the rate of discounting, with small primary reinforcers being discounted more than large primary reinforcers (Estle et al., 2006; Farrar et al., 2003; Green et al., 2004; Ito & Asaki, 1982; Ong & White, 2004). Because the subjective worth of the food reinforcer was unknown for either species, the present experiment assumes that the subjective value was the same for both species.

Finally, there is an anatomical difference that benefited the dwarf hamster. Dwarf hamsters have evolved large internal cheek pouches, an anatomical adaptation that improves their ability to hoard (Lea & Tarpy, 1986). These pouches open inside the lips, extend well back of the shoulders, and can more than double the width of the hamster's head and shoulders when filled (Nowak, 1999). Hamsters have the ability to store food in these pouches and expel it later for storage or consumption. It is possible that the dwarf hamsters in the present experiment were able to pouch enough food to remain satiated throughout the time they were not in their experimental session and perhaps even into the start of it.

The ability to pouch and retain pouched pellets allowed for extra-session feedings for dwarf hamsters while rats did not have such an ability. The deprivation imposed by the closed economy may have been reduced for the dwarf hamsters due to these extra-session feedings. Pouching food for later consumption might diminish the impact of deprivation resulting from the closed economy for dwarf hamsters; however, Ostaszewski and colleagues (2003) and Richards and colleagues (1997) found that food deprivation does not seem to affect the rate of discounting, so the extent of this as a possible limitation is unknown.

It is possible for the experimenter to manually remove food from the cheek pouches (see: Lupfer et al., 2010); however, for the present experiment it was deemed appropriate for dwarf hamsters to retain any pouched food because hamsters need to eat at regular 2-hour intervals (Toates, 1978) and golden hamsters have been known to starve when faced with deprivation (Rowland, 1982). Although this was thought to be a necessary precaution, it does create a limitation of the present experiment, as rats do not have a similar adaptation and were not able to bring food back to their home cages to eat following the experimental session.

Experimental Findings

The main findings of the present experiment were consistent, for the most part, with the hypothesized expectations as well as with the reviewed literature. The first hypothesis of the present experiment was that dwarf hamsters would perform appropriately in an operant choice task and demonstrate temporal discounting. As hypothesized, both dwarf hamsters and rats decreased their selection of the Larger Later alternative as the delay to receive the reinforcer associated with it increased. In other words, subjects successfully switched responding from the Larger Later alternative to the Smaller Sooner alternative as the delay associated with the Larger Later alternative increased. This successful switching of alternatives demonstrates that both dwarf hamsters and rats discount the subjective value of a reinforcer based on its temporal occurrence.

Second, because dwarf hamsters' primary motivation for food is to hoard (store food for the purpose of future consumption) whereas rats' primary motivation seems to be to satisfy immediate satiety, it was further expected that dwarf hamsters would tolerate a longer delay associated with the Larger Later alternative compared to rats. If dwarf hamsters attempt to maximize the amount of food hoarded (inferred in the present experiment by the number of pellets earned), they should be more willing to wait for a larger amount of food. This was demonstrated by dwarf hamsters in the present experiment by a greater tolerance for longer lengths of delay associated with the Larger Later alternative.

Although there was not a statistically significant difference for indifference points in the present experiment, it was approaching statistical significance. The Larger Later delay that was calculated as most equivalent to the Shorter Sooner alternative in terms of time invested per pellet earned was 36 seconds (see Appendix C for an explanation of this computation). Only one dwarf hamster's indifference point exceeded 36 seconds (none of the rats did). More interesting is that the end criterion was at a delay of 36 seconds or less for five of nine rats and only one of eight dwarf hamsters, suggesting that rats were not as sensitive to the schedule demands as the dwarf hamsters were. In other words, dwarf hamsters seemed better able to estimate when the Shorter Sooner and Larger Later alternatives were equivalent compared to the rats.

Although the difference between the rat and dwarf hamster indifference points was not statistically significant, the slope of discounting functions and the delay at which subjects fulfilled the end criteria were. The slope of a discounting function was used as a representation of the shift in preference of choice over time, as the length of the delay associated with the Larger Later alternative increased. For the present experiment, the average percentage of choice of the Larger Later alternative over the 4 days that represented stability at each delay was graphed. The linear slope of this line was used as a representation of the rate of discounting of the Larger Later alternative as the delay associated with it increased. The slopes of this line for dwarf hamsters were statistically different from rats. Combined with the finding that dwarf hamsters had significantly higher delays at which the end criterion was met, dwarf hamsters demonstrated a greater tolerance for delay than rats, that is, greater self-control. Whereas rats responded more impulsively by switching their preference from their Larger Later alternative to the Smaller Sooner alternative at a much shorter delay than dwarf hamsters. This finding, however, will need further supportive research as the effectiveness of reinforcer magnitude for these species is unknown (see Experimental Limitations).

The finding that rats behaved more impulsively when compared to dwarf hamsters in the present experiment supports the finding of Campbell and Persaud (2008) and contradicts the findings of Tobin and Logue (1994). Tobin and Logue (1994) used allometric scaling to predict species differences in self-control to suggest a possible link between metabolic rate and self-control. They postulated a possible negative correlation between the two, because animals with increased metabolic rates face depleting energy reserves at a quicker rate (than those with slower metabolic rates), and therefore are more likely to die if they do not obtain food at regular intervals. They claimed that there might be an adaptive value for animals with higher metabolic rates to behave impulsively, because food presents more of an immediate need. Through a series of simulation studies, Campbell and Persaud (2008), on the other hand, found that species with higher metabolic rates and low energy reserves had a competitive advantage from self-controlled intertemporal choice strategies. The findings of the present experiment support these simulated results.

Finally, there were no sex differences regarding the number of choices made or the number of pellets earned for either species. There was also no difference between the sexes (or between the species) regarding the storage of food. There were no statistically significant effects for sex for any of the measures. Although these findings do not support the hypothesis that there would be a sex difference for these factors and is not consistent with research on food storage, it is consistent with operant research investigating sex differences in golden hamsters (*Mesocricetus auratus*). Rowland (1982) and Wong and Jones (1985) did not find a sex difference regarding food intake. An unpublished study from our laboratory also did not find a sex difference in lever pressing in dwarf hamsters (*Phodopus campbelli*) when faced with different Fixed-Ratio schedules (Wertz, 2007).

Additional Findings

Because operant choice tasks have not been previously conducted with dwarf hamsters, the data were examined for further patterns and interesting findings, specifically in regards to temporal discounting. Because previous research has not investigated temporal discounting in dwarf hamsters, behavioral economic theory was used to predict how dwarf hamsters would respond when faced with a temporal discounting task. Patterns in the data were also noted and compared between the species to evaluate the predictions of the behavioral economic theory.

These findings, in addition to those that were hypothesized, are noteworthy and provide interesting areas on which further research could be conducted.

Response distributions. Because the present experiment was a closed economy and subjects experienced 12.5 hours without food prior to each experimental session, it was assumed that subjects would respond rapidly at the start of the experimental session, until they became satiated. If subjects were well aware of the session schedule and had a good internal clock to monitor time, they might also spend a fair amount of time responding at the end of the session in order to prepare for the 12.5 hours they would spend in their home cages without food.

In addition to responding at specific points of the experimental session, it was further assumed that subjects would prefer one alterative over the other earlier in the session. For example, subjects might choose the Smaller Sooner alternative more often in the beginning until they became satiated, as food was delivered more quickly (without delay) on this option. Conversely, they might choose the Larger Later alternative more often in the beginning in order to maximize the quantity of food earned per lever press (three as opposed to one).

However, investigation of the distribution of choices made on free choice trials did not support these assumptions. There was considerable individual variation in these distributions, and there did not appear to be any dependable pattern to choice distributions. Subjects distributed choices fairly consistently throughout the session. There also did not appear to be a preference for one lever over the other at any specific point during the experimental session. In other words, both species distributed choices to both levers fairly consistently throughout the session.

Even though rats and dwarf hamsters were distributing their responses consistently throughout the session, they each worked for only a limited amount of time. Comparison of the pattern of free choice response distributions showed that rats distributed their choices for longer periods throughout the session, whereas dwarf hamster choices were more consolidated during the session. When the cumulative records for individual lever choice data were investigated, the majority of choices dwarf hamsters made seemed contained within a time span of one half hour to one hour, with additional periods of activity only containing one or two choices.

Timeout Distributions. Amount of time actively responding was inferred from the amount of time each subject spent in a timeout period. A timeout started when a subject did not respond on either lever for 15 minutes. When this occurred, both levers were retracted and remained retracted for an additional 15 minutes, resulting in a 30-minute (total) timeout period in which the subject did not receive reinforcement.

Supporting the response distribution data, assessment of timeout distributions suggested both rats and dwarf hamsters only responded for a limited period during the experimental session, spending less than half their time actively responding for food. Rats actively responded on average for only 4 hours of the 11.5-hour session, whereas dwarf hamsters actively responded for only 2.5 hours of the 11.5-hour session. Considering dwarf hamsters spent an average of 60 minutes to start the experimental phase of their experimental session, they were actively responding for an average of only 1.5 hours. None of the literature reviewed for the present experiment discussed timeouts or their distributions, so this finding cannot be compared to previous findings.

Timeout by trial type. As the length of the delay associated with the Larger Later alternative increased, timeout periods occurred more often on the Larger Later forced choice trials for both rats and dwarf hamsters. Because a timeout represents a 30-minute period without reinforcement (15 minutes of which is forced) and is substantially longer than any of the delays the subject experienced, trial type (forced choice or free choice) should not affect choice. At any delay, reinforcement would be delivered sooner than waiting for the 30-minute timeout period. However, if subjects are discounting the value of reinforcement obtained on the Larger Later alternative as the length of the delay associated with it increases, it could be assumed that this option might become aversive. Therefore, it was assumed subjects would timeout more often on forced choice trials than on free choice trials, as well as timeout more often on the Larger Later forced choice trials (and less often on the Smaller Sooner forced choice trials) as the delay associated with it increased.

Rats did appear to timeout more often on the Larger Later forced choice trials as the schedule delay increased compared to either the Smaller Sooner forced choice trials or the free choice trials. Timeouts also appear to occur less often on the free choice trials compared to either forced choice option. It is harder to discriminate whether the dwarf hamsters showed the same pattern without further analysis; however, it does appear to have the same (although less dramatic) pattern.

Timing out more often on the Larger Later alternative as the length of the delay associated with it increased suggests that subjects understood the contingencies of each lever; this, provides indirect evidence of temporal discounting. It suggests that the subjective value of the Larger Later alterative is being discounted to the extent that they would choose to take a 30-minute break rather than to make this selection. Again, timeouts have not been investigated in the reviewed literature; therefore, it is unknown whether this finding is consistent with other research.

Behavioral Economic Theory

Because temporal discounting has not been researched in hamsters before, behavioral economic theory was used to make predictions (based on previous research with golden hamsters) on how dwarf hamsters might respond in a temporal discounting task. According to behavioral economic theory (Lea, 1978) rats have an inelastic demand for food whereas golden hamsters are considered to have an elastic demand.

Elasticity is a function of the subjective worth of a commodity measured by how hard a subject will work to obtain it. Inelastic demand is demonstrated when, as the cost for a commodity increases, an individual increases their level of effort expended to obtain the same amount of that commodity. In the present experiment, rats were aware of the task demands (schedule) as demonstrated by their successful switch from the Larger Later alternative to the Smaller Sooner alternative as the delay associated with the Larger Later alternative increased. In contrast to inelastic demand, elastic demand refers to a situation in which an individual does not expend more energy to meet an increase in schedule demand.

Considering the present experiment, inelastic demand would be observed when an individual increases the number of choices made during free choice trials when faced with an increased demand[2]. This increase in number of choices would result in a stable amount of reinforcers earned, despite the increase in schedule demand. Conversely, elastic demand would be observed when an individual does not increase the number of choices made when faced with an increased demand, thereby either decreasing or maintaining a constant amount of choices made during free choice trials. This lack of increase in the number of choices despite an increase in schedule demand would result in a decrease in the overall amount of reinforcer earned, and demonstrate an elastic demand for food earned.

According to the behavioral economic theory, it would be expected that rats should increase their number of choices made on free choice trials as the length of delay on the Larger Later alternative increases, therefore maintaining the same number of pellets earned despite changes in delay. This would demonstrate an inelastic demand for food. Also, according to the behavioral economic theory (dwarf hamster response was predicted based on research investigating golden hamsters) it would be expected that dwarf hamsters would maintain (or even decrease) their number of choices made on free choice trials thereby earning fewer reinforcers as schedule delay increased, thus demonstrating an elastic demand for food.

Finally, although not a direct assumption of the behavioral economic theory, the effect of increased schedule demand on body weight can be deduced. If rats maintain a consistent rate of pellets earned by increasing the total number of choices made, it can be expected that they would also maintain a consistent body weight when faced with an increased schedule demand. Conversely, if hamsters earn fewer pellets by not changing (or decreasing) the total number of choices made, it can be expected that they will lose body weight.

Applying the behavioral economic theory to the findings of the present experiment, it is important to keep in mind that most research on which the behavioral economic theory is based does not provide alternative options in the experimental designs, as the present experiment did. Typically subjects are presented with an increasing demand on only one alternative. This experiment, however, allowed subjects the opportunity to switch to another alternative (Shorter Sooner) when the delay associated with the Larger Later lever increased. Further research is necessary to ensure that the difference reported here is not the result of the procedural design.

Although the present research was a choice task that allowed subjects the opportunity to switch from one alternative to another based on each alternative's profitability, having the opportunity to choose between different alternatives does not explain how dwarf hamsters were able to increase their body weight as the delay associated with the Larger Later alternative increased. Further experimentation is necessary to clarify the findings of the present research.

Total choices made by delay. Both rats and dwarfs hamsters increased the total number of choices made on free choice trials per session as the length of the delay associated with the Larger Later alternative increased. As mentioned, behavioral economic theory would predict that rats would increase their number of choices made per session as the length of delay associated with the Larger Later lever increases. Rats in the present experiment behaved consistent with this prediction by increasing the number of choices made in response to an increased demand, demonstrating an inelastic demand for food in rats.

Dwarf hamsters, on the other hand, did not behave as predicted by the behavioral economic theory. Based on previous research in golden hamsters, this theory predicts that dwarf hamsters would either maintain the number of choices made on free choice trials despite the change in delay or may even decrease the number of choices. However in the present experiment, dwarf hamsters increased the number of responses rather than maintain or decrease them. Although this finding is not consistent with the predictions of the behavioral economic theory, it does agree with unpublished research that has been previously conducted in our laboratory. Wertz (2007) found that dwarf hamsters significantly increased their number of active lever presses as an FR schedule increased from a CRF to an FR-5. This is evidence that dwarf hamsters do not respond the same as golden hamsters when faced with operant tasks and therefore need separate consideration when applying the behavioral economic theory.

Pellets earned. As mentioned previously, the behavioral economic theory would predict that rats would earn the same number of pellets overall and that dwarf hamsters would earn fewer pellets overall as the length of the delay associated with the Larger Later alternative increases. However, in the present experiment the impact of increased delay on the number of pellets earned was inconsistent with behavioral economic theory for both rats and dwarf hamsters.

Rats increased (rather than maintained) the total number of pellets earned as the length of the delay associated with the Larger Later alternative increased, and dwarf hamsters maintained the same amount overall (rather than earning fewer pellets). Although this finding contradicts the predictions of the behavioral economic theory of demand for both species concerning the number of pellets earned as schedule delay increased, the data are in the correct direction. That is, rats increased the number of pellets earned more than dwarf hamsters did when faced with increased schedule demand.

Considering the number of pellets earned, this finding is also inconsistent with the reviewed literature. Although Tarte and Vernon (1974) found that rats would increase their rate of responding on an increased FR-schedule, the rats maintained the number of pellets earned. In other words, the demand for pellets earned was inelastic. Although rats in the present experiment also increased their rate of responding when faced with an increased cost (consistent with Tarte and Vernon [1974]), they also increased the number of pellets earned when faced with an increased cost (which is not consistent with Tarte and Vernon [1974]). Taken together, however, these findings are consistent with inelastic demand. Also, Lea and Tarpy (1986) found that golden hamsters earned fewer pellets as an FR schedule increased. In other words, the demand for pellets earned was elastic. Dwarf hamsters in the present experiment maintained the overall amount of pellets earned. Demand for food for both species was inelastic, both demonstrating an ecologically sound response.

This inconsistency with the behavioral economic theory and the reviewed literature might be further indication that dwarf hamsters do not respond the same as golden hamsters (on which the prediction of demonstrating an elastic demand was based) when faced with operant tasks. Unpublished research in dwarf hamsters did demonstrate a trend for subjects to earn fewer pellets as FR schedule increased; however, this trend did not reach statistical significance (Wertz, 2007).

Another possible reason for these inconsistencies might be the result of the procedural design. In the present experiment, subjects were maintained on a closed economy which did not allow dwarf hamsters to successfully hoard (although they were allowed to retain any pouched pellets). In previous research, both golden hamsters (Lea & Tarpy, 1986; Phillips et al., 1989) and dwarf hamsters (Wertz, 2007) were allowed to maintain some level of hoarding. Lea and Tarpy (1986) found that although responding (and as a result the number of pellets earned) decreased as schedule demand increased, subjects were eating from their hoards more, resulting in a consistent amount of food intake despite schedule change.

It might be that dwarf hamsters in the present experiment maintained the same number of pellets earned because they could not hoard. They may have earned and pouched a constant amount despite changes in delay in order to simulate a consistent hoard. In other words, if dwarf hamsters were attempting to maintain a certain number of pellets collected per day to simulate the number they would normally collect to maintain a hoard, then the finding presented here would be consistent with the literature that found an inelastic demand for a hoard. Because Wertz (2007) did not record food intake, it is unknown whether this is relevant for that study.

Weight change by delay. Finally, the maintenance of weight can be deduced from the predictions of the behavioral economic theory. If rats maintain a consistent rate of pellets earned by increasing the total number of choices made as predicted by the behavioral economic theory of demand, it can be expected that they would also maintain a consistent body weight when faced with an increased schedule demand. Conversely, if dwarf hamsters earn fewer pellets by not changing (or decreasing) the total number of choices made, it can be expected that they will lose body weight.

Despite increasing their rate of responding as well as the total number of pellets earned when faced with increasing delay, rats in the present experiment were not able to maintain a steady body weight, instead losing on average four percent of their initial body weight. This finding is inconsistent with both the predictions of the behavioral economic theory as well as previous research. Silverman and Zucker (1976), as well as Tarte and Vernon (1974), found that rats adjusted their rate of responding to maintain their level of food intake in order to maintain a stable body weight.

Because rats in the present experiment were able to match their level of responding to the schedule requirement, it does not seem likely that the present experimental design was too difficult for rats to understand the schedule requirements. Rats successfully switched from the Larger Later alternative to the Smaller Sooner alternative as the delay associated with the Larger Later alternative increased, suggesting that they understood the schedules associated with each alternative and were able to change their choice of alternatives when it became more profitable to do so. Also, previous research has demonstrated that rats are able to successfully complete a concurrent-chains procedure in which choice of an initial link determines the future contingency of a terminal link. That task is far more complicated than the present design and has been used successfully in rats.

Although the present experimental design was an operant choice task in which one choice always resulted in at least one reward, perhaps rats were unable to maintain their body weight as the delay associated with the Larger Later alternative increased because they decreased their response to it. Because this lever provided more pellets per choice and the rats were choosing it less often as schedule demand increased, perhaps they were not able to maintain their body weight on only the Smaller Sooner alternative.

Based on previous experience in our lab, a male rat consumes approximately 23 grams of food per day (females: 19 g.). In order to maintain this level of food intake in the present experiment, a male rat would need to earn about 511 pellets per session (females: 422 pellets). A male rat choosing only the Smaller Sooner alternative for every free choice option would take 4 hours and 38 minutes and 12 seconds (425 responses) to earn 511 pellets (see Appendix C for computations and explanation). Choices made to the Larger Later alternative, at a 173-second delay, would take 8 hour and 57 minutes and 46 seconds (183 responses). Considering rats typically performed for an average of 4 hours and a male rat on average earned only 395 pellets per session (of expected 511; females earned 283 of expected 422), it is clear why rats were not able to maintain their body weight.

One plausible assumption for why rats responded for less time than it would take to earn their free feed daily intake level amounts is that the schedule requirements were too difficult for the rats to respond the necessary 511 responses on the Smaller Sooner (183 Larger Later responses) to maintain their weight. However, in other research conducted in our lab rats responded in a two-step arithmetically progressive ratio (PR) schedule. In that experiment, the first response on an active lever results in a single reinforcer, the next reinforcer requires three responses, the next reinforcer requires five responses, the next, seven, and so on until the subject does not respond for 15 minutes. At this point the subject faces a 30 minute timeout phase and the session is restarted. In this PR experiment, male rats are responding on average 3,431 responses over the course of an 11.5-hour session (females: 2158), and time out on average with a maximum of 48 responses for a single reinforcer (females: 27). This demonstrates that rats should have the physical ability as well as the motivation to be able to maintain their free feed body weight in the present experiment. Also, following the results presented here rats were brought back down through the delays experienced in the present research, in reverse order. Although the rats re-experienced the shorter delays of the present research, their weight continued to decrease rather than recover itself. (Dwarf hamster weights also continued to increase as they re-experienced the shorter delays.) This continued change in weights further suggests that the experimental design (and schedule contingency) were not the sole factor contributing to weight.

