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Is the Lewis (LEW) rat an appropriate control
for the Spontaneously Hypertensive rat (SHR)?

A Thesis in Behavior Analysis

By

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Abstract

The Spontaneously Hypertensive rat (SHR), the most widely accepted rodent-model of Attention Deficit/Hyperactivity disorder (ADHD), is compared with its normotensive control the Wistar Kyoto (WKY) rat looking for between strains differences in impulsive choice. But the WKY is not a proper control for the SHR when the procedure requires locomotion to choose. The SHR has deficiencies in dopamine activity in nucleus accumbens causing lower tolerance to delayed outcomes than the WKY. Locomotion and anomalies in dopamine in the Lewis (LEW) rat are like those in the SHR, suggesting that the LEW is a good control for the SHR. This possibility was analyzed with SHRs and LEWs responding to concurrent-chains procedures. Choice was measured in the initial link where two random interval schedules arranged entries to two terminal links, one delivering 1-food pellet immediately and the other delaying 4-food pellets 0.1, 5, 10, 20, 40, or 80 s. Impulsive choice increased with training, but the SHRs showed faster changes in preference, making more impulsive choices than the LEWs. The hyperbolic-decay model and the generalized matching law fitted the data well. Positive correlations between discounting rate and sensitivity of choice to the immediacy of reinforcement suggests compatibility between the models of choice.

1. Introduction

This research focuses on the study of impulsivity analyzing choice behavior in inbred strains of Lewis (LEW) and Spontaneously Hypertensive (SHR) rats, because these strains of rats display behaviors (e.g., impulsivity, inattention, learning difficulties, and memory deficits) characterizing the Attention Deficit/Hyperactivity Disorder (ADHD) affecting children and adults documented in the Diagnostic and Statistical Manual of Mental Disorders (DSM-V). Accordingly, impulsivity is associated with a preference for immediate rewards and unlikeliness to delay gratification (American Psychiatric Association, 2017). One longitudinal study on delay discounting has shown that preschool children who waited longer for a larger reward instead of choosing a smaller more immediate reward, exhibited higher academic success and better social skills a decade later (Mischel et al., 1988). Related research shows that individuals with ADHD discount money at greater rates than their control group (Barkley et al., 2001).

In the operant laboratory impulsivity is studied by arranging a choice between a smaller sooner reinforcer (SSR) and a larger later reinforcer (LLR) (Logan, 1965), choosing the SSR over the LLR suggests impulsivity (Rachlin and Green, 1972) and choosing the LLR more often than choosing the SSR indicates self-controlled choice (Logue, 1988). Impulsivity is becoming increasingly viewed as the most important characteristic of ADHD research (Sagvolden, 2000). The term delay discounting refers to the finding that the LLR loses its subjective value with the increasing delay to obtain it, with the choices of human and nonhuman animals producing delay discounting functions with hyperbolic shape (Chung and Herrnstein, 1967). It has been shown that normally functioning humans discount relatively larger amounts of the LLR less steeply than small

amounts of it, suggesting a magnitude effect (Grace et al., 2012; Green & Myerson, 2004; Estle et al., 2007). However, the magnitude effect is less common in nonhuman animals including inbred strains of rats (Aparicio et al., 2020; Calvert et al., 2010).

Research in our laboratory shows that nonhuman animals learn to choose impulsively with their experience in the delay discounting task (Aparicio et al., 2015). This finding suggests that naive rats not familiar with the delay discounting procedure will choose less impulsively at the beginning of the study than at the end of the study, and this result will be observed regardless of the genetic and neurophysiological conditions of the rats.

One model used to analyze the effect that increasing the delay to deliver the LLR has on choice, is Mazur's (1987) hyperbolic decay model which is formally expressed as follows:

$$V = \frac{A}{(1+kD)} \quad (1)$$

where V is the value of the LLR, A its amount, D the delay to receive it, and k a free parameter to estimate how quickly the LLR is discounted (i.e., its discounting rate) as a function of the increasing delay to obtain it.