Although the finding of the present experiment that rats did not work enough to maintain their free feed body weight is inconsistent with the predictions of the behavioral economic theory and research in operant research, it is consistent with other literature. First, Lea (1978) found that subjects on schedules of reinforcement rarely make all the responses they are physically capable of making. In studies of risk aversion in foraging behaviors Battalio, Kagel and MacDonald (1985) found that rats did not switch behavioral strategies when faced with negative energy budgets, and Kagel, MacDonald, Battalio, White and Green (1986) found that they did not satisfy long-term survival requirements. These authors suggest that it might be due to the rat's size (referred to as larger mammals). Rats are larger (compared to many of the animals they have been studied with) and are less likely to die from starvation if resources become limited than to die from disease conditions related to malnutrition (i.e. respiratory disease). Because they are less likely to die from starvation, rats might not be as sensitive to changes in the environmental contingencies as animals that are at risk of starvation resulting from these changes (Battalio et al., 1985). Rats in the present experiment were also not as sensitive to the schedule contingencies as evidenced by steeper slopes of discounting functions and shorter delays at which the end criterion was satisfied.

The body weight of dwarf hamsters was also inconsistent with expectations based on predictions of the behavioral economic theory. It was inferred that dwarf hamsters would lose overall body weight as the length of the delay associated with the Larger Later alternative increased because they were predicted to earn fewer pellets. However, in the present experiment, dwarf hamsters actually increased their body weight, gaining on average 17% of their initial body weight.

This weight increase is surprising considering that although dwarf hamsters in the present experiment increased the number of choices they were making as the length of the delay associated with the Larger Later lever increased, they maintained the same number of pellets earned overall. Also, based on previous experience in our lab, a male dwarf hamster consumes approximately 3.5 grams of food per day (females: 4.2 g.). In order to maintain this level of food intake, a male dwarf hamster would need to earn about 78 pellets per session (females: 94 pellets). In the present experiment, both male and female dwarf hamsters earned these expected amounts (males: 87; females: 93). Both of these findings suggest that dwarf hamsters were maintaining a consistent amount of food as compared to pre-experimental free feed food consumption, and despite an increase in schedule demand.

Because dwarf hamsters in the present experiment maintained the same amount of pellets earned overall, it should be expected that their weight should stay the same (or decrease slightly as they had to exert more energy to earn the same amount). It is difficult to assess whether this finding is consistent with previous research as the research with golden hamsters and dwarf hamsters reviewed did not list weight as a dependent variable.

The most likely reason that dwarf hamsters were able to gain weight despite earning fewer pellets is again their ability to pouch food (see Experimental Limitations). If hamsters were pouching food and using this food as a temporary hoard in their home cage, it is conceivable that they pouched an amount in excess of what they required to maintain a stable body weight, providing further evidence that they may have been earning/pouching enough to simulate the number of pellets they would get to maintain a hoard, rather than solely intake of food. This amount may have remained in excess of what was typically fed on, despite the fact that dwarf hamsters earned fewer pellets as the length of delay associated with the Larger Later Lever increased. If this were occurring, they would have enough food despite earning fewer pellets during the experimental session, comparable to Lea and Tarpy's (1986) finding that golden hamsters increase hoard consumption when faced with increased demand.

This finding for dwarf hamsters is even more interesting when compared to research concerning deprivation and the effect of increasing schedule demand in golden hamsters. In experiments considered for the present research, golden hamsters were either allowed to maintain a hoard to some extent (Lea & Tarpy, 1986; Phillips et al., 1989; Wong & Jones, 1985), or else were deprived food for some amount of time (72 hours, Rowland, 1982; every other 24 hours, Silverman & Zucker, 1976) and then were re-introduced to food. All of these studies found some form of post-fast anorexia with the general conclusion that golden hamsters were incapable of increasing their meal size in the face of deprivation or increased schedule demand, and that instead of increasing responses to earn more food, golden hamsters would eat from their hoards to maintain the same level of food intake while not having to work as hard. Lea and Tarpy (1986) explained it in economic terms as an elastic demand for food because golden hamsters maintain a hoard from which they feed in times of need, and then being inelastic in their consumption of the hoard.

The present experiment, on the other hand, did not allow dwarf hamsters the opportunity to hoard (although food could be maintained in the food hopper during the experimental session and pouched for future consumption). Dwarf hamsters may have increased responding, maintained the same total number of pellets earned, and increased their weight despite increasing schedule demand because they adapted to not being able to hoard. Although this requires further investigation, it disagrees with previous research statements that hamsters are unable to adjust to deprivation and increasing schedule demand (Lea & Tarpy, 1986; Phillips et al., 1989; Rowland, 1982; Silverman & Zucker, 1976; Wong & Jones, 1985). Although dwarf hamsters in the present experiment did not increase the number of choices or the number of pellets earned when faced with an increased delay, they were able to adjust as evidenced by their ultimate gain in weight. This might, again be evidence that dwarf hamsters were maintaining the amount of food they would typically maintain in a hoard in what they consumed and pouched during the experimental session.

Most interesting, this finding strongly disagrees with the current research contention that hamsters are so evolutionarily adapted to hoarding that they are not able to compensate without it (Rowland, 1982; Silverman & Zucker, 1976). The findings of the present experiment would suggest that not only were dwarf hamsters able to adjust to an increased schedule demand but they were also able to compensate for a lack of hoard. When faced with a lack of ability to maintain a hoard, the dwarf hamsters in this experiment gained body weight in excess of their initial body weight. This finding would seem to suggest that dwarf hamsters in the present experiment were able to overcome the need for a hoard, perhaps by using their ability to pouch in order to do so. Whereas previous research has shown that golden hamsters do not respond to deprivation by increasing the amount of food they eat (although they do build a larger hoard; Lea & Tarpy, 1986), the present experiment would suggest that they might when faced with long-term hoard loss.

Conclusion

This explanation is supported by the findings of the present experiment when behavioral economic theory is applied to temporal discounting. Both rats and dwarf hamsters in the present experiment demonstrated an inelastic demand for food. Although this finding does not agree with research investigating the behavioral economic theory in golden hamsters, it does support the hypothesis and findings of the present experiment when demand is considered in terms of temporal discounting.

Inelastic demand is generally observed with essential commodities, whereas elastic demand is typically observed with non-essential commodities or where another commodity can be readily substituted for the original one. Food (reinforcer for the present experiment) is an essential commodity, and as such dwarf hamsters in the present experiment, unlike golden hamsters in previous research, responded to it appropriately and demonstrated an inelastic demand. Also, research investigating temporal discounting, when considered from a reinforcer magnitude perspective, has demonstrated that the more incentive value a reinforcer (commodity) has, the slower the rate of discounting (the shallower the discounting function; Estle et al., 2006; Farrar et al., 2003; Green et al., 2004; Ito & Asaki, 1982; Killeen, 1985; Ong & White, 2004). Dwarf hamsters in the present experiment had shallower discounting functions, when compared to rats, suggesting that despite potential difference in reinforcer magnitude which might result from different body weight between the species dwarf hamsters valued the reinforcer associated with the Larger Later alternative more when compared to the rats. Finally, the procedural design of the present experiment increased how essential earning food was for the dwarf hamsters by not allowing them to maintain any type of hoard. Considering all of these factors, the data are accurately explained and strongly support most of the hypotheses for which this research was conducted.

Although further research would be necessary, it may be that hamsters have an elastic demand for food consumption dependent on what opportunities are available. They may consume lesser amounts of food when they have the security of a hoard to guard against body weight loss, and might increase their amount of food intake when unable to maintain an adequate hoard. Stevens and Stephens (2009) proposed an ecological theory of changing tactics when faced with changes in environmental opportunity. They discuss "cream-skimming" whereby an animal quickly takes something from a foraging opportunity and "bowl-licking" whereby an animal stays at a foraging patch until all the resources are consumed. (2009, p. 363) "Cream-skimming" results in far ranging travel and numerous quality items being left behind, whereas "bowl-licking" produces numerous quality items, but more time is wasted by extracting the last dregs from a source. Foraging techniques (and demand for food) might depend on the richness of the environment, with rich environments encouraging cream-skimming and lean environments requiring thorough exploitation (Kagel et al., 1986; Stevens & Stephens, 2009). For example, in lean periods (when a forager faces a net deficit for a resource) an individual may consume prey that it might pass by in better times (Kagel et al., 1986; Stevens, & Stephens, 2009). Similarly, a hamster may build an ample hoard when the resources and the environment allow for it, and adjust hoarding if not.

Although the findings of the present experiment requires further experimentation, they provide evidence for a need to consider dwarf hamsters separately from golden hamsters in regard to performance in operant tasks as well as behavioral economic theory, as well as an expansion in the understanding of a hamster's compensatory reaction to the absence of a hoard.

References

Ainslie, G. (1975). Specious reward: A behavioral theory of impulsiveness and impulse control. *Psychological Bulletin*, *82(4),* 463-496.

Bateson, M., & Kacelnik, A. (1996). Rate currencies and the foraging starling: the fallacy of the averages revisited. *Behavioral Ecology, 7(3),* 341-352.

Battalio, R.C., Kagel, J.H., & MacDonald, D.N. (1985). Animals' choices over uncertain outcomes: Some initial experimental results. *The American Economic Review, 75(4),* 597-613.

Beach, F.A. (1950). The snark was a boojum. *American Psychologist, 5,* 115-124.

Campbell, T.G., & Persaud, N. (2008). The adaptiveness of self-control: Simulation of foraging mice. *Journal of Comparative Psychology*, *122(4),* 368-372.

Calhoun, J.B. (1963). *The Ecology and Sociology of the Norway Rat*. Bethesda, MD: U.S. Dept. of Health, Education and Welfare.

Estle, S.J., Green, L., Myerson, J., & Holt, D.D. (2006). Differential effects of amount on temporal and probability discounting of gains and losses. *Memory & Cognition, 34(4),* 914-928.

Etienne, A.S., Matathia, R., Emmanuelli, E., Zinder, M., & Crapon de Caprona, D. (1982). The sequential organization of hoarding its ontogeny in the golden hamster. *Behaviour, 83,* 80-112.

Fantino, E. (1969). Choice and rate of reinforcement. *Journal of the Experimental Analysis of Behavior*, *12(5),* 723-730.

Farrar, A.M., Kieres, A.K., Hausknecht, K.A., de Wit, H., & Richards, J.B. (2003). Effects of reinforcer magnitude on an animal model of impulsive behavior. *Behavioural Processes, 64,* 261-271. doi: 10.1016/S0376-6357(03)00139-6.

Grace, R.C. (1999). The matching law and amount-dependent exponential discounting as accounts of self-control choice. *Journal of the Experimental Analysis of Behavior, 71,* 27-44.

Green, L., Myerson, J., Holt, D.D., Slevin, J.R., & Estle, S.J. (2004). Discounting of delayed food rewards in pigeons and rats: Is there a magnitude effect. *Journal of the Experimental Analysis of Behavior, 81,* 39-50.

Green, L., Myerson, J., Shah, A.K., Estle, S.J., & Holt, D.D. (2007). Do adjusting-amount and adjusting-delay procedures produce equivalent estimates of subjective value in pigeons? *Journal of the Experimental Analysis of Behavior, 87,* 337-347.

Henly, S.E., Ostdiek, A., Blackwell, E., Knutie, S., Dunlap, A.S., & Stephens, D.W. (2008). The discounting-by-interruptions hypothesis: model and experiment. *Behavioural Ecology, 19(1),* 154-162.

Ito, M., & Asaki, K. (1982). Choice behavior of rats in a concurrent-chains schedule: amount and delay of reinforcement. *Journal of the Experimental Analysis of Behavior, 37(3),* 383-392.

Kagel, J.H., MacDonald, D.N., Battalio, R.C., White, S., & Green L. (1986). Risk aversion in rats (*Rattus norvegicus*) under varying levels of resource availability. *Journal of Comparative Psychology, 100(2),* 95-100.

Killeen, P.R. (1985). Incentive theory: IV. Magnitude of reward. *Journal of the Experimental Analysis of Behavior, 43(3),* 407-417.

Killeen, P.R., Posadas-Sanchez, D., Johansen, E.B., & Thrailkill, E.A. (2009). Progressive ratio schedules of reinforcement. *Journal of Experimental Psychology: Animal Behavior Processes, 35(1),* 35-50.

Lea, S.E.G. (1978). The psychology of economics of demand. *Psychological Bulletin, 85(3),* 441-466.

Lea, S.E.G., & Tarpy, R.M. (1986). Hamsters' demand for food to eat and hoard as a function of deprivation and cost. *Animal Behaviour, 34,* 1749-1768.

Lupfer-Johnson, G., Murphy, E.S., Blackwell, L.C., LaCasse, J.L., & Drummond, S. (2010). Operant behavior in dwarf hamsters (*Phodopus campbelli*): Effects of rate of reinforcement and reinforcer flavor variety. *Behavioural Processes, 84(2)*, 573-580.

Madden, G.J., Dake, J.M., Mauel, E.C., & Rowe, R.R. (2005). Labor supply and consumption of food in a closed economy under a range of fixed- and random-ratio schedules: Test of unit price. *Journal of the Experimental Analysis of Behavior, 83(2),* 99-118.

Marx, M.H. (1950). A stimulus-response analysis of the hoarding habit in the rat. *Psychological Review, 57(2),* 80-93.

Mazur, J.E. (1984). Tests of an equivalence rule for fixed and variable reinforcer delays. *Journal of Experimental Psychology: Animal Behavior Processes, 10(4),* 426-436.

Mazur, J.E. (1987). An adjusting procedure for studying delayed reinforcement. In M.L. Commons, J.E. Mazur, J.A. Nevin, & H. Rachlin (Eds.), *Quantitative analyses of behavior: Vol. 5. The effect of delay and of intervening events on reinforcement value* (pp. 55-73). Hillsdale, NJ: Erlbaum.

Mazur, J.E. (1991). Choice with probalistic reinforcement: Effect of delay and conditioned reinforcers. *Journal of the Experimental Analysis of Behavior, 55(1),* 63-77.

Mazur, J.E. (1995). Conditioned reinforcement and choice with delayed and uncertain primary reinforcers. *Journal of the Experimental Analysis of Behavior, 63(2),* 139-150.

McNamara, J.M., & Houston, A.I. (1987). A general framework for understanding the effects of variability and interruptions on foraging behaviour. *Acta Biotheoretica, 36,* 3-22.

Miller, G.A. (1945). Concerning the goal of hoarding behavior in the rat. *Journal of Comparative & Physiological Psychology, 38,* 209-212.

Morgan, C.T. (1947). The hoarding instinct. *Psychological Review, 54(6),* 335-341.

Nowak, R.M. (1999). *Walker's Mammal of the World* (6th Ed., Vol. II). Baltimore and London: The John Hopkins University Press.

Ong, E.L., & White, K.G. (2004). Amount-dependent temporal discounting? *Behavioural Processes, 66,* 201-212.

Ostaszewski, P., Karzel, K., & Szafrańska, P. (2003). Changes in discounting rates as adaptation to food deprivation in rats: the role of age and deprivation level. *Polish Psychological Bulletin, 34(4),* 203-211.

Phillips, J.H., Robinson, A., & Davey, G.C.L. (1989). Food hoarding behaviour in the Golden hamster (*Mesocricetus auratus*): Effects of body weight loss and hoard-size discrimination. *The Quarterly Journal of Experimental Psychology, 41B(1),* 33-47.

Richards, J.B., Mitchell, S.H., de Wit, H., & Seiden, L.S. (1997). Determination of discounting functions in rats with an adjusting-amount procedure. *Journal of the Experimental Analysis of Behavior, 67(3),* 353-366.

Rodriguez, M.L., & Logue, A.W. (1988). Adjusting delay to reinforcement: Comparing choice in pigeons to humans. *Journal of Experimental Psychology: Animal Behavior Processes, 14(1),* 105-117.

Rosati, A.G., Stevens, J.R., & Hauser, M.D. (2006). The effect of handling time on temporal discounting in two New World primates. *Animal Behaviour, 71(6),* 1379-1387.

Rowland, N. (1982). Failure by deprived hamsters to increase food intake: Some behavioural and physiological determinants. *Journal of Comparative and Physiological Psychology, 96(4),* 591-603.

Shapiro, M.S., Schuck-Paim, C., & Kacelnik, A. (2012). Risk sensitivity for amounts of and delays to rewards: Adaptation for uncertainty or by-product of reward rate maximising? *Behavioural Processes, 89(2),* 104-114.

Shapiro, M.S., Siller, S., & Kacelnik, A. (2008). Simultaneous and sequential choice as a function of reward delay and magnitude: Normative, descriptive and process-based models tested in the European starling (*Sturnus vulgaris)*. *Journal of Experimental Psychology: Animal Behavior Processes, 34(1),* 75-93.

Siegel, S., & Castellan, N.J. (1988). Nonparametric statistics for the behavioral sciences. New York: McGraw-Hill.

Silverman, H.J., & Zucker, I. (1976). Absence of post-fast food compensation in the golden hamster (*Mesocricetus auratus*). *Physiology and Behavior, 17,* 271-285.

Stevens, J.R., & Stephens, D.W. (2009). The adaptive nature of impulsivity. In Madden, G.J., Bickel, W.K. (Eds.), *Impulsivity: the Behavioral and Neurological Science of Discounting* (pp. 361-387). APA Press, Washington, DC.

Tarte, R.D., & Vernon, C.R. (1974). Rat's barpressing in the presence of free food as a function of fixed-ratio schedules. *Bulletin of the Psychonomic Society, 3,* 34-36.

Toates, F.M. (1978). A circadian rhythm of hoarding in the hamster. *Animal Behaviour, 26,* 631.

Tobin, H. & Logue, A.W. (1994). Self-control across species (*Columba livia, Homo sapiens,* and *Rattus norvegicus*). *Journal of Comparative Psychology, 108(2)*, 126-133.

Waddell, D. (1951). Hoarding behavior in the Golden hamster. *Journal of Comparative and Physiological Psychology, 44(4),* 383-388.

Wertz, K.A. (2007). Operant conditioning and hoarding behavior in Djungarian hamsters *(Phodopus campbelli).* Unpublished master's thesis, Kansas State University, Manhattan.

Wong, R., & Jones, C.H. (1985). A comparative analysis of feeding and hoarding in hamsters and gerbils. *Behavioural Processes, 11,* 301-308.

Footnotes

[1] Graphs in Appendix B represent responses made on warm-up and free choice trials, but not on forced choice trials. Diamond symbols (blue) represent responses made on the Shorter Sooner alternative. Square symbols (red) represent responses made on the Larger Later alternative. Triangle symbols (green) symbols represent timeouts, with each triangle corresponding with a half of an hour. Graphs present performance of each individual at a 10 sec. delay, their indifference point, and at the delay at which they met the end criterion. Graphs represent individual data for each subject, for one session, and are not averages for the four days of stability. Two rats did not reach an indifference point or end criterion and are represented on the same page.

[2] Elasticity is typically considered using ratio schedule of demand, in which the number of responses required for reinforcement is the price imposed by the schedule. The present experiment used interval schedules for which, traditionally, time is the price for a commodity. (See Lea [1978] for further considerations.) However, because the present experiment contrasts 2 different interval schedules and compares the preference for one compared to the other, it makes the assumption that demand would be measured by the number of choices made, similar to that measure for ratio schedules of demand.

Figure Captions

Figure 1. Box plots of means of indifference points, linear slope and end criteria by species. Plots demonstrate the existence of outliers in the data, supporting the use of non-parametric testing.

Figure 2. Box plots of means of indifference points, linear slope and end criteria by sex. Plots show no meaningful differences between the sexes for either species.

Figure 3. Box plots of means of indifference points, linear slope and end criteria by group. Plots show no meaningful differences between the groups for the species. Because Group 3 consisted of only one subject and was run consecutively with some subjects from Group 2, Group 3 data was collapsed into Group 2.

Figure 4. Mean number of timeouts for each trial type by species across each delay. SS: Shorter Sooner Forced Choice Trial; LL: Larger Later Forced Choice Trial; Free: Free Choice Trial. Timeouts occurred more often on Larger Later force choice trials as the delay to reinforcement increased. Timeouts occurred least often on Free Choice trials throughout the experiment.