Moreover, research on delay discounting (i.e., Aparicio et al., 2015; 2020) has been using concurrent-chain procedures and a modified version of Baum's (1974) Generalized Matching Law (GML) to estimate sensitivity of choice to the immediacy of reinforcement (i.e., the reciprocal of delay) as follows:

$$\log \left(\frac{BLL}{BSS} \right) = s * \log \left(\frac{DSS}{DLL} \right) + \log b \quad (2)$$

Where BLL and BSS represent the behaviors of pressing the levers associated with the LLR and SSR, respectively, DSS and DLL the delays to deliver the SSR and LLR reinforcers, respectively, b is a free parameter to estimate the bias toward one lever or the other arising from

factors other than the delay to deliver the reinforcers (DSS and DLL), and s is a free parameter estimating sensitivity of the behavior ratio (BLL/BSS) to the ratio of immediacies of reinforcement (DSS/DLL). In this linear equation (Eq. 2) the steeper the slope of the regression line, the higher the sensitivity of choice to the immediacy of reinforcement. Studies comparing the hyperbolic decay model (Eq. 1) with the generalized matching law (Eq. 2) fitting delay discounting data from non-human animals, found positive correlations between estimates of discounting rate (k in Eq. 1) and estimates of sensitivity of choice to immediacy of the LLR (s in Eq. 2), suggesting some consistencies between these two models of choice (Aparicio, 2015; Aparicio et al., 2015; 2020).

A variety of procedures have been developed to study impulsivity. Choosing an optimal procedure to assess impulsivity is challenging (Bergh et al., 2006) because different factors can affect the results of the study, such as the type of the method used to estimate impulsivity. Some procedures have produced mixed results, with some individuals discounting the LLR at high rates and others discounting the LLR at low rates. For instance, it has been shown that the SHR chooses more impulsively than its normotensive control the Wistar-Kyoto (WKY) rat (Aparicio et al., 2019; Fox et al., 2008; Orduña, 2015). The SHR and WKY strains of rats were derived from the same colony of outbred Wistar rats (WIS). The SHR was selectively bred from the WIS rats that had higher than normal systolic blood pressure, with the goal of developing a hypertensive strain of rats (Okamoto & Aoki, 1963). Studies reporting that the SHR displays behaviors characterizing symptoms of ADHD, show inconsistencies in the impulsive behavior of the SHR across different tests, questioning the validity of the SHR as a rodent model of ADHD (Bergh et al., 2006). The DSM-V characterizes ADHD as inattentive (ADHD-PI), hyperactive/impulsive (ADHD-HI), or combined subtype (ADHD-C) (American Psychiatric Association, 2017). Research on delay

discounting suggests that the SHR is a rodent model of ADHD-C (Miller et al., 2012, Sagvolden et al., 1992).

Other factors that can affect the results of an experiment examining impulsive choice, are the age of the rats and their experience in the choice situation. Since impulsive choice in nonhuman animals increases as a function of learning, allowing the rats to have enough experience with the delay discounting procedure is important to assess impulsivity (Aparicio et al., 2015). Some studies show that the SHR chooses more impulsively than the WKY responding to discrete trial procedures (Adriani et al., 2003; Fox et al., 2008), multiple two-component concurrent-chains procedures (Orduña, 2015; Orduña and Mercado-III, 2017), and novel concurrent chains procedures (Aparicio et al., 2019), suggesting that the WKY is an appropriate control for the SHR (Adriani et al., 2003; Russell, 2007; Sagvolden, 2000) to study impulsivity and cognitive deficits associated with ADHD. However, other research has been questioning the validity of the WKY as an appropriate control for the SHR when the procedure requires locomotion, showing significant behavioral differences in choice behavior between the SHR and the WKY (Clements, 2006; Diana, 2002; Ferguson et al., 2007; Grundt et al., 2009; Meneses et al., 2011). For this reason, other strains of rats have been considered as potential controls for the SHR, arguing that the WKY is hypoactive rather than being a normotensive rat (Alsop, 2007; Robertson et al., 2008). In addition, some genetic differences between the WKY and the SHR may make the WKY an unsuited control for the SHR (Drolet et al., 2002; Johnson et al., 1995). To this date little research has been conducted to identify a more appropriate control for the SHR than the WKY. The present study will explore the possibility that the LEW rat is an appropriate control for the SHR.

Additionally, it has been suggested that hypertension is not the only factor that contributes to learning deficits in the SHR (Diana, 2002). The SHR shows irregular activity of dopamine in

the striatum and mesolimbic system (Nakamura et al., 2001; Oades et al., 2005), and suffers from irregular activity of norepinephrine (Heal et al., 2008) and serotonin neurotransmitters (Toot et al., 2004) like those characterizing individuals diagnosed with ADHD. An organism's ability to tolerate the delay to reinforcement requires a properly functioning nucleus accumbens that maintains regular activity of dopamine, norepinephrine, and serotonin (Cardinal et al., 2001). The irregular activities of these neurotransmitters could also affect the expression of genes involved in ADHD, creating genetic differences between the WKY and SHR (DasBanerjee et al., 2008).

One study examining the dopamine activity of the SHR and WKY has shown that there are drastic differences in the striatum and nucleus accumbens between the two strains (Miller et al., 2012). The SHR showed faster dopamine uptake in the ventral striatum and nucleus accumbens which plays a role in impulsive behavior. Also, the SHR showed lower dopamine release in the dorsal striatum which plays a role in motor activity.

Research examining the neurochemical systems of two groups of SHRs, one group exhibiting high impulsivity and other low impulsivity, found the same levels of serotonin (5-HT) in the medial frontal cortex (MFC) and cingulate cortex (CC) for both sub-groups, however, the low impulsive group of SHRs showed lower 5-HT turnover in the MFC, lower noradrenaline levels in the MFC and CC, and the same dopamine levels in the MFC and CC than the high impulsive group of SHRs. The variability in these two groups is compared to the two subtypes of ADHD, inattentive (ADHD-PI) and hyperactive/impulsive (ADHD-HI), respectively (Adriani et al., 2003).

The Lewis (LEW) rat which was also derived from the Wistar (WIS) rat, suffers from irregular dopamine levels in comparison to its control strain, the Fischer 344 (F344) rat (Kosten et al., 1997), and irregular activity at hippocampal and frontal cortical serotonin (5HT1A) receptor binding sites (Burnet et al., 1996). Compared to the Fischer 344 rat (F344), the LEW rat also shows

a higher preference for alcohol and self-administration of alcohol (Suzuki et al., 1988), nicotine (Brower et al., 2002), cannabis (Gardener and Lowinson, 1991), cocaine (Kosten et al., 1997), etonitazene (Suzuki et al., 1992), and morphine (Ambrosio et al., 1995; Martin et al., 2003). This type of drug seeking behavior characterizing the LEW rat is linked to impulsivity (Garcia-Lecumberri et al., 2011).

Studies on anxiety have shown that the LEW and the SHR do not differ from one another in terms of locomotor activity, with both strains showing similar activities of 5-HT_{1a} (serotonin) receptors (Kulikov et al., 1997; Ramos et al., 1997). Thus, the purpose of the present study is to demonstrate that the LEW rat might be an appropriate control for the SHR rat. It will explore the possibility that the LEW rat chooses less impulsively than the SHR on a delay discounting task implemented by concurrent-chain procedures. This is important because it has been suggested that the WKY is hypoactive instead of normotensive, and an appropriate control for the SHR (i.e., the LEW) should exhibit a similar level of hyperactivity characterizing the SHR.