Figures

Figure 1

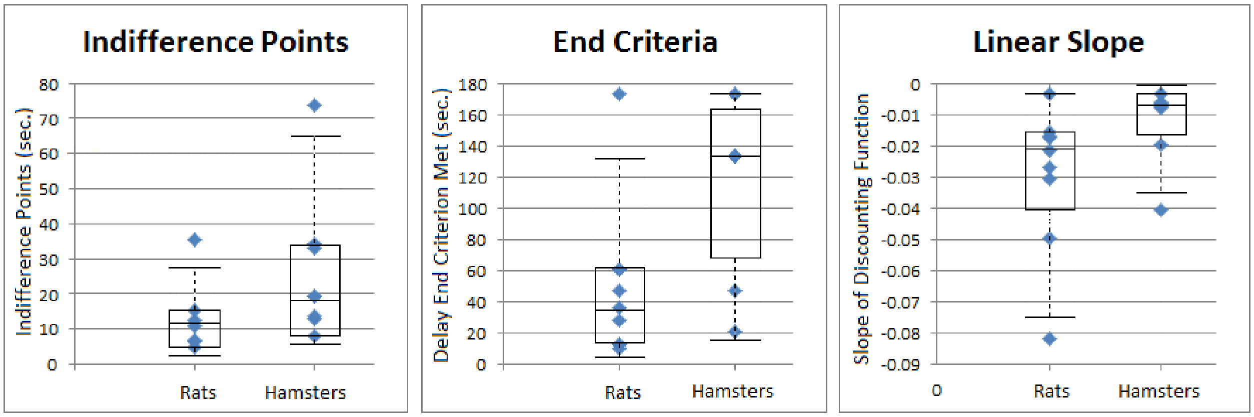
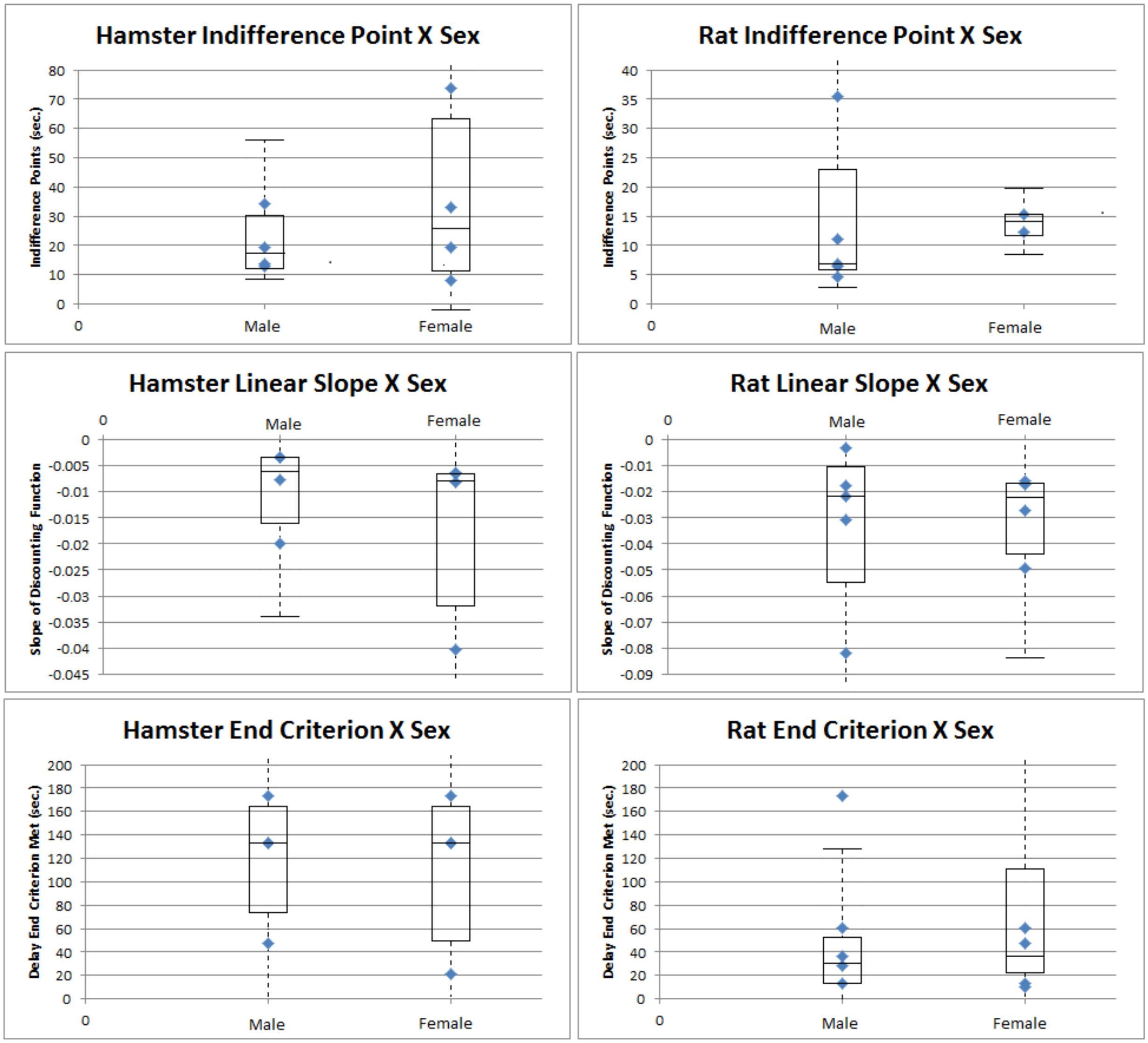


Figure 2


Hamster Indifference Point X Sex

Rat Indifference Point X Sex

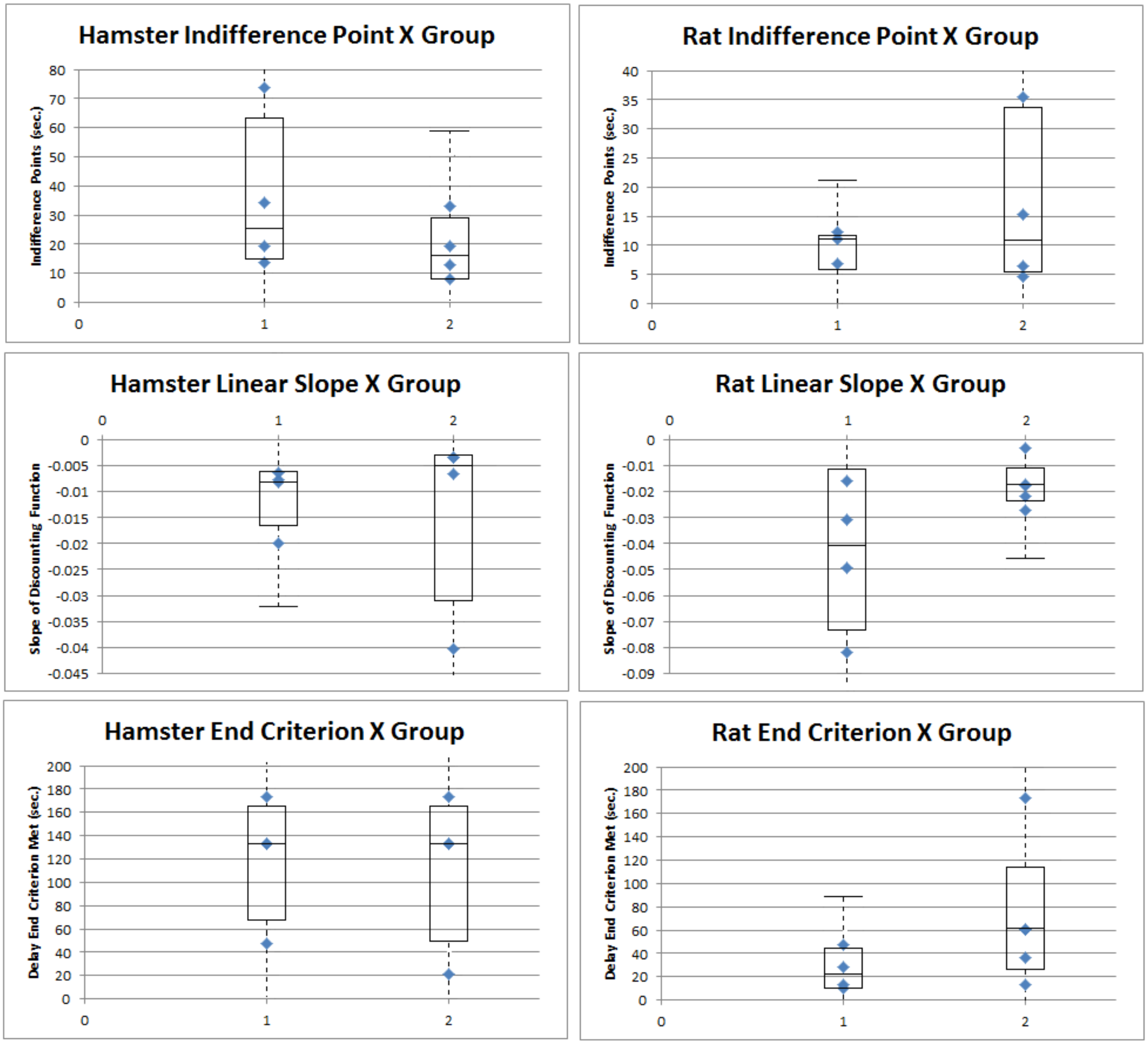
Hamster Linear Slope X Sex

Rat Linear Slope X Sex

Hamster End Criterion X Sex

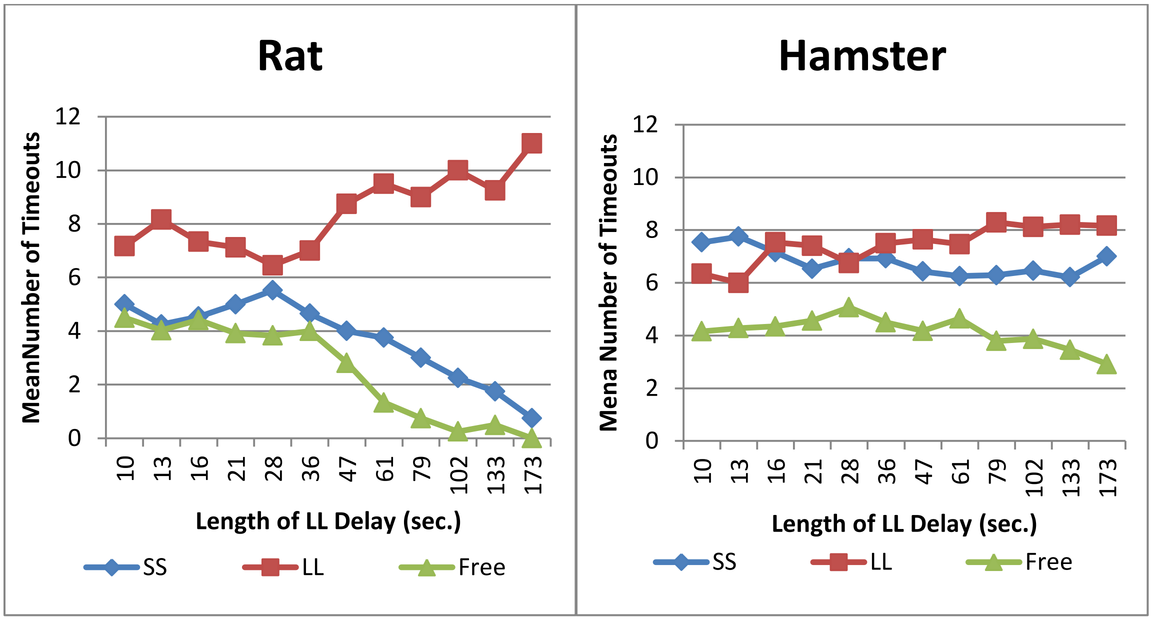
Rat End Criterion X Sex

Figure 3



Hamster Indifference Point X Group
Indifference Points (sec.)
80
70
60
50
40
30
20
10
0
0
1
2
Rat Indifference Point X Group
Indifference Points (sec.)
40
35
30
25
20
15
10
5
0
0
1
2
Hamster Linear Slope X Group
Slope of Discounting Function
0
1
2
0
-0.005
-0.01
-0.015
-0.02
-0.025
-0.03
-0.035
-0.04
-0.045
Rat Linear Slope X Group
Slope of Discounting Function
0
1
2
0
-0.01
-0.02
-0.03
-0.04
-0.05
-0.06
-0.07
-0.08
-0.09
Hamster End Criterion X Group
Delay End Criterion Met (sec.)
200
180
160
140
120
100
80
60
40
20
0
0
1
2
Rat End Criterion X Group
Delay End Criterion Met (sec.)
200
180
160
140
120
100
80
60
40
20
0
0
1
2

Figure 4


Rat
MeanNumber of Timeouts
12
10
8
6
4
2
0
10
13
16
21
28
36
47
61
79
102
133
173
Length of LL Delay (sec.)
SS
LL
Free
Hamster
Mena Number of Timeouts
12
10
8
6
4
2
0
10
13
16
21
28
36
47
61
79
102
133
173
Length of LL Delay (sec.)
SS
LL
Free

Tables

Table 1.

Percent Choice of LL Lever X Delay

	Delay (sec.)											
Subject	10	13	16	21	28	36	47	61	79	102	133	173
						Hamster						
22-10	98%	87%	70%	71%	71%	44%	35%	38%	14%	8%	1%	
18-10	52%	49%	50%	38%	22%	11%	1%					
01-11	57%	41%	52%	29%	30%	24%	17%	11%	7%	5%	4%	
06-11	43%	60%	66%	40%	41%	41%	21%	22%	12%	13%	13%	3%
10-10	91%	100%	93%	86%	80%	80%	83%	56%	47%	33%	9%	4%
13-10	95%	78%	77%	35%	29%	26%	17%	19%	12%	13%	6%	
14-11	35%	19%	22%	6%								
12-11	85%	84%	77%	63%	61%	43%	38%	40%	28%	10%	5%	
						Rat						
A1	61%	33%	29%	16%	8%							
A2	29%	10%	13%	9%	7%	6%						
A3	39%	26%	33%	45%	45%	46%	26%	33%	22%	11%	11%	7%
B1	13%	8%										
B2	85%	84%	92%	91%	75%	48%	28%	4%				
A4	12%	7%										
B3	80%	67%	46%	37%	35%	12%	11%	5%				
B5	58%	48%	32%	31%	32%	17%	6%					

Table 2.

Indifference Points, Linear Slopes of Discounting Functions, and Delays at End Criteria

Subject	Species	Sex	Shift	Group	Indifference Point	Linear Slope	End Criteria
22-10	Hamster	M	AM	1	34.2	-0.0076	133
18-10	Hamster	M	PM	1	13.8	-0.0198	47
01-11	Hamster	M	PM	2	13.1	-0.0033	133
06-11	Hamster	M	AM	2	19.5	-0.0034	173
10-10	Hamster	F	AM	1	73.8	-0.0063	173
13-11	Hamster	F	PM	1	19.3	-0.0081	133
14-11	Hamster	F	AM	2	8.2	-0.0404	21
12-11	Hamster	F	PM	2	32.9	-0.0065	133
A1	Rat	M	PM	1	11.2	-0.0307	28
A2	Rat	M	PM	2	6.5	-0.0217	36
A3	Rat	M	PM	3	4.7	-0.0033	173
B1	Rat	M	AM	1	6.8	-0.0818	13
B2	Rat	M	AM	2	35.5	-0.0174	61
A4	Rat	F	PM	2		-0.0271	13
A5	Rat	F	PM	1		-0.0495	10
B3	Rat	F	AM	2	15.4	-0.0170	61
B5	Rat	F	AM	1	12.4	-0.0158	47

Table 3.

Summary Statistics for Discounting Task X Sex

		Females			Males		
Species	Test	M	SD	n	M	SD	n
Hamster	Indifference Points	33.6	28.7	4	20.2	9.8	4
	Linear Slopes	-0.0153	0.0167	4	-0.0085	0.0078	4
	Delays at End Criteria	115.0	65.4	4	121.5	53.1	4
Rat	Indifference Points	13.9	2.1	2	12.9	12.8	5
	Linear Slopes	-0.0274	0.0156	4	-0.031	0.0301	5
	Delays at End Criteria	32.8	25.2	4	62.2	64.3	5

Table 4.

Summary Statistics for Discounting Task X Group

		Group 1			Group 2		
Species	Test	M	SD	n	M	SD	n
Hamster	Indifference Points	32.3	27.1	4	18.4	10.7	4
	Linear Slopes	-.0105	.0063	4	-.0134	.0181	4
	Delays at End Criteria	121.5	53.1	4	115.0	65.4	4
Rat	Indifference Points	10.1	3.0	3	15.53	14.11	4
	Linear Slopes	-.0445	.0285	4	-.0173	.0088	5
	Delays at End Criteria	24.5	16.9	4	68.8	61.6	5

Table 5.

Average Number of Pellets Left in Food Tray X Delay

		Delay (sec.)											
Subject	Sex	10	13	16	21	28	36	47	61	79	102	133	173
Hamster													
22-10	M	1	1	0	0	0	0	0	1	1	0	0	
18-10	M	0	0	0	0	0	0	0					
01-11	M	3	0	0	0	0	0	1	0	0	0	0	
06-11	M	0	3	3	2	1	1	0	0	0	2	0	0
10-10	F	0	0	0	0	0	0	0	0	1	0	0	0
13-11	F	0	0	0	0	0	0	1	0	0	0	0	
14-11	F	1	0	1	1								
12-11	F	0	0	0	0	0	0	0	0	0	0	0	
Rat													
A1	M	0	0	0	0	0							
A2	M	1	0	0	2	0	0						
A3	M	0	0	0	0	0	0	0	0	0	0	0	0
B1	M	0	0										
B2	M	0	0	0	1	0	0	0	0				
A4	F	0	0										
A5	F	1											
B3	F	2	1	0	0	0	0	0	0				
B5	F	2	2	0	0	0	1	0					

Table 6.

Number of Subjects That Experienced a Given Delay X Species

	Delay (sec.)											
Species	10	13	16	21	28	36	47	61	79	102	133	173
Hamster	8	8	8	8	7	7	7	6	6	6	6	2
Rat	8	8	6	6	6	5	4	3	1	1	1	1

Table 7.

Average Number of Timeouts per Session X Delay

	Delay (sec.)											
Subject	10	13	16	21	28	36	47	61	79	102	133	173
Hamster												
22-10	18	18	20	20	21	21	21	17	20	19	19	
18-10	18	18	19	20	19	19	19					
01-11	17	17	18	18	18	19	18	19	18	19	19	
06-11	19	19	19	19	19	18	17	19	19	18	17	18
10-10	19	17	20	16	19	19	17	18	18	18	17	17
13-11	16	17	18	18	17	18	17	18	17	17	16	
14-11	18	19	19	19								
12-11	20	20	20	20	19	20	19	20	19	21	19	
Rat												
A1	17	16	16	16	15							
A2	17	17	16	16	15	16						
A3	14	15	15	15	15	15	15	13	13	13	12	12
B1	15	15										
B2	18	18	19	18	18	17	17	15				
A4	17	17										
B3	19	19	19	18	18	17	16	16				
B5	17	15	15	13	15	14	15					

Table 8.

Average Latency to Start the Warm-up and Experimental Phases at a 10-sec. Delay and the Delay at End Criterion

	Warm-up Phase (sec.)		Experimental Phase (sec.)	
Subject	10-sec. Delay	End Criterion Delay	10-sec. Delay	End Criterion Delay
		Hamster		
22-10	335	59	4981	427
18-10	109	1272	1408	2388
01-11	1147	20	7016	3033
06-11	61	725	2644	2854
10-10	130	1150	1731	3073
13-11	836	151	6578	766
14-11	250	159	1462	831
12-11	336	38	2920	326
		Rat		
A1	3	1	49	67
A2	1	3	50	70
A3	1	0	51	173
B1	1	2	44	44
B2	1	1	70	96
A4	19	3	79	49
B3	17	170	62	8
B5	1	2	65	100

Table 9.

Average Type of Trial Timed Out On X Delay

		Delay (sec.)											
Species	Type of Trial	10	13	16	21	28	36	47	61	79	102	133	173
	SS forced	8	8	7	7	7	7	6	6	6	6	6	7
Hamster	LL forced	6	6	8	7	7	8	8	7	8	8	8	8
	Free choice	4	4	4	5	5	5	4	5	4	4	3	3
	SS forced	5	4	5	5	6	5	4	4	3	2	2	1
Rat	LL forced	7	8	7	7	6	7	9	10	9	10	9	11
	Free choice	5	4	4	4	4	4	3	1	1	0	1	0

Table 10.