2. *Methods*

2.1 *Subjects*

Two strains of inbred male rats, 8-SHR and 8-LEW (Charles River, Wilmington, MA), 218- and 187-days old, respectively, were the subjects. All rats had experience on auto-shaping procedures establishing the acquisition and maintenance of lever pressing (Aparicio et al., 2020). The rats were individually housed in plastic cages with water always available in a temperate controlled vivarium (ranging from 68 to 72 degrees F) maintaining a 12:12-h light dark cycle (lights on at 0700). Animals were maintained on a regimen of food restriction in which 20 minutes after the end of each experimental session the rats were weighed and fed with approximately 10 g (+/- 2 g) of Purina Chow (Mazuri®). At the beginning of the study, the weights of the SHRs ranged

from 263 to 296 g (M = 280 g) and the weights of the LEWs from 327 to 345 g (M = 336 g); when the study ended, the weights of the SHRs ranged from 287 to 345 g (M = 315 g) and the weights of the LEWs from 375 to 394 g (M = 384g). The sessions were conducted daily about the same time (12:00).

2.2 Apparatus

Eight Coulbourn Instruments® (Whitehall, PA) test cages for rats (E10-11R TC), each measuring 30 cm x 33 cm x 25 cm, were used. Two retractable levers (E23-17RA), 3.3 cm x 1.5 cm, were mounted on the front wall of each cage 6 cm above the floor; the edge of one lever (left-lever) was 2.3 cm from the left side wall of the cage and edge of the other (right-lever) 2.3 cm from the right wall of the cage. A third non-retractable back lever (H21-03R) was centered on the back wall of each cage 6 cm above the floor. All levers required a force of 0.2 N to be operated. One 24-V DC stimulus light (H11-03R) was placed 3.5 cm above each retractable lever. A 24-V DC house-light (H11-01R) was centered on the back wall of the cage, 19 cm above the non-retractable lever, provided the illumination of the chamber. A dry-food dispenser (H14-23R), placed behind the front wall of each cage, delivered 45-mg grain-based pellets (BioServ®, F0165) into a 3 cm x 4 cm food cup (E14-01R) centered between the left- and right retractable levers, 4.5 cm from the left lever and 4.5 cm from the right lever at 2 cm from the floor. A white noise generator (E12-08) was installed on the back wall of each cage at 20 cm from the floor, 1 cm from the left sidewall and 1 cm below the ceiling and connected to a 2.6 cm x 4.0 cm speaker (H12-01R) to deliver a continuous white noise of 20 kHz (+/- 3 dB). Two computers each linked to 4-cages using Habitest Lincs (H02-08), delivered the stimuli and recorded the responses executing Coulbourn Instruments® software (Graphic State Notation, V 3.03) at a 0.01-s resolution.

2.3. Procedure

All rats were directly exposed to a novel concurrent-chains procedure developed in our laboratory (Aparicio et al., 2015, 2019). It consisted of six different delay components (.01, 5, 10, 20, 40, 80 s) arranging 60-choice cycles for each session. Delay components were selected and presented in random order during the session to arrange 10-choice cycles each. The session started with the illumination of the house light signaling the beginning of the choice cycle. One response on the back lever extended the front left and right levers into the chamber, turning on the lights above them and turning off the house light. Choice was measured in the initial link of the concurrent-chains procedure, recording the number of responses that the rats emitted on the extended left and right levers. Two random interval schedules, averaging 11 s each and operating concurrently on the levers (con RI 11 s RI 11 s), arranged entries to two terminal links. One RI was associated with the left or SS lever and the other RI with the right or LL lever. When the SS lever was selected by one RI 11 s as the operative lever, the first response on the SS lever advanced the cycle to the terminal link causing the other non-operative LL lever to retract from the chamber. The next response on the operative SS lever produced the SSF (1-food pellet) after a 0.1 s delay. After the delivery of the SSF, the operative SS lever was retracted from the chamber and the light above it turned off signaling the end of the choice cycle. After that, the house light was turned on signaling the beginning of the next choice cycle, requiring the rat to move from the front wall to the back wall of the chamber and to press the back lever again to repeat the same sequence of actions completing the cycle. For choice cycles where the LL lever was selected as the operative lever by one RI 11 s, the first response on the LL lever caused the SS lever to retract from the chamber turning off the light above it. The next response on the LL lever started a fixe time (FT) of 0.1, 5, 10, 20, 40, or 80 s to deliver the LLF (4-food pellets). The responses on the LL lever during the FT (i.e., the delay to LLF) had no scheduled consequences. The LLF was delivered at