Average Number of Total Choices Made per Subject X Delay

	Delay (sec.)											
Subject	10	13	16	21	28	36	47	61	79	102	133	173
						Hamster						
22-10	20	37	34	36	25	36	36	50	42	50	57	
18-11	18	18	19	20	19	19	19					
01-11	19	22	18	19	29	35	39	39	32	37	32	
06-11	19	17	21	18	17	22	30	25	39	36	31	39
10-10	20	22	22	23	31	26	25	37	41	35	50	55
13-11	29	42	43	44	42	46	62	50	56	53	52	
14-11	30	31	35	41								
12-11	14	13	13	14	15	17	15	13	17	17	22	
						Rat						
A1	153	195	195	177	290							
A2	163	204	200	216	231	241						
A3	150	157	170	147	178	158	184	203	225	251	255	266
B1	236	250										
B2	92	101	86	109	111	140	166	211				
A4	128	172										
B3	78	74	87	97	97	135	152	178				
B5	112	123	144	150	144	166	189					

Table 11.

Average Number of Pellets Earned X Delay

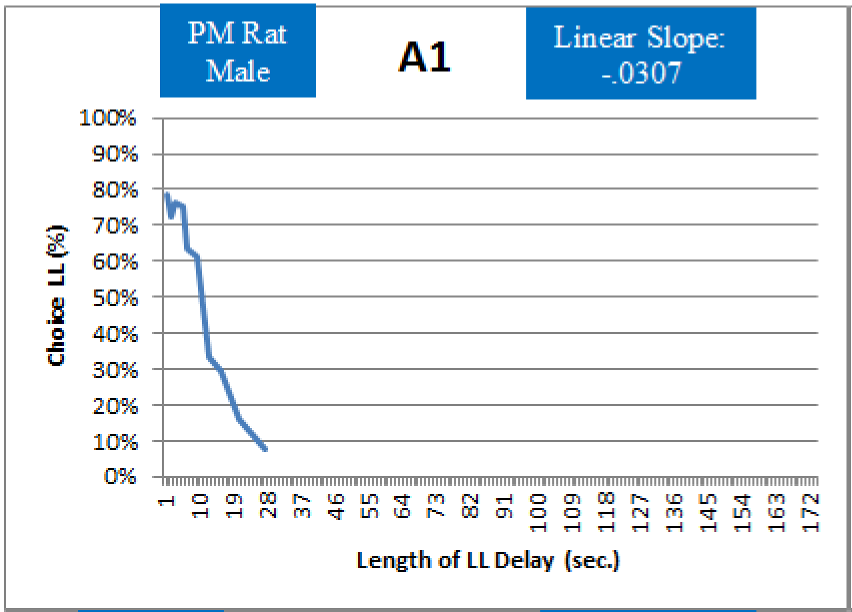
	Delay (sec.)											
Subject	10	13	16	21	28	36	47	61	79	102	133	173
						Hamster						
22-10	93	146	112	120	93	96	93	132	91	96	99	94
18-10	96	92	97	100	96	97	83					
01-11	72	80	67	62	85	88	91	90	74	80	70	
06-11	67	70	77	62	59	76	77	72	80	79	75	79
10-10	88	96	94	96	105	105	102	123	117	98	111	113
13-10	120	158	154	118	108	110	123	113	117	109	101	
14-11	86	74	91	81								
12-11	61	63	61	62	63	61	53	54	53	53	52	
						Rat						
A1	443	434	419	464	496							
A2	357	362	377	379	398	412						
A3	354	325	340	367	426	397	402	448	442	440	447	441
B1	426	436										
B2	315	344	343	394	363	362	353	338				
A4	236	293										
B3	258	231	232	233	236	259	281	294				
B5	318	325	328	338	326	323	319					

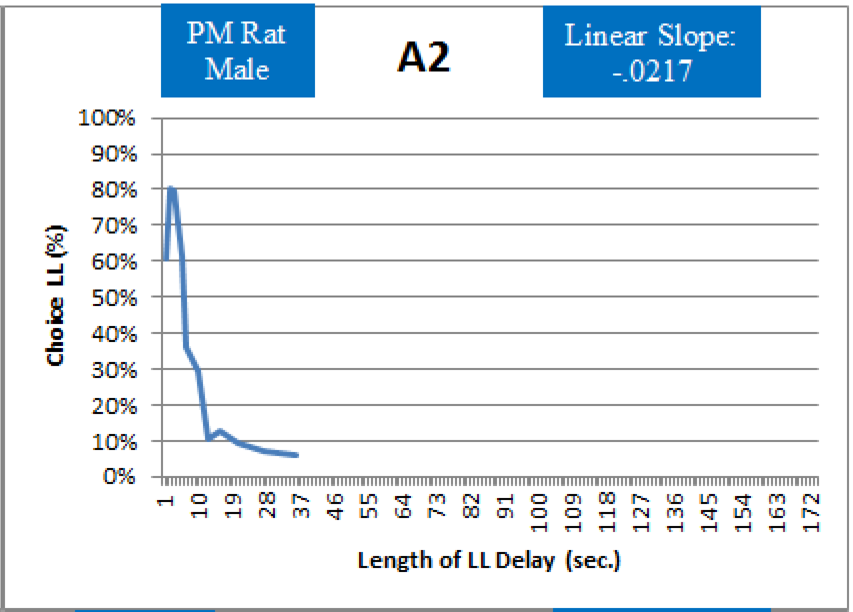
Table 12.

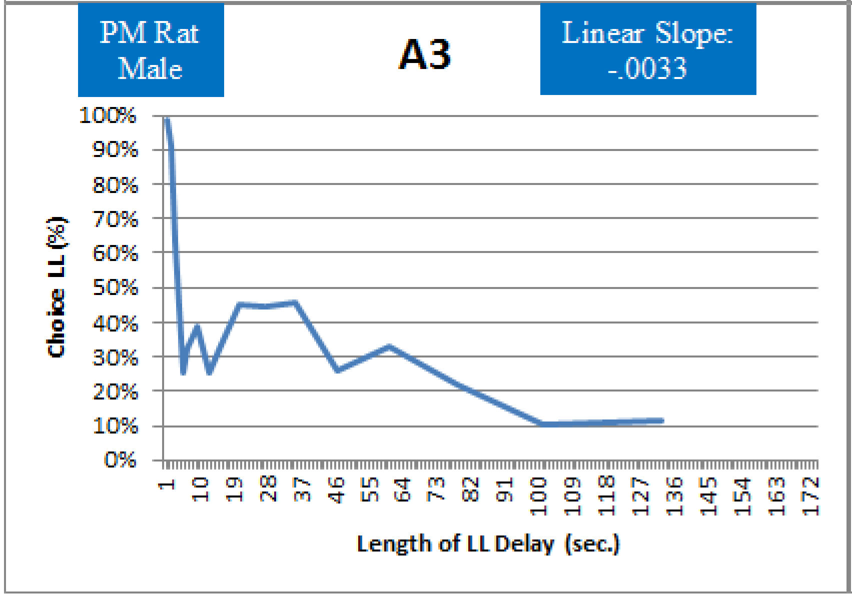
Average Weight (g.) at Shaping and the End of Experiment and Their Difference

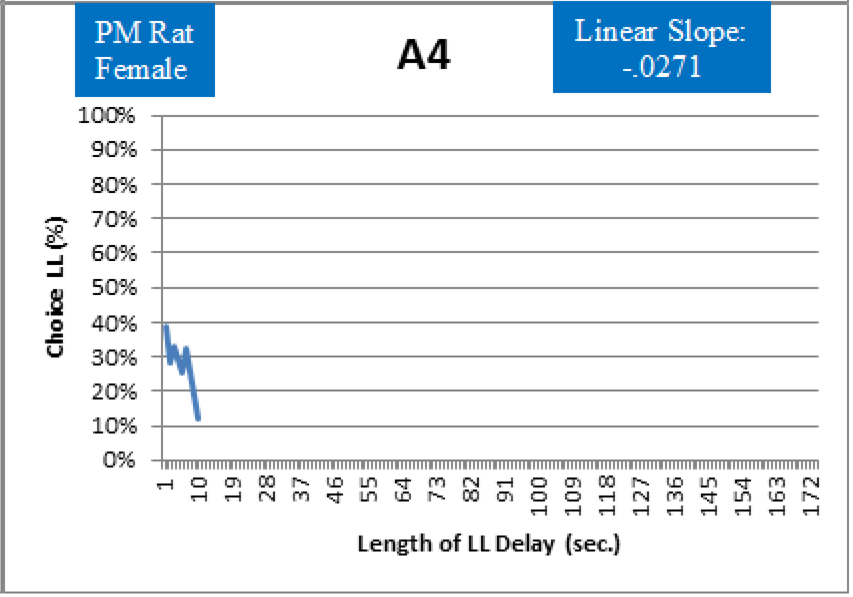
	Weight (g)			
Subject	Start	End	Difference	% Difference
		Hamster		
22-10	18	19	2	10%
18-10	30	38	8	26%
01-11	35	37	2	4%
06-11	30	35	5	17%
10-10	33	37	5	14%
13-11	28	39	11	38%
14-11	31	34	4	12%
12-11	25	27	2	9%
Ave.	30	27	5	17%
		Rat		
A1	540	518	-22	-4%
A2	694	644	-50	-7%
A3	706	647	-59	-8%
B1	502	492	-10	-2%
B2	528	516	-12	-2%
A4	370	338	-32	-9%
A5	229	225	-4	-2%
B3	403	356	-47	-12%
B5	228	247	19	8%
Ave.	467	443	-24	-4%

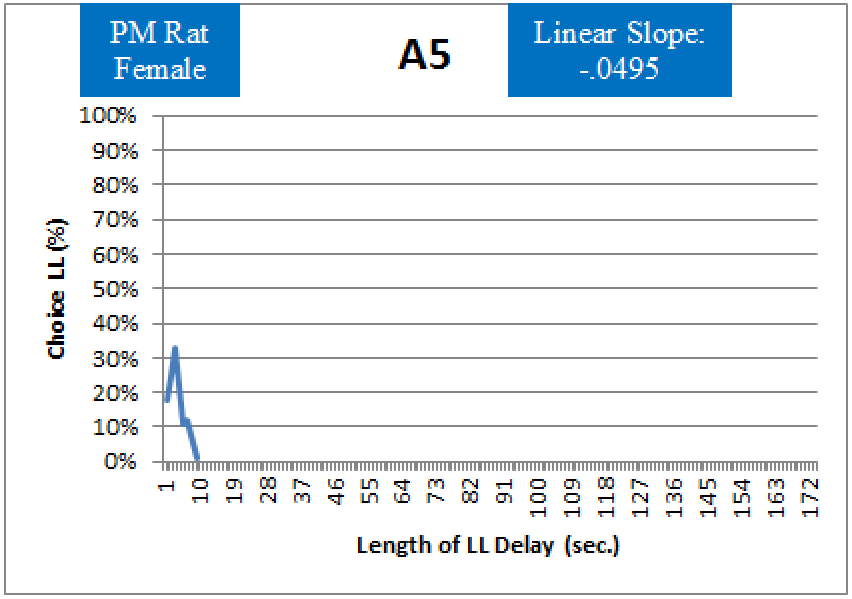
Appendix A - Discounting Functions

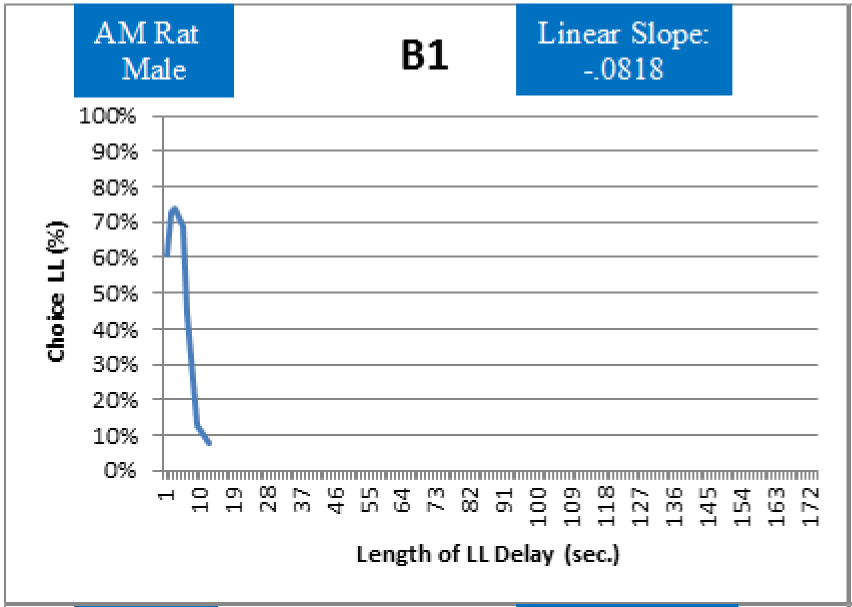

PM Rat Male
A1
Linear Slope: -.0307
Choice LL (%)
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
1
10
19
28
37
46
55
64
73
82
91
100
109
118
127
136
145
154
163
172
Length of LL Delay (sec.)

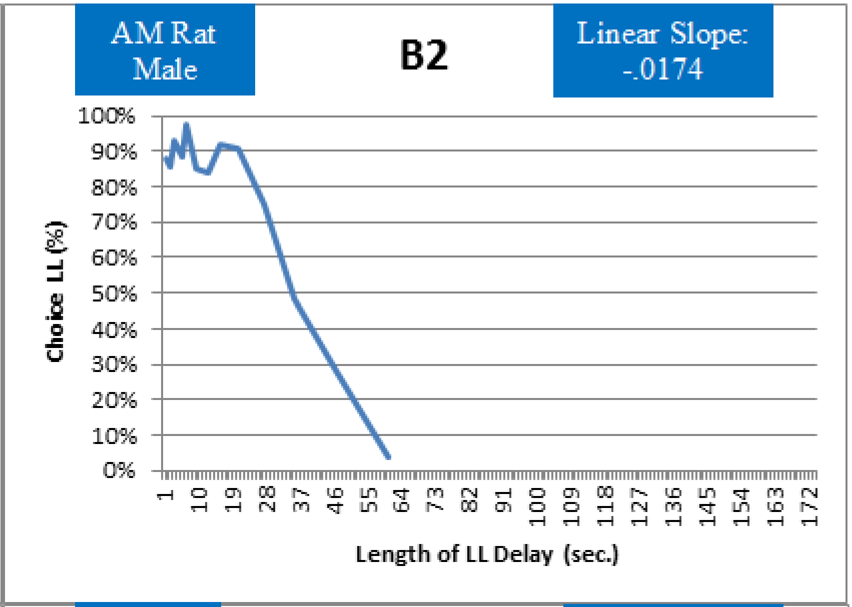

PM Rat Male
A2
Linear Slope: -.0217
Choice LL (%)
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
1
10
19
28
37
46
55
64
73
82
91
100
109
118
127
136
145
154
163
172
Length of LL Delay (sec.)

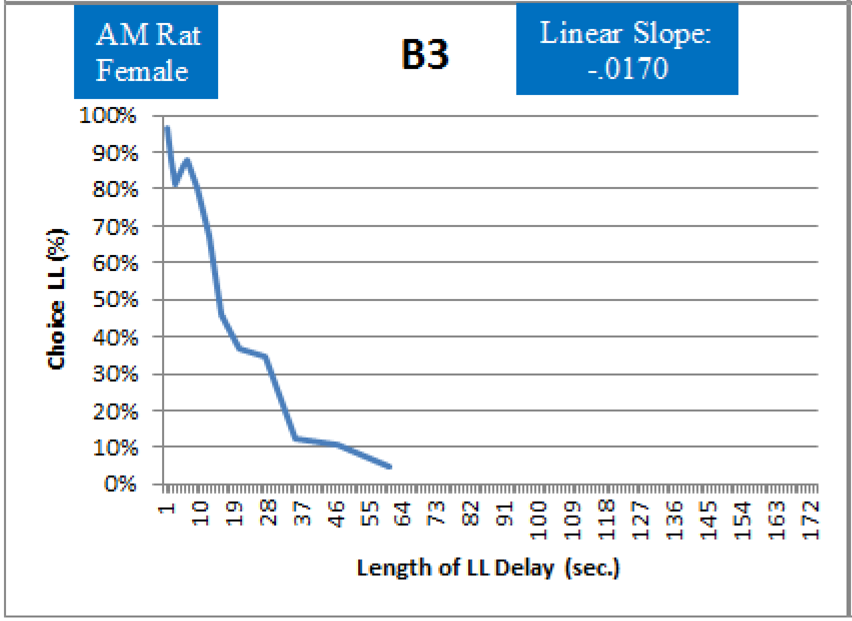

PM Rat Male
A3
Linear Slope: -.0033
Choice LL (%)
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
1
10
19
28
37
46
55
64
73
82
91
100
109
118
127
136
145
154
163
172
Length of LL Delay (sec.)

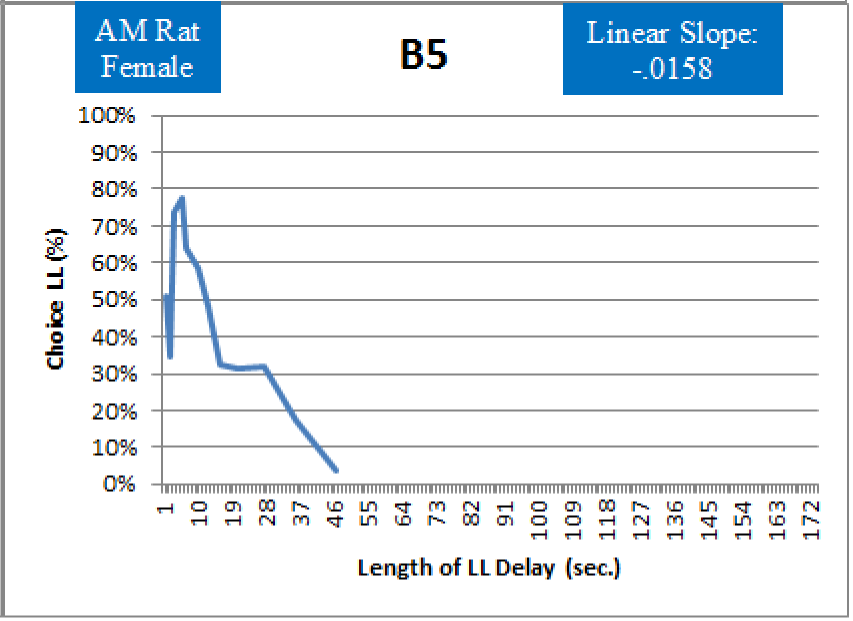

PM Rat Female
A4
Linear Slope: -.0271
Choice LL (%)
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
1
10
19
28
37
46
55
64
73
82
91
100
109
118
127
136
145
154
163
172
Length of LL Delay (sec.)

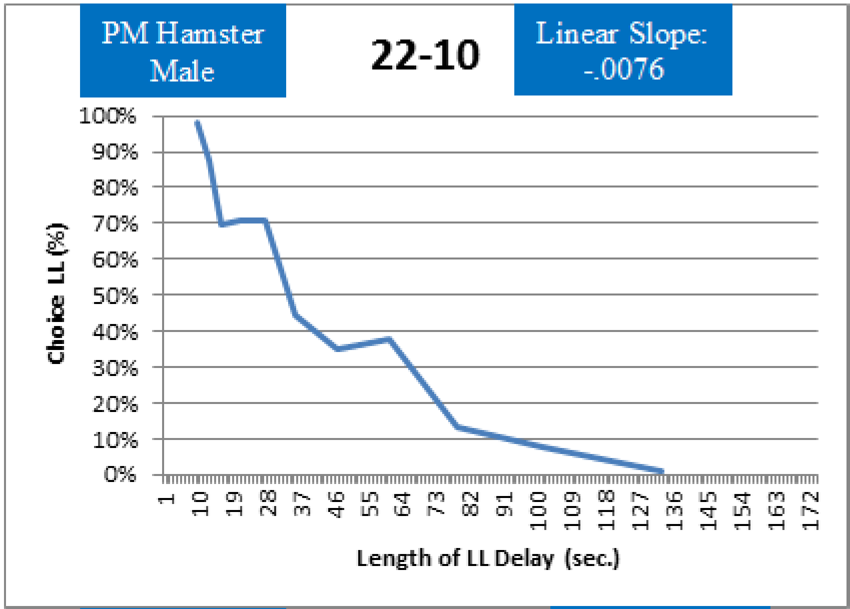

PM Rat
Female
A5
Linear Slope:
-.0495
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
Choice LL (%)
1
10
19
28
37
46
55
64
73
82
91
100
109
118
127
136
145
154
163
172
Length of LL Delay (sec.)

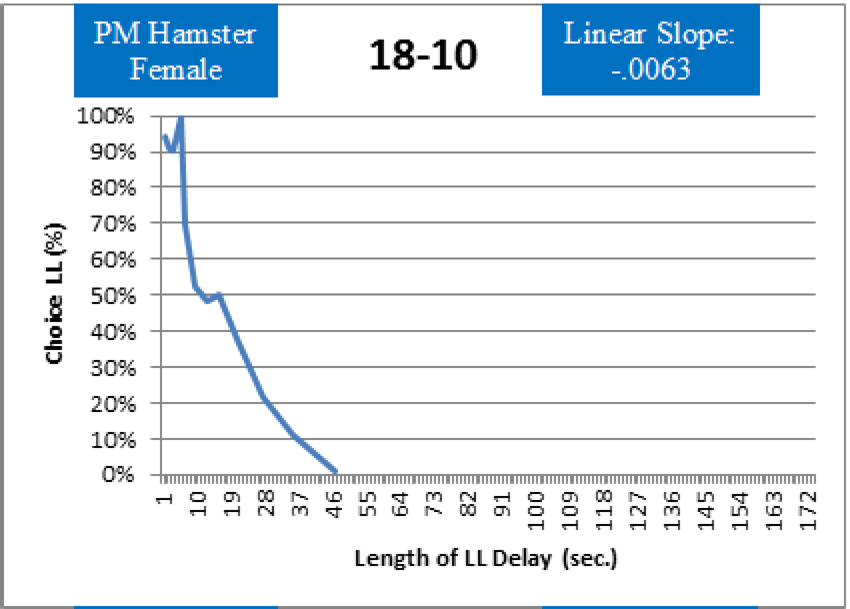

AM Rat Male
B1
Linear Slope: -.0818
Choice LL (%)
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
1
10
19
28
37
46
55
64
73
82
91
100
109
118
127
136
145
154
163
172
Length of LL Delay (sec.)

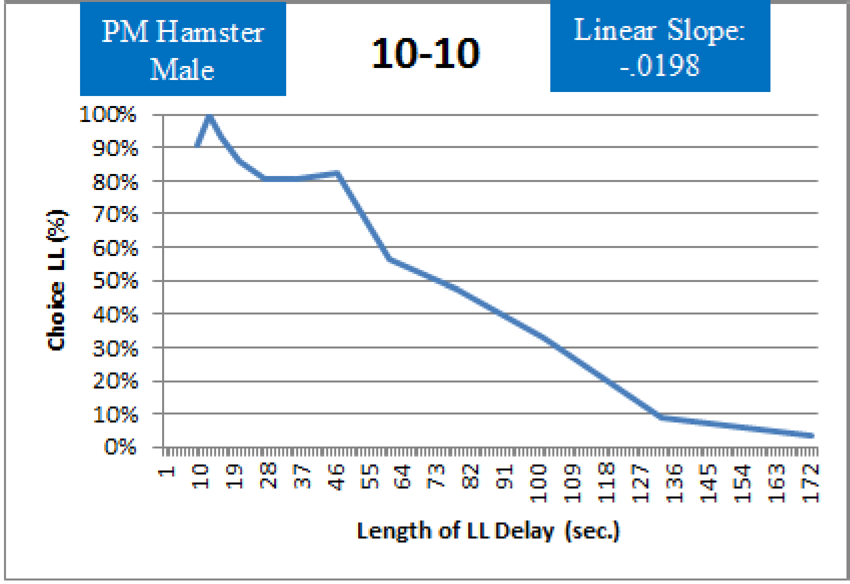

AM Rat Male
B2
Linear Slope: -.0174
Choice LL (%)
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
1
10
19
28
37
46
55
64
73
82
91
100
109
118
127
136
145
154
163
172
Length of LL Delay (sec.)

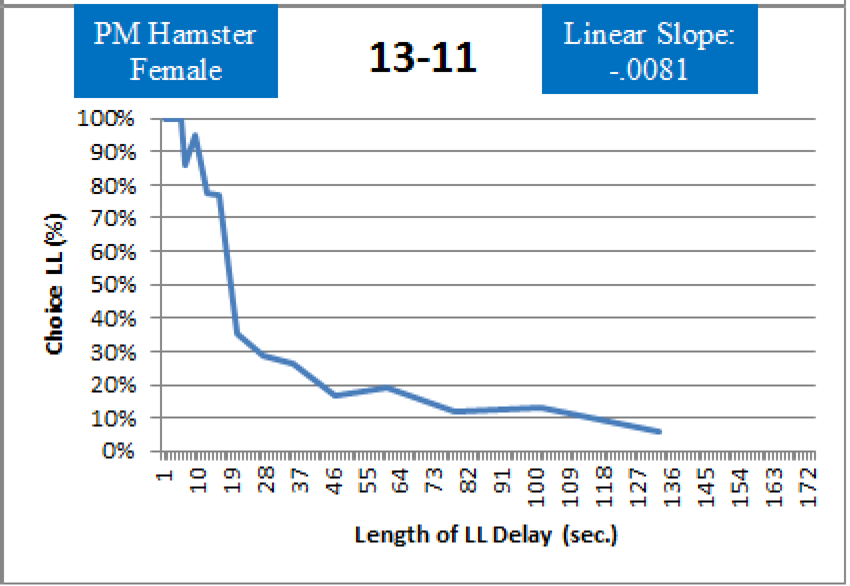

AM Rat Female
B3
Linear Slope: -.0170
Choice LL (%)
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
1
10
19
28
37
46
55
64
73
82
91
100
109
118
127
136
145
154
163
172
Length of LL Delay (sec.)

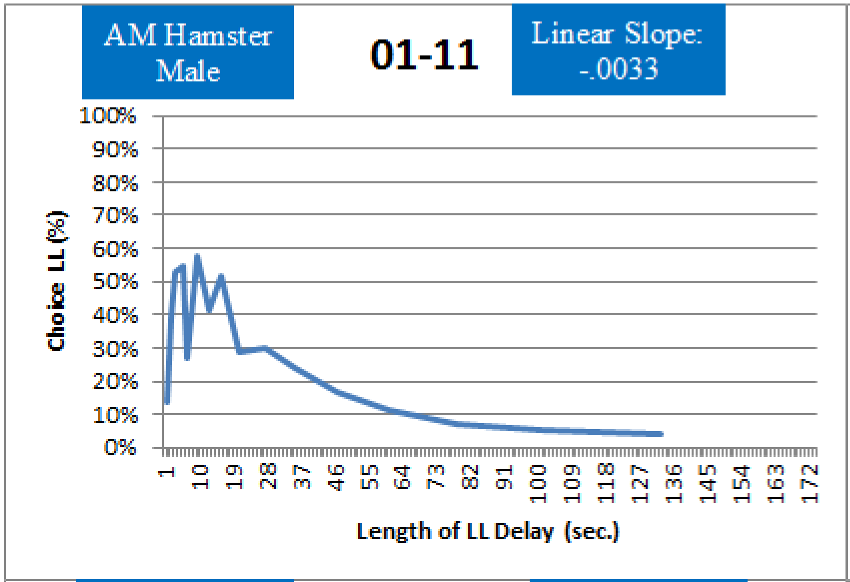

AM Rat Female
B5
Linear Slope: -.0158
Choice LL (%)
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
1
10
19
28
37
46
55
64
73
82
91
100
109
118
127
136
145
154
163
172
Length of LL Delay (sec.)

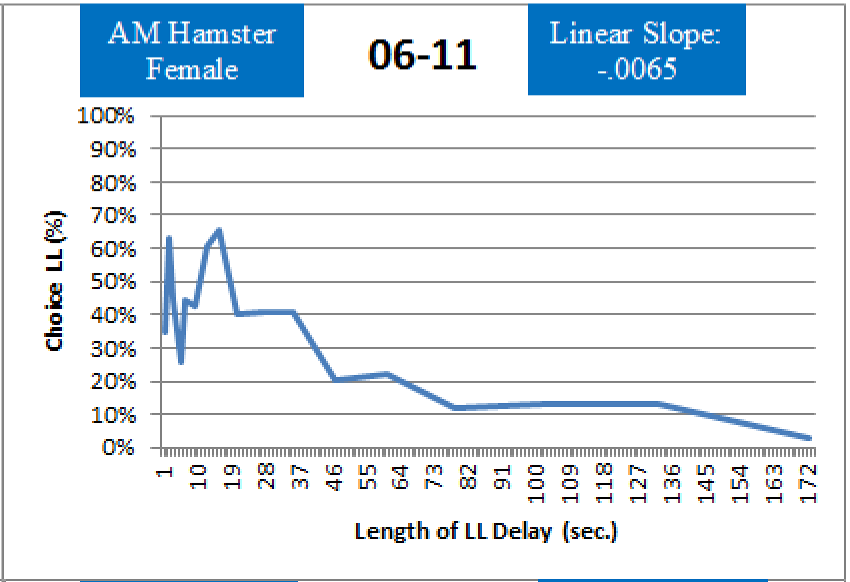

PM Hamster Male
22-10
Linear Slope: -.0076
Choice LL (%)
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
1
10
19
28
37
46
55
64
73
82
91
100
109
118
127
136
145
154
163
172
Length of LL Delay (sec.)

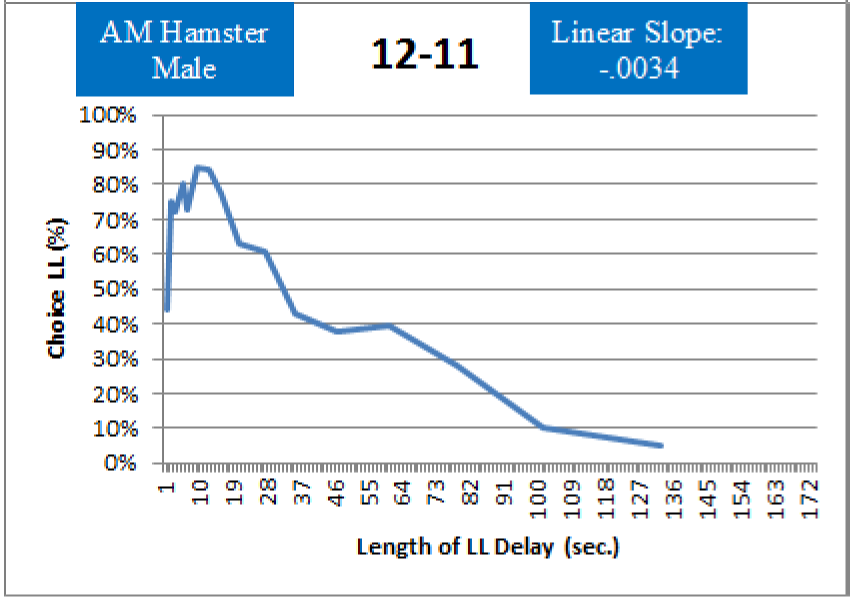

PM Hamster Female
18-10
Linear Slope: -.0063
Choice LL (%)
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
1
10
19
28
37
46
55
64
73
82
91
100
109
118
127
136
145
154
163
172
Length of LL Delay (sec.)

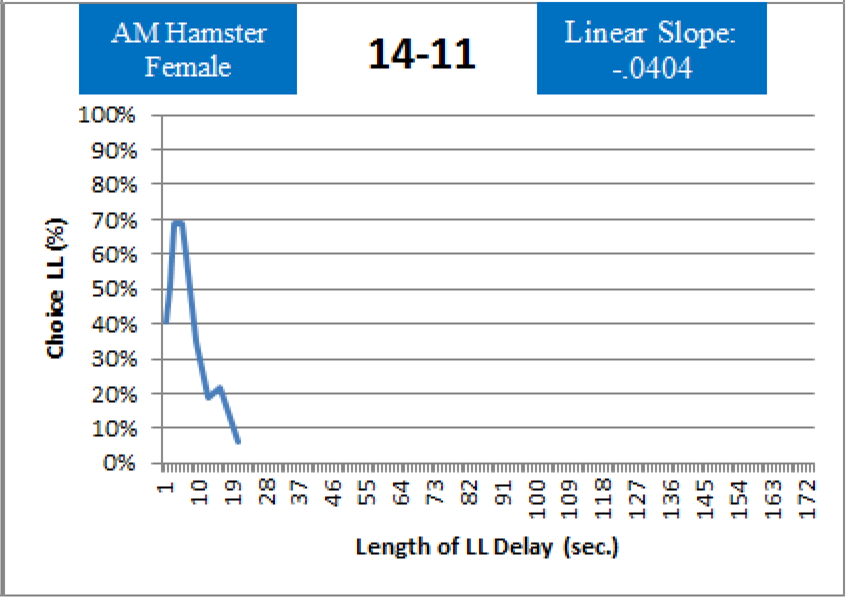

PM Hamster Male
10-10
Linear Slope: -.0198
Choice LL (%)
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
1
10
19
28
37
46
55
64
73
82
91
100
109
118
127
136
145
154
163
172
Length of LL Delay (sec.)


PM Hamster Female
13-11
Linear Slope: -.0081
Choice LL (%)
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
1
10
19
28
37
46
55
64
73
82
91
100
109
118
127
136
145
154
163
172
Length of LL Delay (sec.)


AM Hamster Male
01-11
Linear Slope: -.0033
Choice LL (%)
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
1
10
19
28
37
46
55
64
73
82
91
100
109
118
127
136
145
154
163
172
Length of LL Delay (sec.)

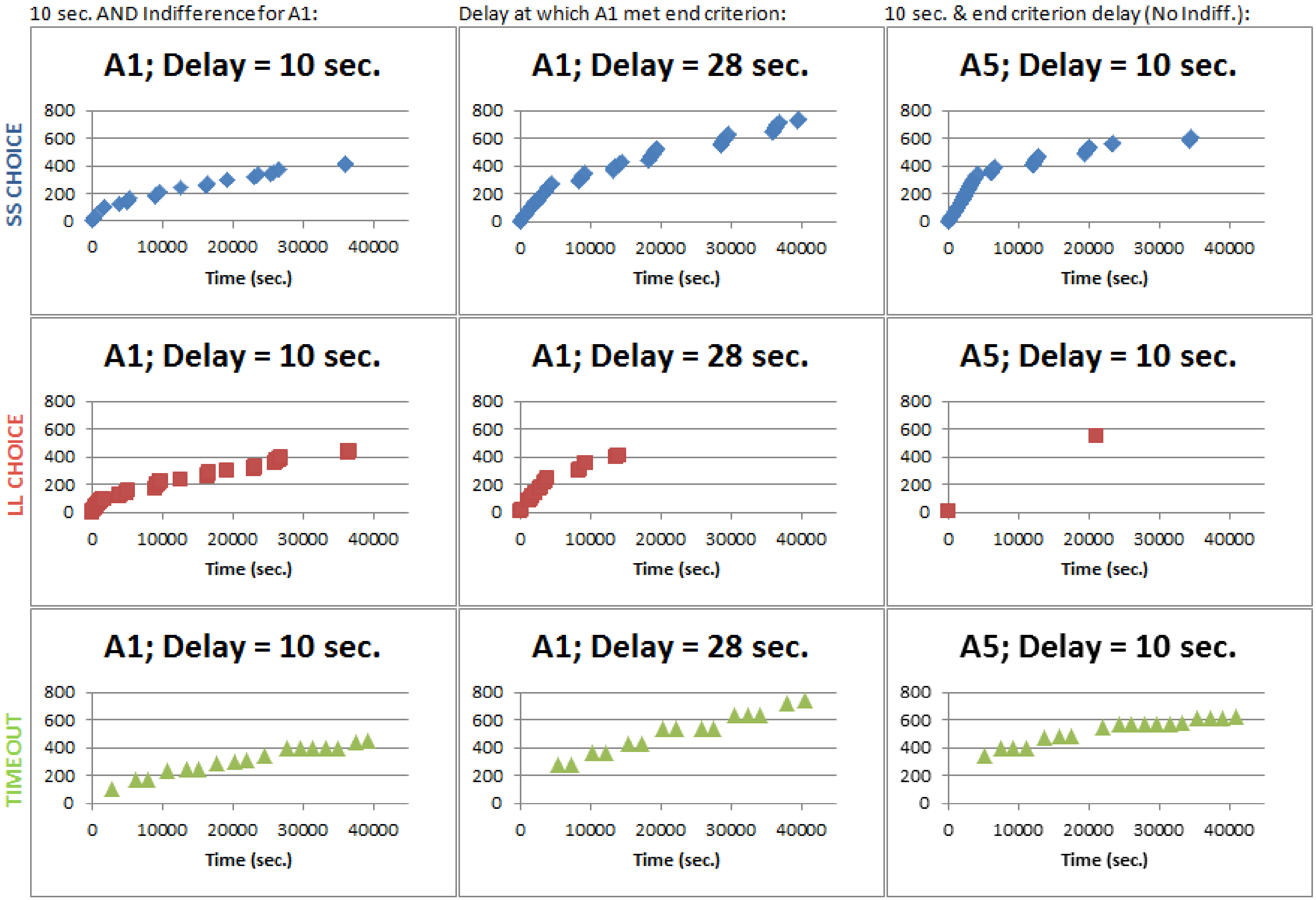

AM Hamster Female
06-11
Linear Slope: -.0065
Choice LL (%)
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
1
10
19
28
37
46
55
64
73
82
91
100
109
118
127
136
145
154
163
172
Length of LL Delay (sec.)

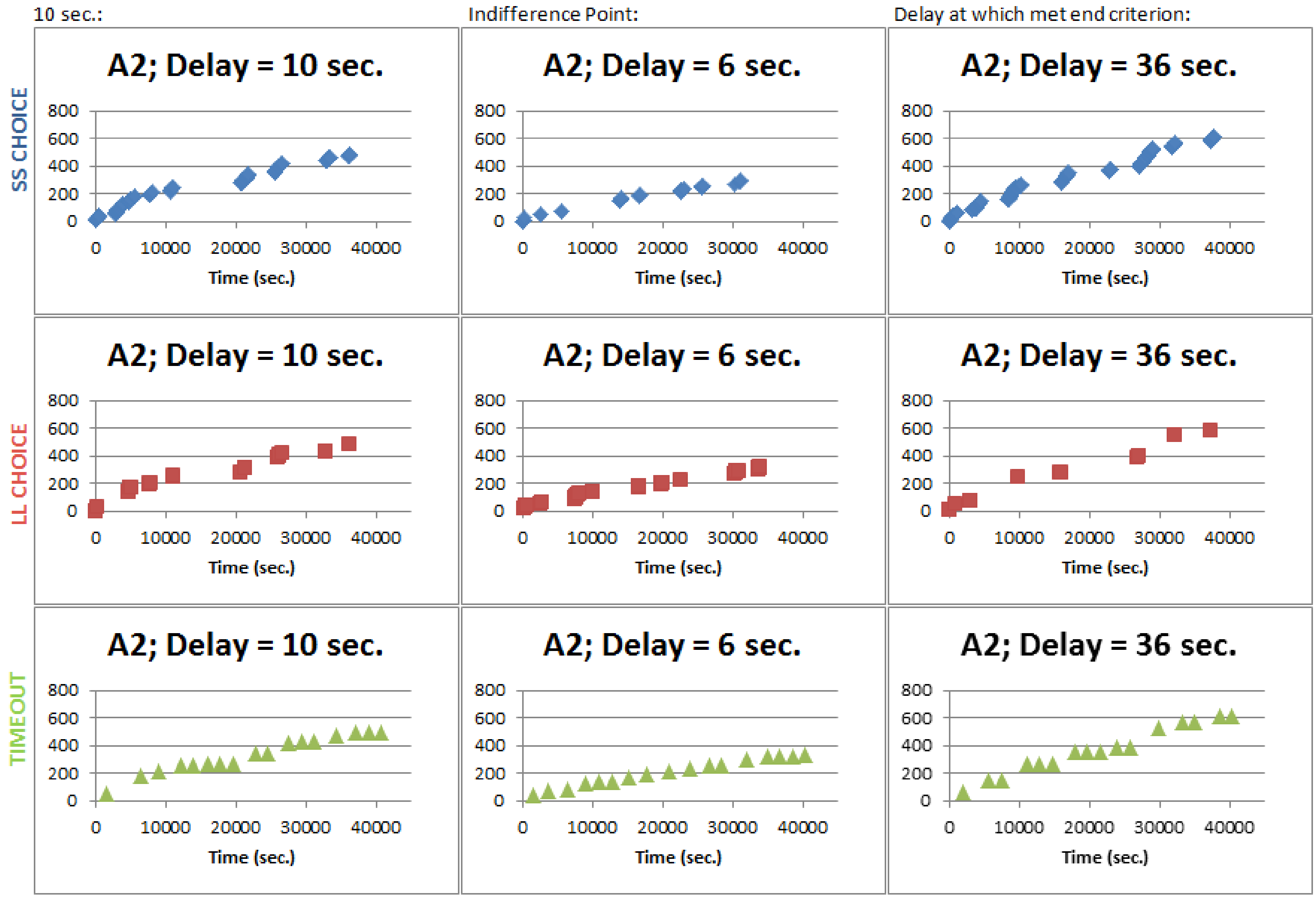

AM Hamster Male
12-11
Linear Slope: -.0034
Choice LL (%)
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
1
10
19
28
37
46
55
64
73
82
91
100
109
118
127
136
145
154
163
172
Length of LL Delay (sec.)