the end of the delay, retracting the LL lever from the chamber, turning of the light above it, and signaling the end of the choice cycle. Ten foods delivered with the same delay component (5-SSF with the SS lever and 5-LLF with the LL lever), were followed by a 60- s blackout after which a different delay component was randomly selected for another 10 cycles. To prevent a possible bias that the rats might have for one lever over the other, for four rats of each strain the left lever produced the SSF and the right lever the LLF. These relations were reversed for the other four rats of each strain, the left lever produced the LLF and the right lever the SSF. With the rats responding to the concurrent-chains procedure, these conditions were studied for 180 consecutive days.

2.4. Data Analysis

The data from all 180 consecutive sessions were used for data analysis. Global analyses organized the data in 12 blocks of 15 sessions each, and local analyses used the data from all 180 sessions sorted by delay component to analyze choice food by food delivery within a delay component (0.1, 5, 10, 20, 40, or 80 s). All computations of choice used initial-link responses emitted on the LL and SS levers. For the analyses across blocks of sessions, the responses that the rats emitted on the LL and SS levers were counted separately for each delay component and aggregated across 15-sessions of the same block. For each delay component, 6-proportions of LL choice ($(LL \text{ responses} / (LL \text{ responses} + SS \text{ responses}))$) and 6-ratios of responses ($LL \text{ responses} / SS \text{ responses}$) were computed for each rat within a strain and the mean of the group. To compute the number of responses that the rats emitted food by food delivery within a delay component, the data were pooled across all 180 sessions of the same delay component, counting responses on the LL and SS levers separately for each food regardless of whether it was a LLF (4-food pellets) or SSF (1-food pellet). Ten proportions of LL choice and ten ratios of responses could be computed, resulting in 60 proportions of LL choice and 60 response ratios for the six delay components. Thus,

the independent variable was the delay to deliver the LLR (.1, 5, 10, 20, 40, and 80 s) and dependent variable choice estimated with the proportion of LL choice and the ratio of LL and SS responses.

Because the data in delay discounting are not normally distributed (Myerson & Green, 1995), nonparametric statistical methods were used to analyze possible between strain differences in discounting rate (k in Eq. 1) and sensitivity of choice to the immediacy of reinforcement (s in Eq. 2). Nonlinear fitting, linear curve fitting, and statistical tests at the alpha level of .05, were executed with Origin® software. Equations 1 and 2 were entered into the Origin software (version 2020) as a user defined equation, with the former providing nonlinear curve fitting to the proportions of LL choice and the latter providing linear fitting to the ratios of responses. The parameter A was free in Eq.1 (it was not assumed to be 1.0 at the y-intercept). For linear regression (Eq. 2), the ratios of responses (LL responses / SS responses) were transformed into base-2 logarithms, and the least square method was conducted with the \log_2 of response ratios plotted against delay ratios (SS / LL) transformed into base-2 logarithms, the y-intercept estimated bias (Baum, 1974).

3. Results

3.1. Preference

Preference was estimated with the proportion of LL choice ($(LL/(LL+SS))$). It was plotted against 12-blocks of sessions in Figure 1 (i.e., the global analysis) and as a function of 10-food deliveries in Figure 2 (i.e., the local analysis) regardless of whether each food was a SSF or LLF. The unfilled symbols show the proportions of LL choice computed for the individuals and filled circles and squares with error bars the average proportion of LL choice produced by the group of

SHRs and the group of LEWs, respectively. From top to bottom the graphs are organized by delay component. The left graphs display the data produced by the SHRs and the right graphs the data produced by the LEWs. The dotted line intercepting the y-axis at 0.5 is the indifference line, indicating that a similar number of responses were emitted on the SS and LL levers. Proportions of LL choice greater than 0.5 indicate preference for the LL lever, more responses were emitted on the LL lever than on the SS lever, and proportions of LL choice smaller than 0.5 indicate preference for the SS lever, more responses were emitted on the SS lever than on the LL lever.