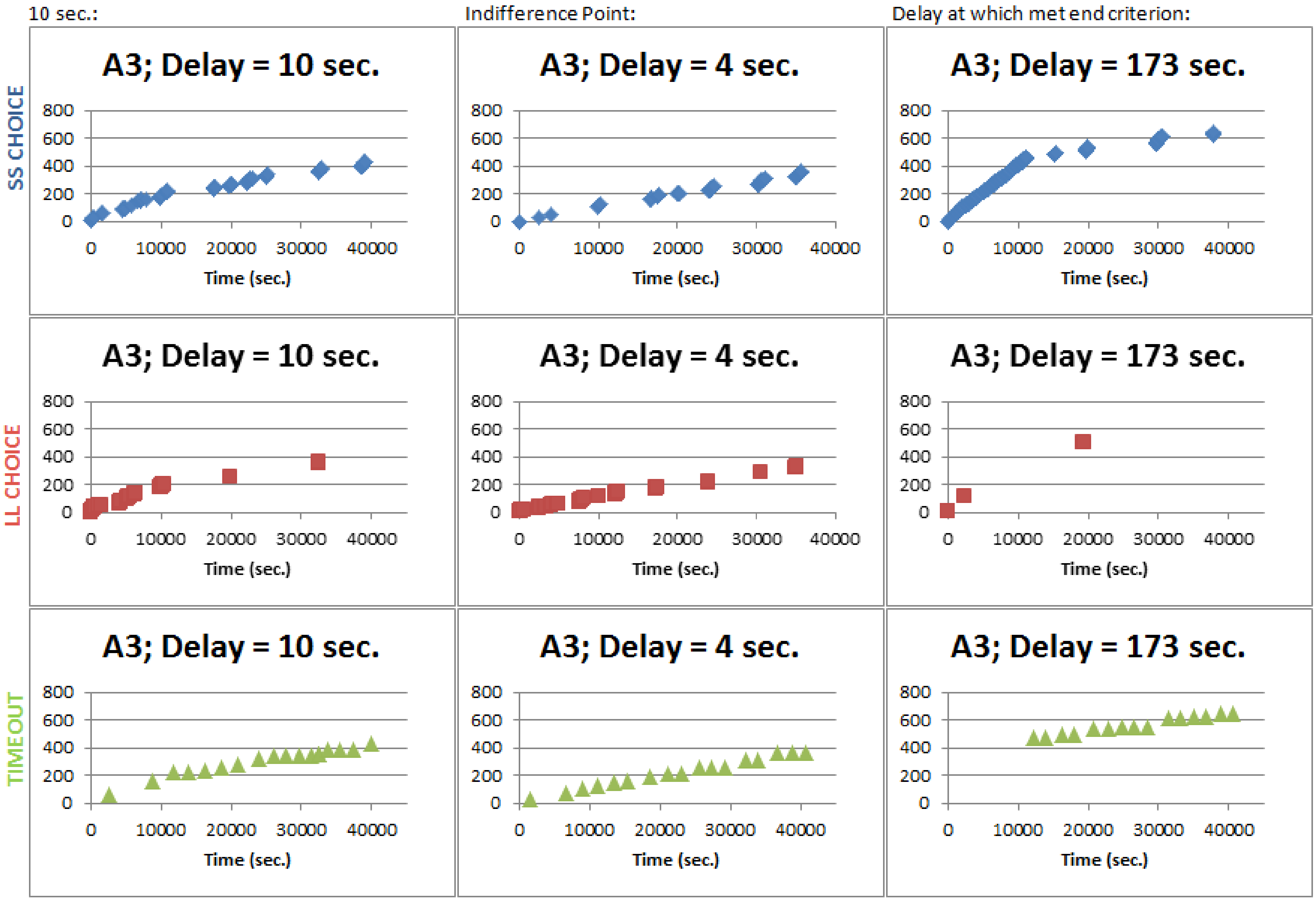

AM Hamster Female
14-11
Linear Slope: -.0404
Choice LL (%)
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
1
10
19
28
37
46
55
64
73
82
91
100
109
118
127
136
145
154
163
172
Length of LL Delay (sec.)

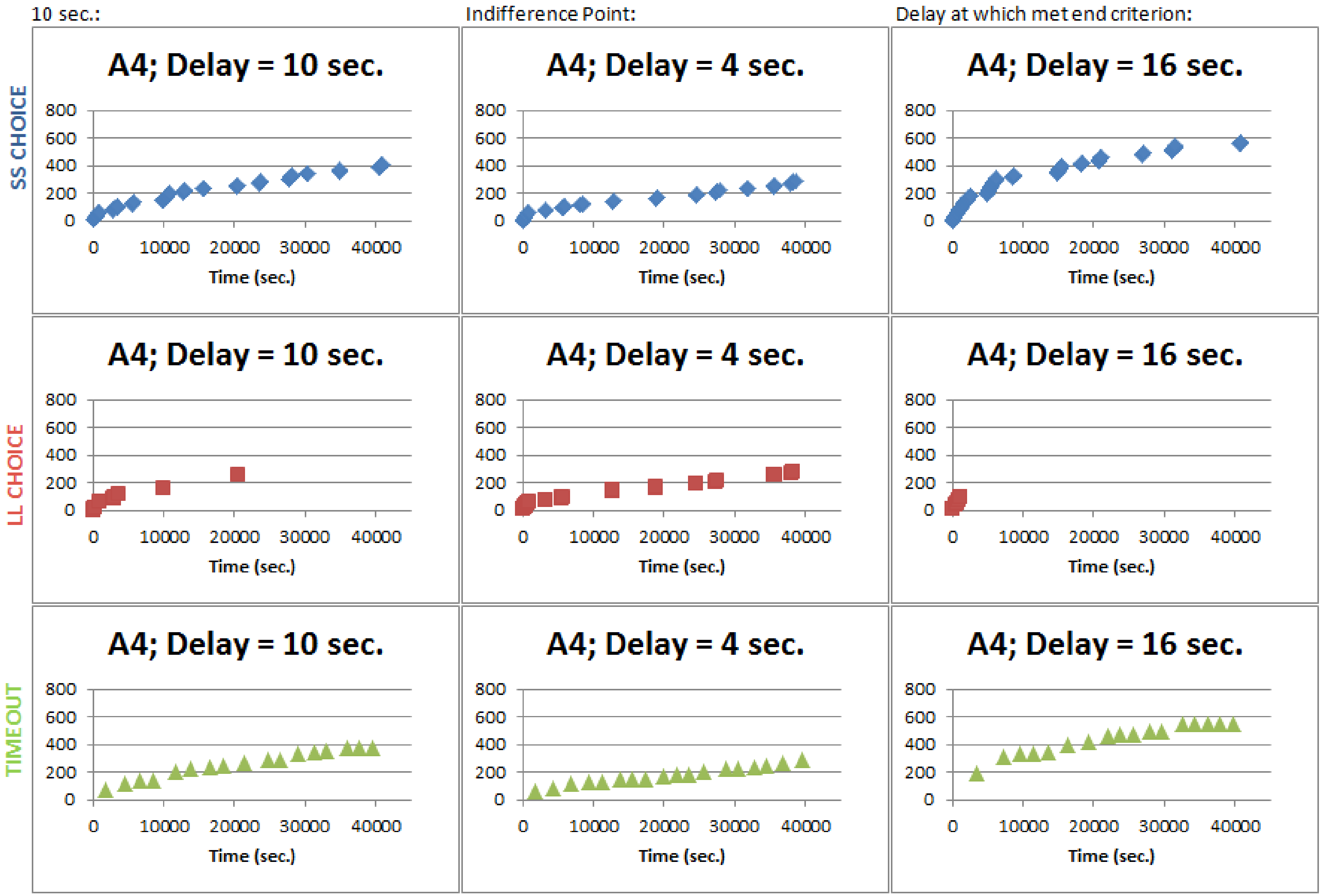
Appendix B - Response and Timeout Occurrence Distribution

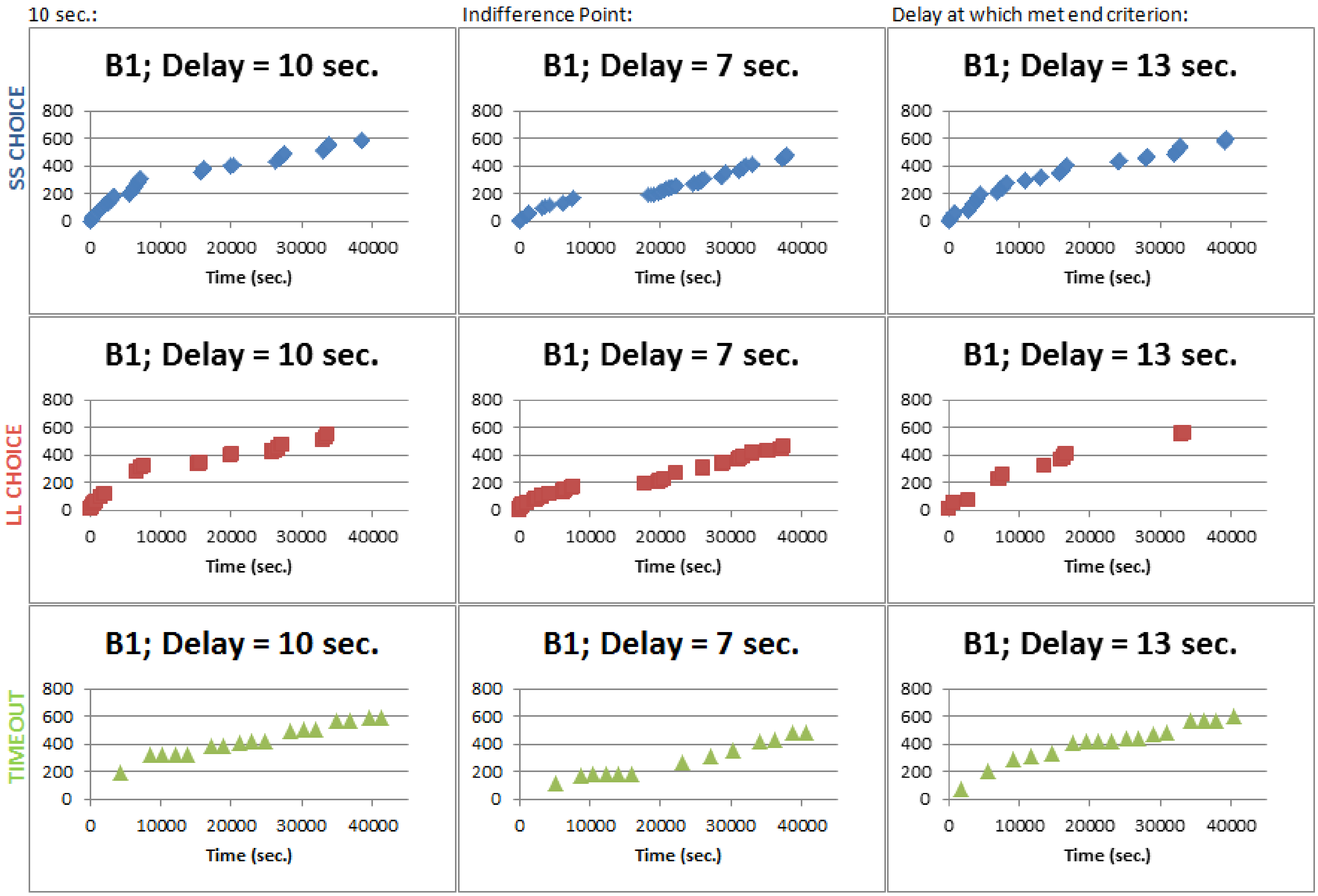
Graphs in this appendix represent responses made on warm-up and free choice trials, but not on forced choice trials. Diamond symbols (blue) represent responses made on the Shorter Sooner alternative. Square symbols (red) represent responses made on the Larger Later alternative. Triangle symbols (green) symbols represent timeouts, with each triangle corresponding with a half of an hour. Graphs present performance of each individual at a 10 sec. delay, their indifference point, and at the delay at which they met the end criterion. Graphs represent individual data for each subject, for one session, and are not averages for the four days of stability. Two rats did not reach an indifference point or end criterion and are represented on the same page.

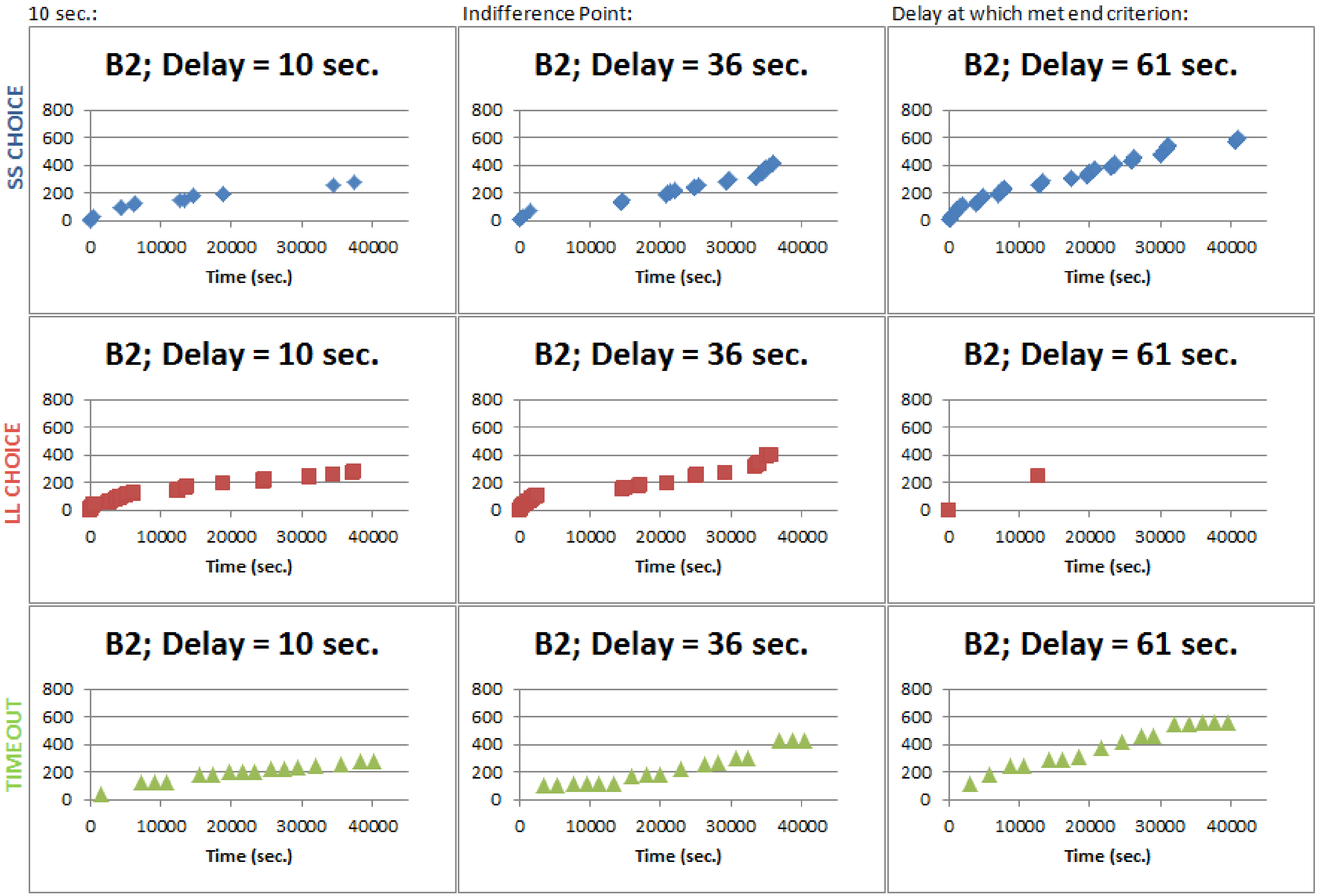

10 sec. AND Indifference for A1:
Delay at which A1 met end criterion:
10 sec. & end criterion delay (No Indiff.):
SS CHOICE
LL CHOICE
TIMEOUT
A1; Delay = 10 sec.
A1; Delay = 28 sec.
A5; Delay = 10 sec.
800
600
400
200
0
0
10000
20000
30000
40000
Time (sec.)

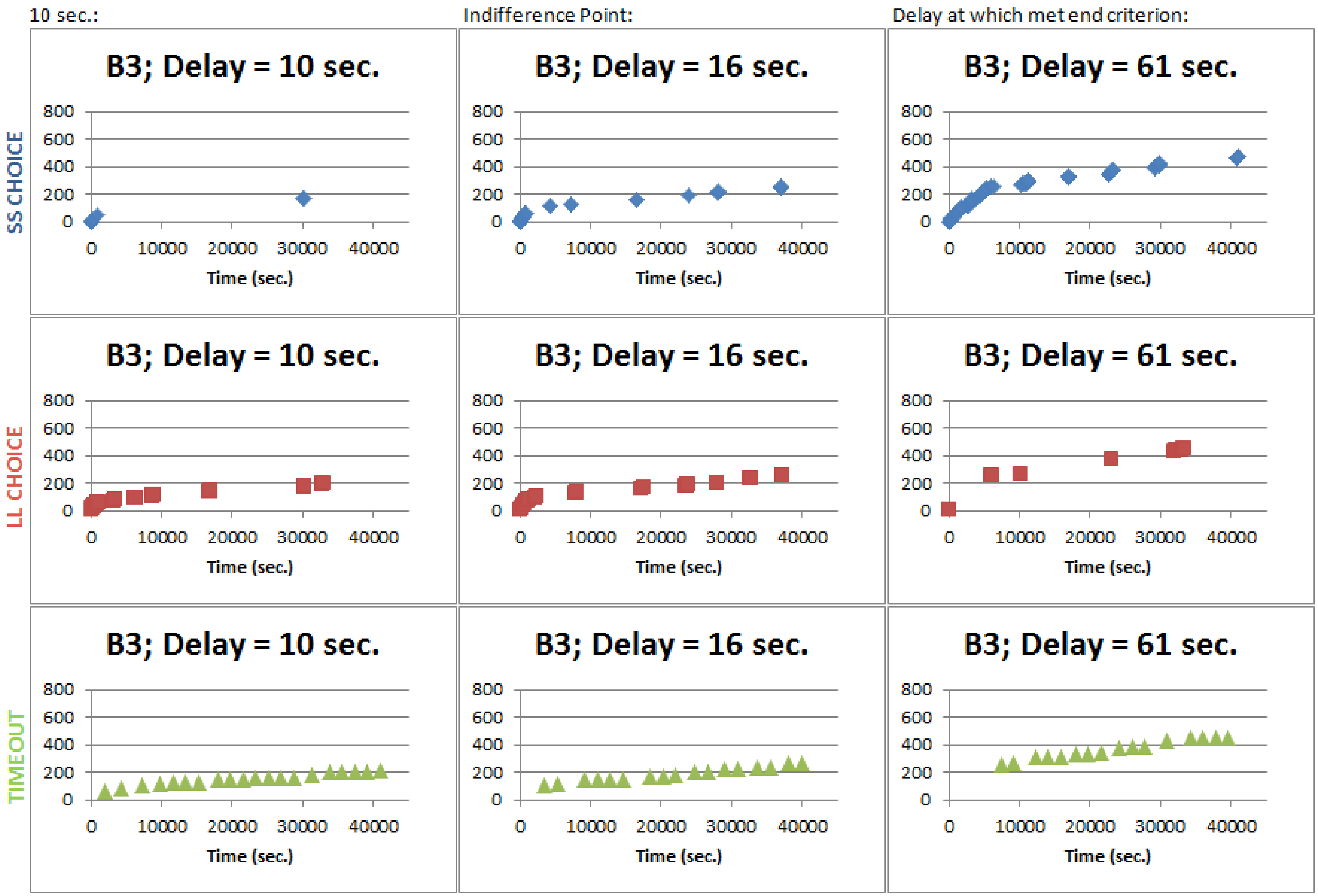

10 sec.:
Indifference Point:
Delay at which met end criterion:
SS CHOICE
LL CHOICE
TIMEOUT
A2; Delay = 10 sec.
A2; Delay = 6 sec.
A2; Delay = 36 sec.
0
200
400
600
800
0
10000
20000
30000
40000
Time (sec.)