Figure 1 shows that the SHRs and LEWs developed a clear preference for the LL lever when one terminal link of the concurrent chains delivered the LLF with a negligible delay (0.1 s). The LEWs' preference for the LL lever ($M = .70$) was like that the SHRs developed ($M = .69$) with increasing blocks of sessions. Two rats of each strain produced proportions of LL choice close to the indifference line, but other rats produced proportions of LL choice greater than .70 indicating a strong preference for the LL lever. Both strains showed a slight decrease in their preference for the LL lever (i.e., from .70 to about .65) when its terminal link delayed the LLF either 5 or 10 s. In these components, two rats of each strain produced proportions of LL choice indicating either indifference or slight preference for the SS lever. However, there were other rats maintaining a clear preference for the LL lever when its terminal link delayed the LLF either 5 or 10 s. Preference for the LL lever moved to indifference when the LLF was delayed the 20 s. The choices of the SHRs show proportions of LL choice indicating stable indifference across blocks of sessions ($M = .50$), with block 2 showing a slight preference for the LL lever ($M = .56$). The choices of the LEWs show proportions of LL choice suggesting a small preference for the LLF lever ($M = .55$) across blocks of sessions. Yet, block 1 shows preference for the SS lever ($M = .45$). When the LLF was delayed 40 s and 80 s, the SHRs and the LEWs emitted more responses

on the SS lever than on the LL lever, producing mean proportions of LL choice showing that their preference for the SS lever gradually increased with increasing blocks of sessions. For the choices that the SHRs made responding to the 40 s delay component, blocks 1 and 2 show mean proportions of LL choice close to indifference ($M = .48$) and blocks 3 to 12 mean proportions of LL choice indicating preference for the SS lever ($M = .29$). The SHRs' choices in the 80 s delay component, produced proportions of LL choice ($M = .18$) indicating that their preference to press on the SS lever was strengthened across blocks of sessions; the data points produced by the individuals overlapped with the average data produced by the group indicating a small within group variability in choice. For the choices that the LEWs made in the 40 s delay component, block 1 shows proportions of LL choice indicating a small preference for the SS lever ($M = .40$) and blocks 3-4 indifference ($M = .51$). The LEWs' preference for the SS lever was re-established in block 5 and increased slightly ($M = .45$) from blocks 6 to 12. There were 3 rats maintaining a preference for the LL lever across blocks of sessions. When the LLF was delayed 80 s, all LEWs produced proportions of LL choice indicating their preference to press on the LL lever ($M = .30$). Two LEWs produced proportions of LL choice showing indifference across blocks of sessions.

Figure 2 shows the proportions of LL choice that the SHRs and LEWs produced food by food delivery within a delay component. This local analysis calculated the number of responses that the rats emitted food by food delivery within a delay component, polling the data across all 180 sessions of the same delay component to count responses on the LL and SS levers separately for each food delivery, regardless of whether it was a LLF or SSF. Ten proportions of LL choice were computed for each delay component, resulting in 60 proportions of LL choice.

All graphs show that preference changed food by food with the SHRs and LEWs tracking the LLF. Both strains pressed on the SS and LL levers to obtain the first food that each delay

component delivered, producing proportions of choice indicating either indifference ($M = .50$) or a slight preference for the SS lever ($M = .48$). This result was likely caused by delay components occurring in random order during the session, making it difficult for the rats to anticipate the first food (1- or 4-pellets) to be obtained with the current delay component. Two or more consecutive foods delivered by the same component were required for the rats to confirm the amount of food obtained. When the delay to obtain the LLF was 0.1 s, both strains pressed more on the LL lever than on the SS lever. The SHRs produced proportions of LL choice increasing from .47 with the first food to .70 with the last 5-foods that they obtained with 0.1 s delay component. Two SHRs shown a preference for the LL lever increasing from .55 with the first food to .80 with the last 5-foods, and one SHR proportions of LL choice indicating indifference across food deliveries of the 0.1 s delay component. The LEWs developed an initial preference for the LL lever with the first food ($M = .51$), it was confirmed with each consecutive food and reached asymptotical level ($M = .75$) with the last 5-foods. Two LEWs produced proportions of LL choice indicating a weak preference for the LL lever ($M = .54$) across food deliveries, contrasting with two other LEWs producing proportions of LL choice indicating a clear preference for the LL lever that increased from .55 with the first food to about .90 with the last 5-foods.

Choosing between the SSF and the LLF delivered by the 5 s delay component, the SHRs and LEWs produced proportions of LL choice like those they produced with food deliveries of the 0.1 s delay component. The exception was one LEW developing a weak preference SS lever with consecutive food deliveries of the 5 s delay component. For both strains a small decrease in their preference for the LL lever is observed with consecutive foods of the 10 s delay component, the proportions of LL choice produced by the SHRs ($M = .61$) and LEWs ($M = .65$) are closer to indifference line. With consecutive foods delivered by the 20 s delay component, most SHRs and

LEWs produced proportions of LL choice showing indifference ($M = .50$ and $.51$, respectively). The exceptions were two rats of each strain maintaining a preference for the LL lever across food deliveries ($M = .70$), and three rats, one LEW and two SHRs, developing a preference for the SS lever with the second and consecutive foods delivered by the 20 s delay component. The rats' preference to press more on the SS lever than on the LL lever, emerged with foods delivered by the 40 s delay component, and it was strengthened with consecutive foods delivered by the 80 s delay component. For the choices that the SHRs made with the 40- and 80-s delay components, the left-lower graphs of Figure 2 show proportions of LL choice decreasing from $.50$ with the first food to $.28$ and $.15$ with the last 5-foods delivered by the 40- and 80-s delay components, respectively. The only exception was one SHR producing proportions of LL choice with the 40 s delay component, showing a decrease from $.65$ with first food to $.40$ with the last food delivered by the 40 s delay component. The right-lower graphs show that the choices that the LEWs made with foods delivered by the 40 s delay component, moved slowly from indifference ($M = .50$) with the first two foods to a weak preference for the SS lever ($M = .40$) with the last 5-foods. Two LEWs, however, maintained their preference for the LL lever with the consecutive foods delivered by the 40 s delay component. Contrasting with another LEW showing an increasing preference for the SS lever with each consecutive food delivered by the 40 s delay component. Yet, all LEWs developed a clear preference for pressing on the SS lever with each consecutive food delivered by the 80 s delay component, producing proportions of LL choice with values decreasing from about $.51$ with the first food delivery to $.30$ with the last 5-foods delivered by the 80 s delay component. One LEW developed a strong preference for the SS lever, producing proportions of LL choice with values close to zero for the last 6-foods delivered by the 80 s delay component.

3.2 Discounting Rate

The proportions of LL choice computed for each group of SHRs (circles) and LEWs (squares) are plotted in Figure 3 as a function of the delay to the LLF. The graphs show discounting functions produced by the SHRs and LEWs pressing on the SS and LL levers to choose between the SSF and LLF. Graphs are organized by blocks of sessions, from block-1 upper left-corner to block-12 lower right-corner. The solid and dashed lines are best fits of Eq. 1 to the data produced by the SHRs and LEWs, respectively. Estimates of discounting rate (k in Eq. 1) for the mean data produced by the SHRs (k_{SHR}) and LEW (k_{LEW}) appear in the upper right corner of each graph. All graphs show that the hyperbolic-decay model (Eq. 1) nicely fitted the data produced by the SHRs and LEWs in blocks 1 to 12, accounting for most of the variability in the proportion of LL choice that occurred as a function of the delay to deliver the LLF, with R^2 ranging from .819 to .983 ($M = .953$) for the data produced by the SHRs and ranging from .872 to .995 ($M = .972$) for the data produced by the LEWs. Estimates of y-intercept (A in Eq. 1) ranged from .56 to .74 ($M = .68$) for the discounting functions produced by the SHRs and from .54 to .72 ($M = .68$) for the discounting functions produced by the LEWs.