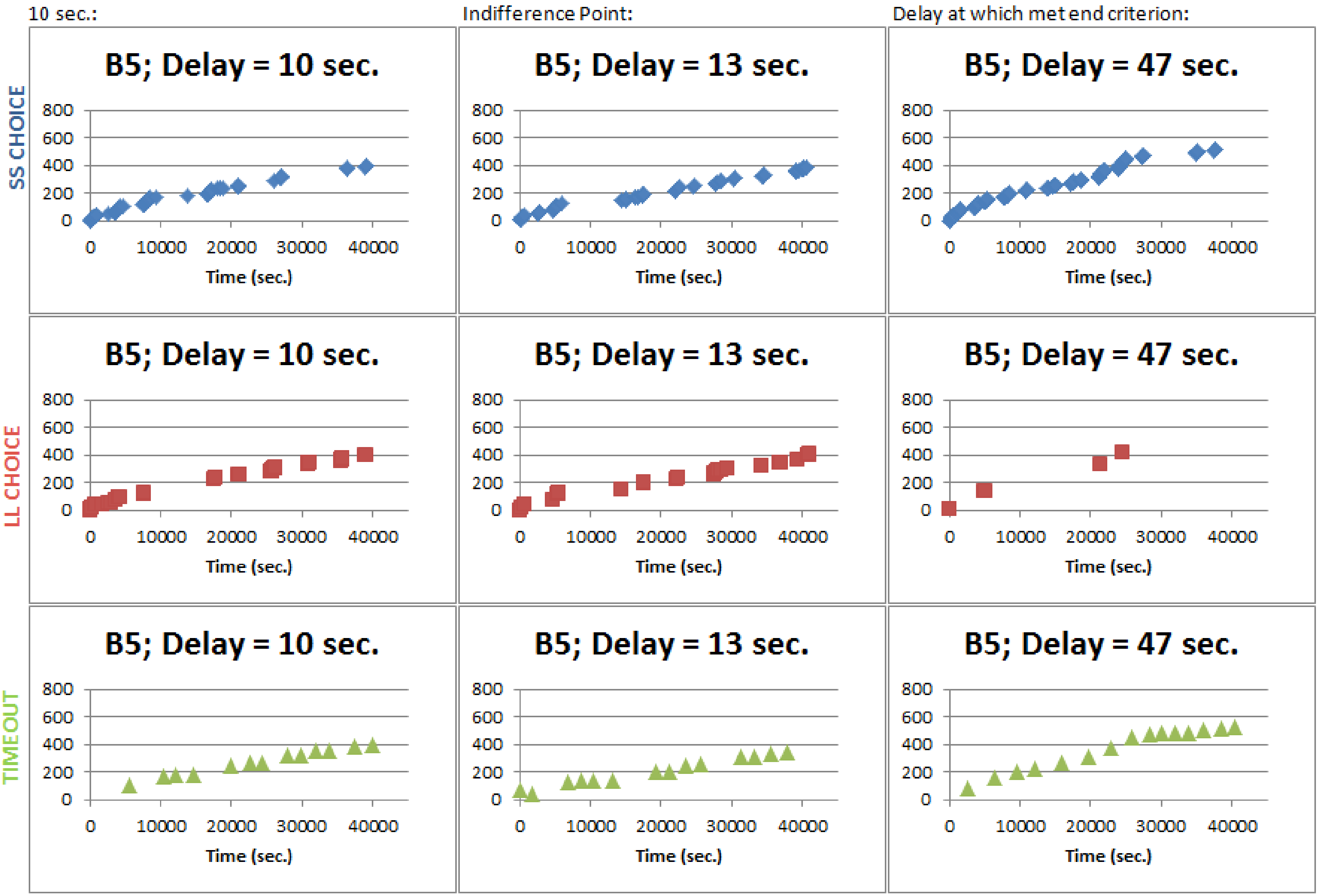

10 sec.:
Indifference Point:
Delay at which met end criterion:
SS CHOICE
LL CHOICE
TIMEOUT
A3; Delay = 10 sec.
A3; Delay = 4 sec.
A3; Delay = 173 sec.
0
200
400
600
800
0
10000
20000
30000
40000
Time (sec.)

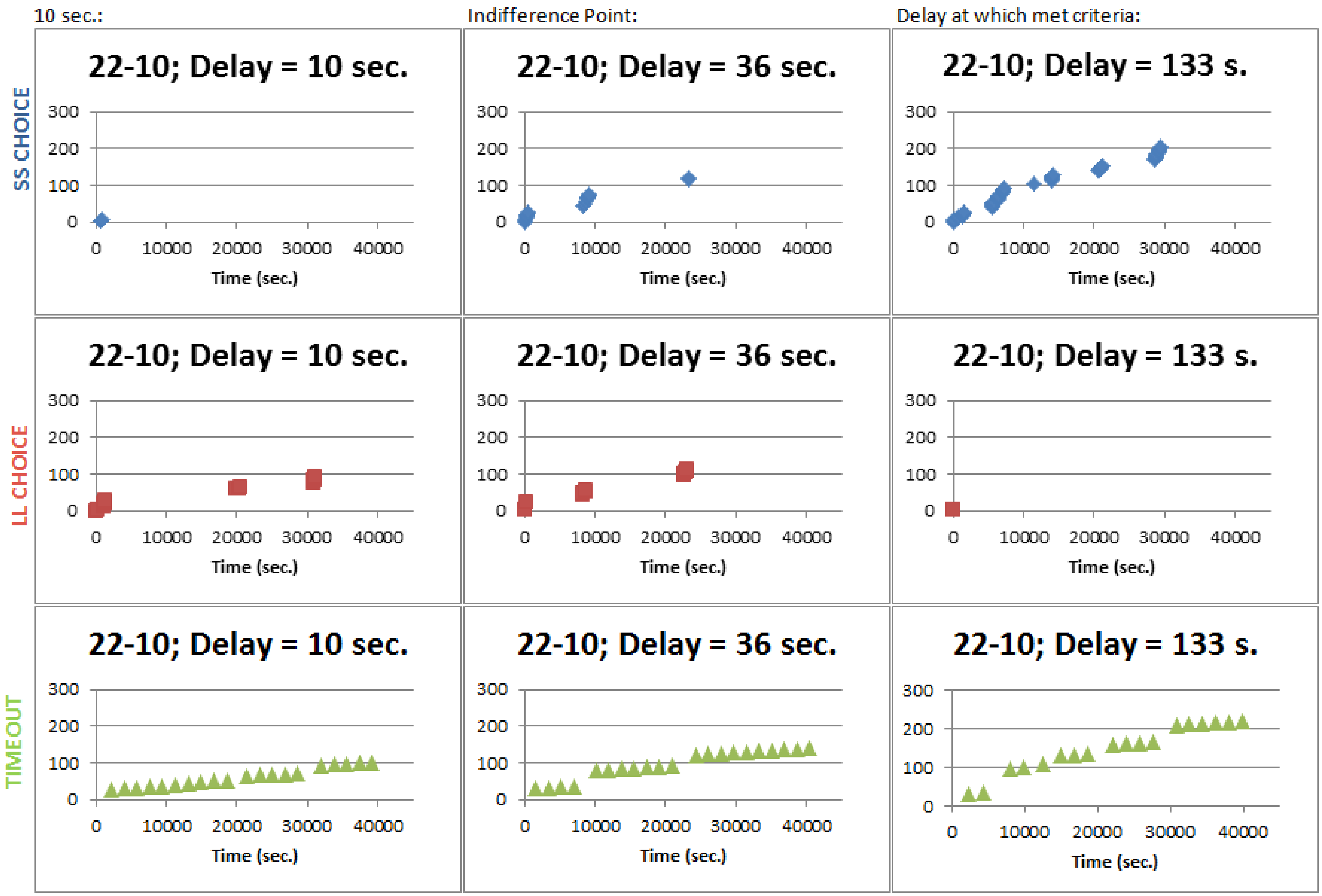

10 sec.:
Indifference Point:
Delay at which met end criterion:
SS CHOICE
LL CHOICE
TIMEOUT
A4; Delay = 10 sec.
A4; Delay = 4 sec.
A4; Delay = 16 sec.
800
600
400
200
0
10000
20000
30000
40000
Time (sec.)

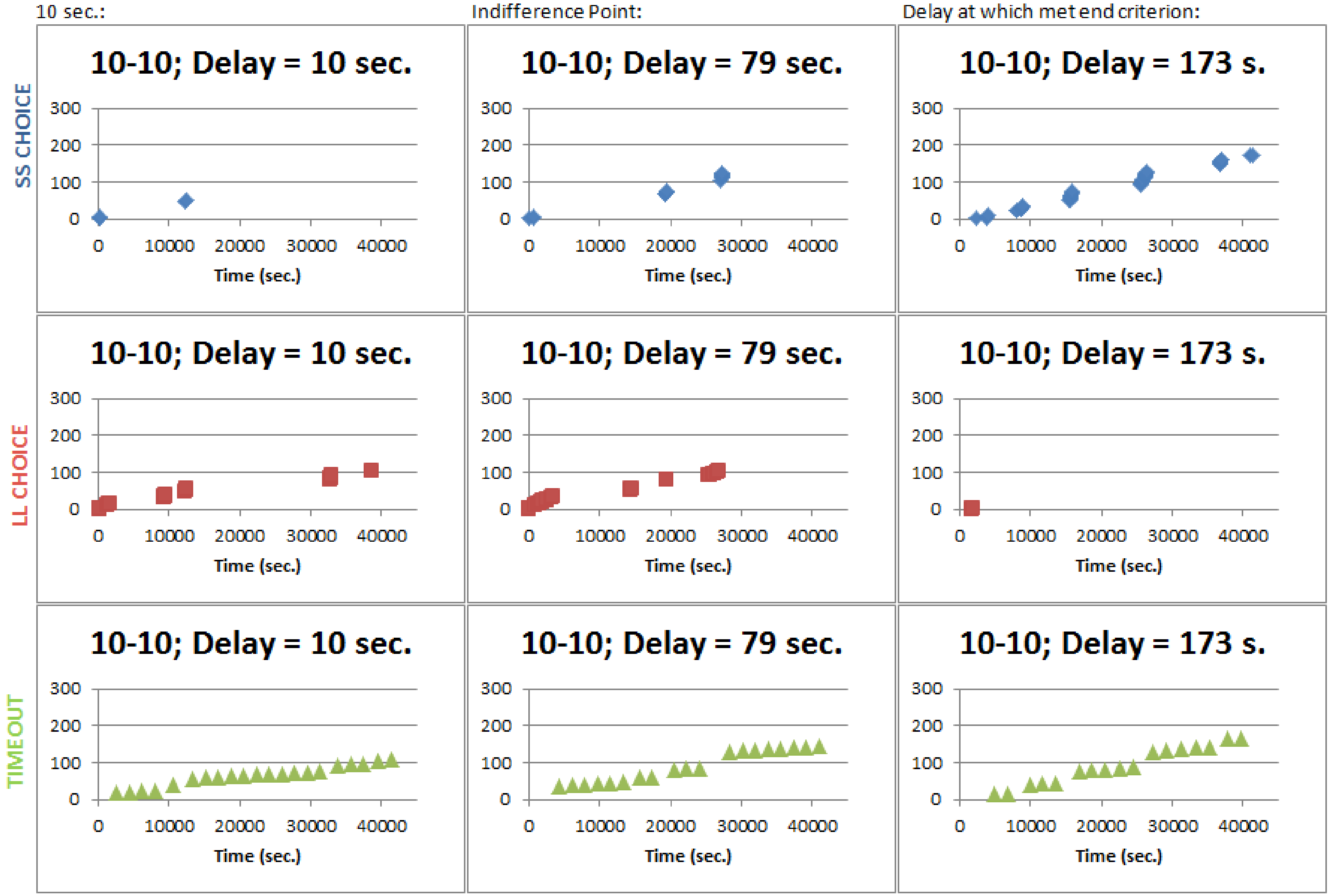

10 sec.:
Indifference Point:
Delay at which met end criterion:
SS CHOICE
LL CHOICE
TIMEOUT
B1; Delay = 10 sec.
B1; Delay = 7 sec.
B1; Delay = 13 sec.
800
600
400
200
0
0
10000
20000
30000
40000
Time (sec.)

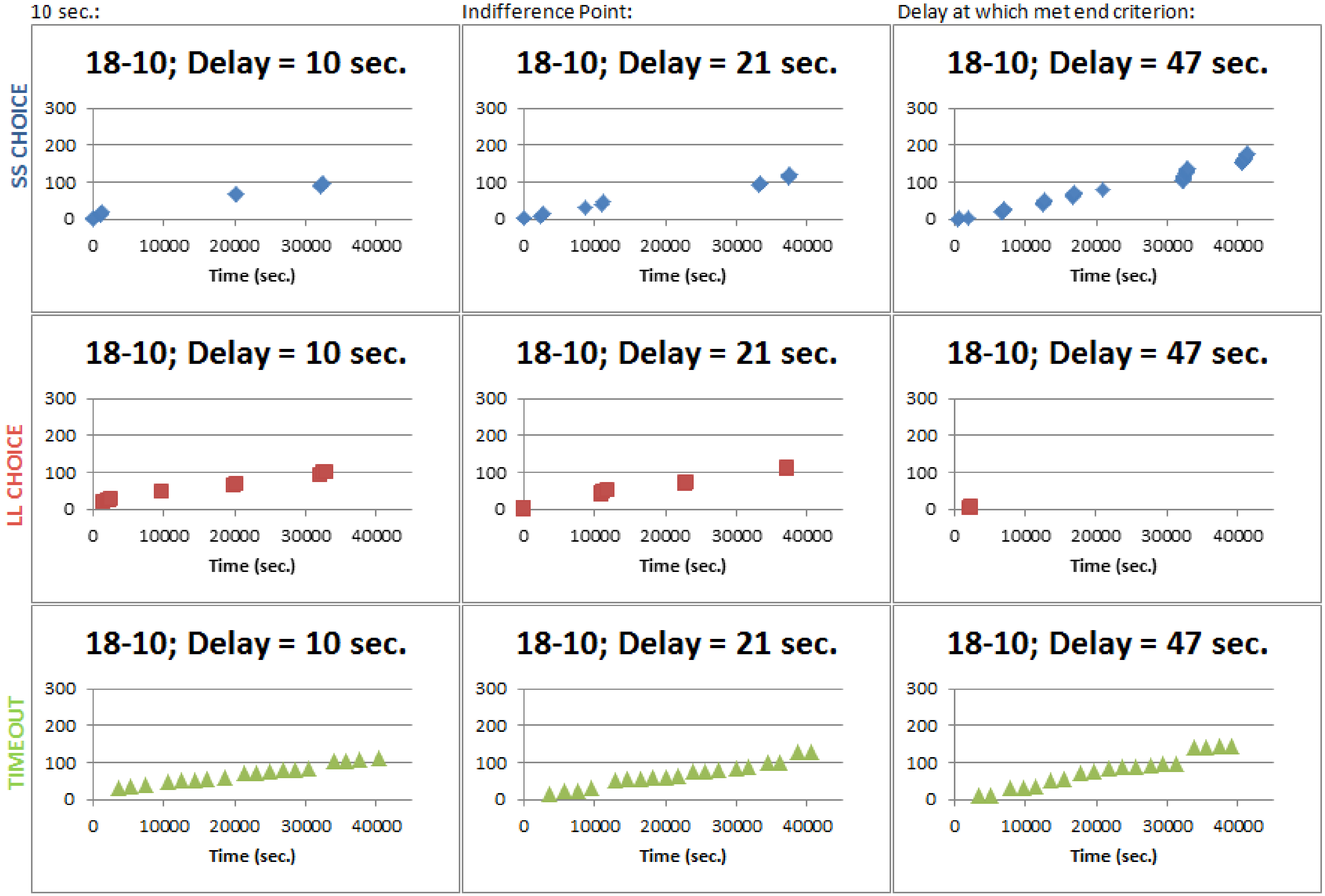

10 sec.:
Indifference Point:
Delay at which met end criterion:
SS CHOICE
LL CHOICE
TIMEOUT
B2; Delay = 10 sec.
B2; Delay = 36 sec.
B2; Delay = 61 sec.
B2; Delay = 10 sec.
B2; Delay = 36 sec.
B2; Delay = 61 sec.
B2; Delay = 10 sec.
B2; Delay = 36 sec.
B2; Delay = 61 sec.
0
200
400
600
800
0
10000
20000
30000
40000
Time (sec.)

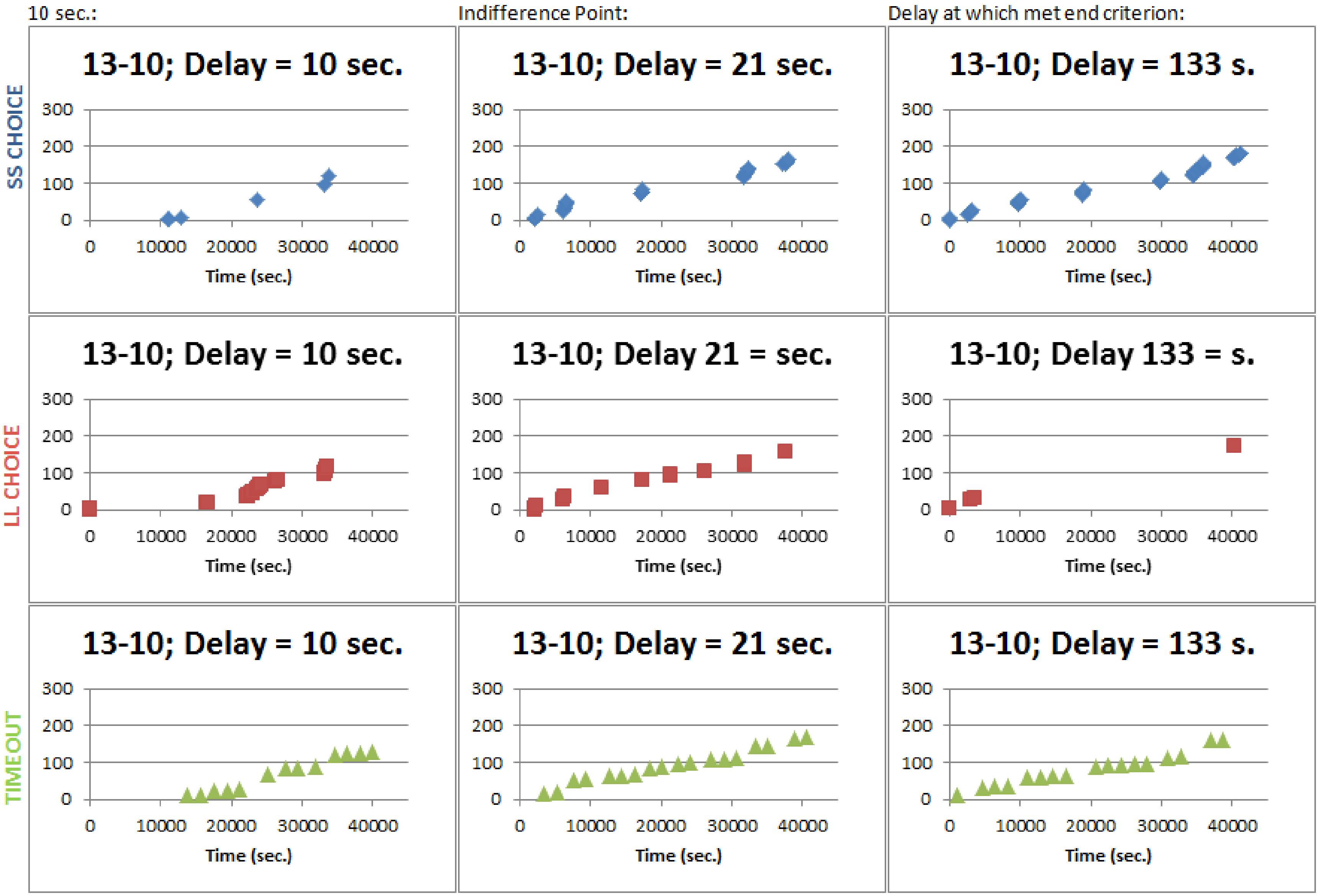

10 sec.:
Indifference Point:
Delay at which met end criterion:
SS CHOICE
LL CHOICE
TIMEOUT
B3; Delay = 10 sec.
B3; Delay = 16 sec.
B3; Delay = 61 sec.
800
600
400
200
0
0
10000
20000
30000
40000
Time (sec.)

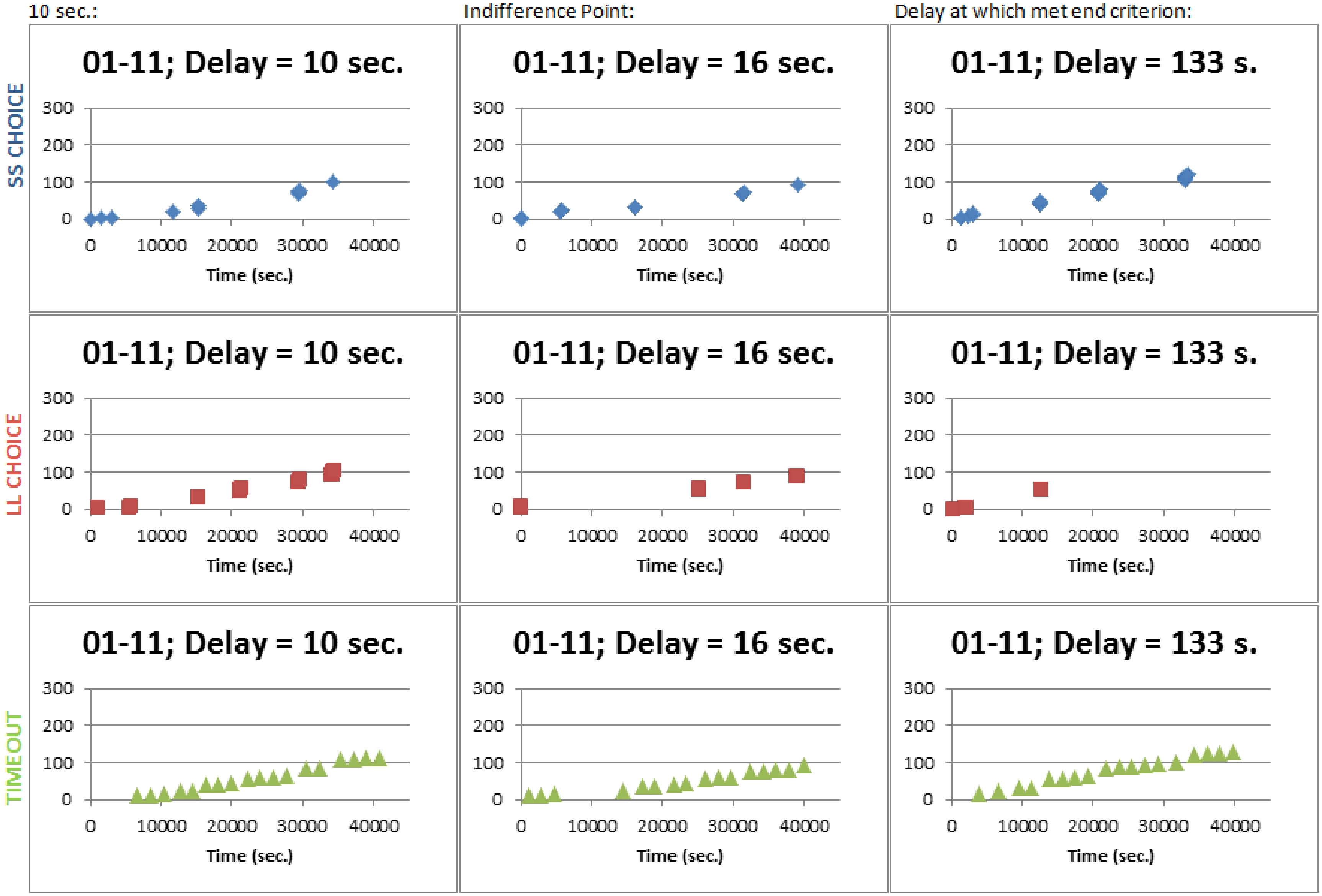

10 sec.:
Indifference Point:
Delay at which met end criterion:
SS CHOICE
LL CHOICE
TIMEOUT
B5; Delay = 10 sec.
B5; Delay = 13 sec.
B5; Delay = 47 sec.
800
600
400
200
0
0
10000
20000
30000
40000
Time (sec.)

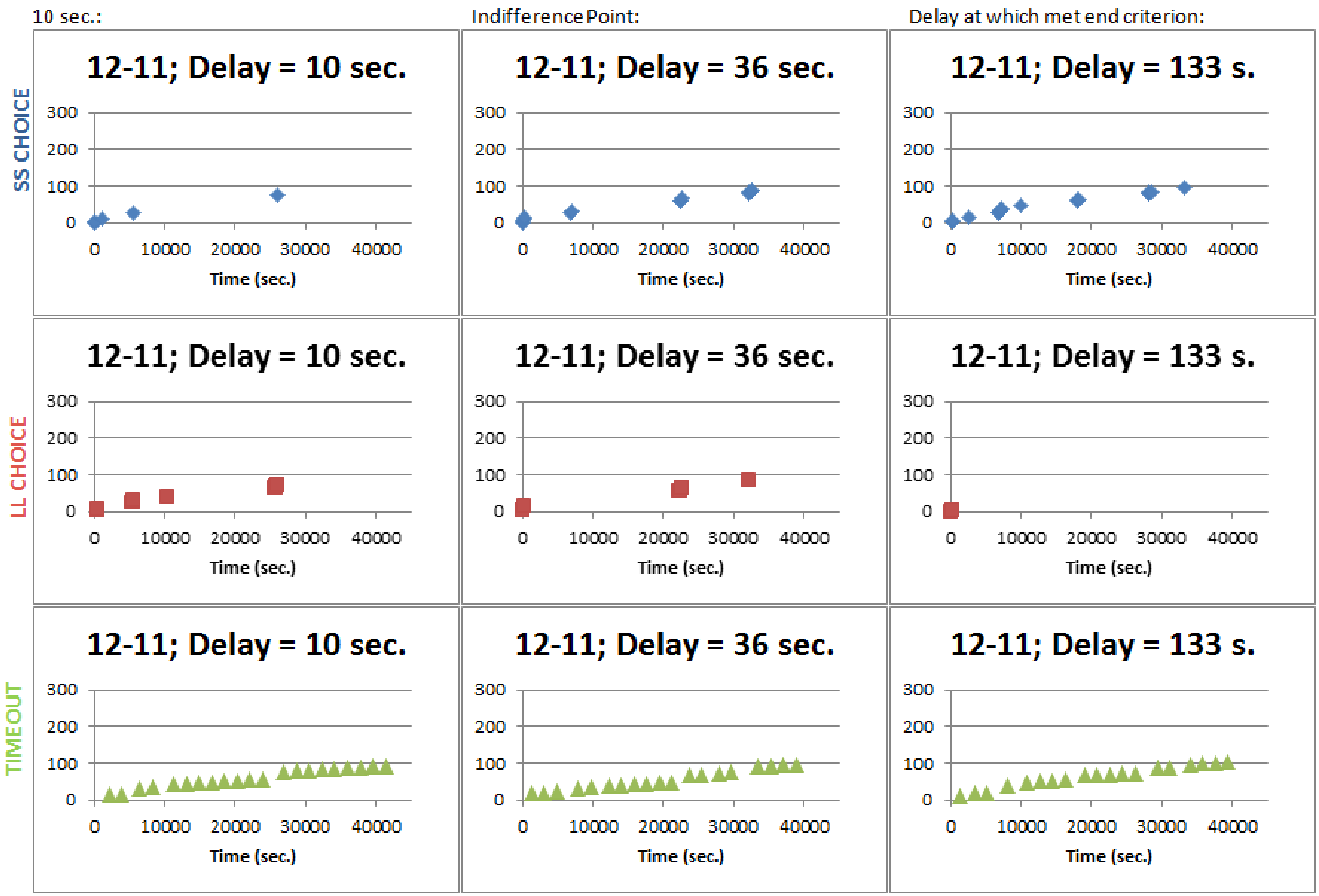

10 sec.:
Indifference Point:
Delay at which met criteria:
SS CHOICE
LL CHOICE
TIMEOUT
22-10; Delay = 10 sec.
22-10; Delay = 36 sec.
22-10; Delay = 133 s.
300
200
100
0
0
10000
20000
30000
40000
Time (sec.)

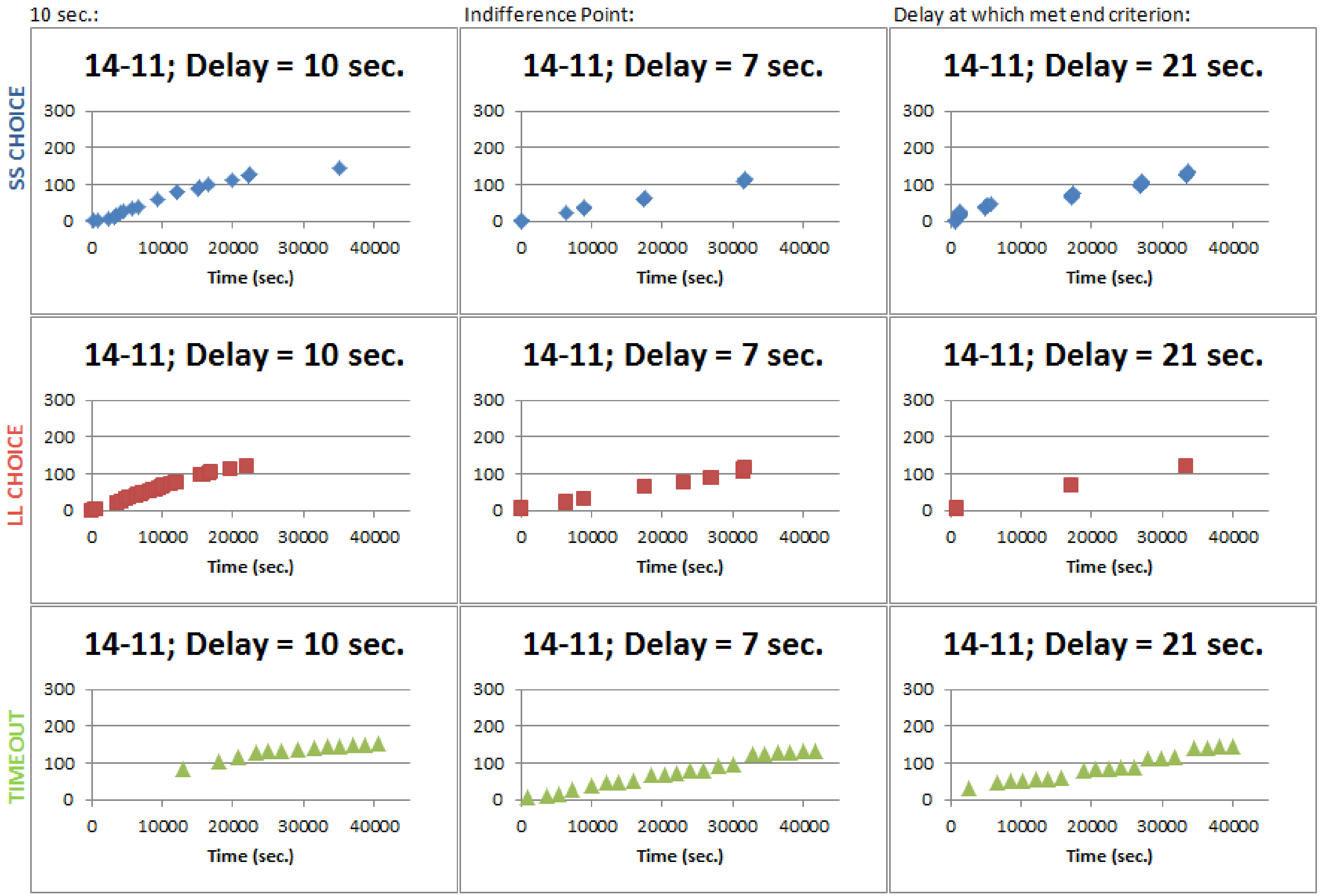

10 sec.:
Indifference Point:
Delay at which met end criterion:
SS CHOICE
LL CHOICE
TIMEOUT
10-10; Delay = 10 sec.
10-10; Delay = 79 sec.
10-10; Delay = 173 s.
300
200
100
0
0
10000
20000
30000
40000
Time (sec.)

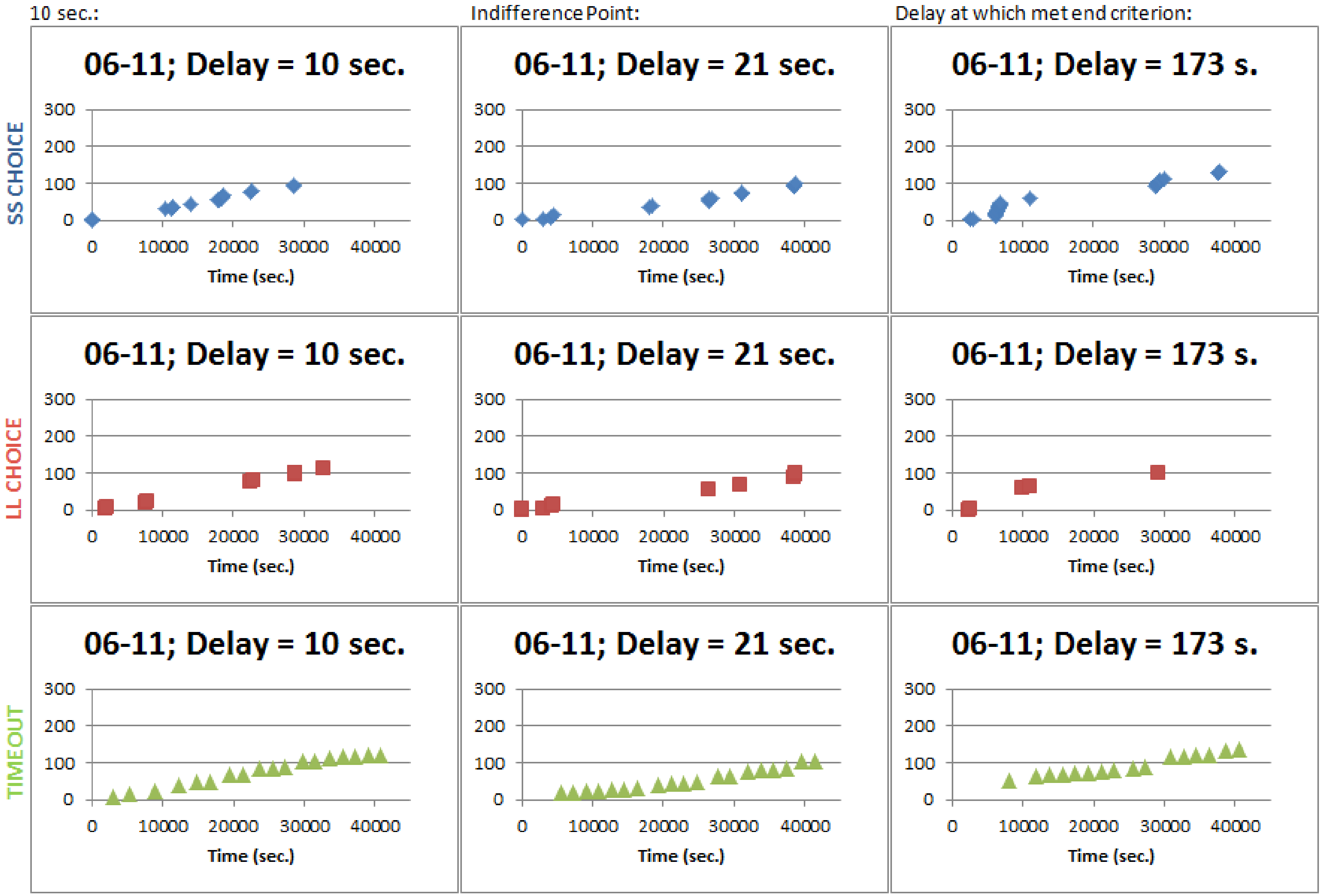

10 sec.:
Indifference Point:
Delay at which met end criterion:
SS CHOICE
LL CHOICE
TIMEOUT
18-10; Delay = 10 sec.
18-10; Delay = 21 sec.
18-10; Delay = 47 sec.
0
100
200
300
0
10000
20000
30000
40000
Time (sec.)


10 sec.:
Indifference Point:
Delay at which met end criterion:
SS CHOICE
LL CHOICE
TIMEOUT
13-10; Delay = 10 sec.
13-10; Delay = 21 sec.
13-10; Delay = 133 s.
13-10; Delay = 10 sec.
13-10; Delay 21 = sec.
13-10; Delay 133 = s.
13-10; Delay = 10 sec.
13-10; Delay = 21 sec.
13-10; Delay = 133 s.
300
200
100
0
0
10000
20000
30000
40000
Time (sec.)


10 sec.:
Indifference Point:
Delay at which met end criterion:
SS CHOICE
LL CHOICE
TIMEOUT
01-11; Delay = 10 sec.
01-11; Delay = 16 sec.
01-11; Delay = 133 s.
300
200
100
0
0
10000
20000
30000
40000
Time (sec.)


10 sec.:
Indifference Point:
Delay at which met end criterion:
SS CHOICE
LL CHOICE
TIMEOUT
12-11; Delay = 10 sec.
12-11; Delay = 36 sec.
12-11; Delay = 133 s.
300
200
100
0
0
10000
20000
30000
40000
Time (sec.)


10 sec.:
Indifference Point:
Delay at which met end criterion:
SS CHOICE
LL CHOICE
TIMEOUT
14-11; Delay = 10 sec.
14-11; Delay = 7 sec.
14-11; Delay = 21 sec.
300
200
100
0
0
10000
20000
30000
40000
Time (sec.)


10 sec.:
Indifference Point:
Delay at which met end criterion:
SS CHOICE
LL CHOICE
TIMEOUT
06-11; Delay = 10 sec.
06-11; Delay = 21 sec.
06-11; Delay = 173 s.
300
200
100
0
0
10000
20000
30000
40000
Time (sec.)

Appendix C - Necessary Calculations

Ideal Indifference Point calculation Based on Inter-Response Time (IRT)

Inter-response time (IRT) is the length of time a subject has to wait between responses. In the present experiment the IRT was calculated for each delay subjects experienced using the length of each delay, plus the 20-second ITI, plus an additional 1 second for pellet delivery. IRT's for both lever alternatives at each delay are presented in the Table below. For example, by selecting the Smaller Sooner alternative a subject would need to wait 21 seconds before being able to make another response. If the subject chose the Larger Later alternative at a 36-second delay, they would need to wait 57 seconds before they could make their next response. An estimate of time investment per pellet was calculated by dividing IRT's for the Larger Later alternative by 3 (except for the 1 second delay associated with the Smaller Sooner alternative).

Based on these calculations the Larger Later delay that is equivalent to the Shorter Sooner alternative in terms of time invested per pellet earned is 36 seconds. In other words, the total time invested for one pellet on the Smaller Sooner lever (21 seconds) is most equivalent to the time invested for 3 pellets on the Larger Later lever at a 36 second delay (3 pellets/57 seconds); approximately 19 seconds for every 1 pellet. Because this delay is the most qualitatively equivalent to the investment for a Smaller Sooner reinforcer, it is logical to assume it would be the ideal delay for indifference.

Pellets Earned Per Lever X Delay

Delay (sec.)	(SS)	0	3	6	1	8	6	7	1	9	02	33	73
3 pellets every ___ sec.	N|A	1	4	7	2	9	7	8	2	00	23	54	94
1 pellet every ___ sec.	2	0.3	1.3	2.3	4	6.3	9	2.7	7.3	3.3	1	1.3	4.7

Earning Potential of the Smaller Sooner and Larger Later Alternatives

Using the information in the Table above, the earning potential was estimated for how much a subject could earn over the course of the session on the greatest delay achieved by subjects (173 seconds; two dwarf hamsters and one rat) if they responded non-stop throughout the session.

The present experiment consisted of blocks: 2 forced choice trials, one Smaller Sooner and one Larger Later, followed by eight free choice trials. Time to complete a block was calculated by multiplying the amount of time for each trial according to the table above. There is a 22 second IRT for the forced Smaller Sooner trial and 194 seconds for the Larger Later forced choice trial (216 seconds total for both forced choice trials). If the subject chose the Smaller Sooner alternative for all free choice trials it would take 176 seconds (22*8). If the subject chose the Larger Later alternative for all free choice trials it would take 1552 seconds (194*8). This results in a total of 392 seconds to complete a block for which on the Smaller Sooner alternative was chosen on all free choice trials on which 12 pellets would be earned, and 1768 seconds to complete a block for which on the Larger Later alternative was chosen on all free choice trials on which 28 pellets would be earned.

Calculating Amount of Pellets Needed to Earn Average Daily Free Feed Amount

Based on experience in our lab, a male rat will consume 23g/day on average. This number is divided by the weight of a pellet (.045 g.) to determine how many pellets would be equivalent; 511 pellets/session are necessary for an average male rat to maintain the daily average of 23g/day of food consumed in the experiment.

Calculating Time and Number of Responses Needed to Earn 511 Pellets

Since 12 pellets are earned during a block that consists of only Smaller Sooner free choice trials (see above), it would take 42.58 trials to earn 511 pellets. Multiplying 42.58 by the 392 seconds it take to complete a block that consists of only Smaller Sooner free choice trials, it would take 16693 seconds (4 hours, 38 minutes, and 12 seconds) to earn 511 pellets (if the subject responded non-stop throughout the session)

Since 28 pellets are earned during a block that consists of only Larger Later free choice trials, it would take 18.25 trials to earn 511 pellets. Multiplying 18.25 by the 1768 seconds it take to complete a block that consists of only Smaller Sooner free choice trials, it would take 32266 seconds (8 hours, 57 minutes, and 46 seconds) to earn 511 pellets (if the subject responded non-stop throughout the session).