All discounting functions indicate that the SHRs and LEWs discounted the LLF as a function of the delay to deliver it. The slopes of the discounting functions indicate that discounting rate (k in Eq. 1) increased with increasing blocks of sessions. Block 1 shows that the slope of the discounting function produced by the LEWs is steeper ($k = .008$) than the slope of the discounting functions produced by the SHRs ($k = .004$), suggesting that the LEWs chosen more impulsively than the SHRs early in training. Both strains produced similar discounting functions in block 2, the slope of the discounting function produced by the LEWs is slightly steeper ($k = .007$) than the slope of the discounting function produced by the SHRs ($k = .005$). Nonetheless, the slope of the discounting function produced by the SHRs in block 3 is steeper ($k = .013$) than the slope of the

discounting function ($k = .008$) produced by the LEWs, indicating that the SHRs made more impulsive choices than the LEWs. In blocks 4 and 5 impulsive choice increased substantially in the SHRs ($k = .027$ and $.028$, respectively), contrasting with the choices made by the LEWs showing a slight increment in discounting rate ($k = .013$). For the discounting functions that the LEWS produced in blocks 6 to 12, estimates of k ranging from $.013$ to $.016$ ($M = .014$) indicated that impulsive choice in the LEWs either did not change or changed insignificantly. In contrast, estimates of k for the discounting functions produced by the SHRs in blocks 6 to 12, ranging from $.032$ to $.046$ ($M = .037$), indicated that impulsive choice in the SHRs increased substantially as a function of increasing blocks of sessions (i.e., their experience with the choice situation).

3.3 Sensitivity of Choice to Immediacy of Reinforcement

This analysis extended the generality of findings showing that the GML (Eq. 2) fits delay discounting data produced by nonhuman animals (Aparicio, 2015; Aparicio et al., 2017). Initial link responses that the rats emitted on the LL and SS levers, were counted separately for each delay component, and aggregated across 15-sessions of the same block. Six ratios of responses (LL responses / SS responses) were computed for each rat and the mean of the group. Response ratios produced by the group of SHRs (circles) and LEWs (squares), were transformed into base-2 logarithms and plotted in Figure 3 as a function of delay ratios (SS/LL) transformed into base-2 logarithms. Where 0 on the x-axis (right side) is the \log_2 of the delay ratio ($0.1 / 0.1$) and -9.6 (close to the origin) the \log_2 of the delay ratio ($0.1 / 80$). The dotted line intercepting the y-axis at 0 is the indifference line, where the ratio of responses is 1 and the \log_2 of it 0. Values greater than 0 on the y-axis indicate preference for the LL lever (i.e., response ratios > 1) and values smaller than 0 preference for the SS lever (i.e., response ratios < 1). The graphs show the data from 12 blocks of sessions increasing in clusters of 15 days each from left to right and top to bottom. Solid

and dashed lines are best fits from Eq. 2 to the response ratios produced by the SHRs and LEWs, respectively. Eq. 2 expressed as a power law appears in bottom part of each graph showing empirical parameters for bias (b) and sensitivity of choice to the immediacy of reinforcement (s).

The multiple graphs of Figure 3 show that the GML (Eq. 2) fitted the data produced by the SHRs and LEWs, accounting for the variability in response ratios that occurred as a function of dynamic changes in the immediacy of reinforcement or delay ratio. Goodness of fit (R^2) for the response ratios produced by the SHRs ranged from .433 to .990 ($M = .617$) and from .593 to .840 ($M = .676$) for the data produced by the LEWs. Both strains developed a bias for pressing on the LL lever. It increased across blocks of sessions, with estimates of bias (b in Eq. 2) ranging from 0.59 to 2.38 ($M = 1.69$) for the response ratios produced by the SHRs and from 0.54 to 2.05 ($M = 1.53$) for the response ratios produced by the LEWs. The rats' bias for the LL lever caused choice to deviate from matching, with results consistent with undermatching where changes in response ratios were slower than those predicted by the GML (Eq. 2) varying the delay ratio.

Blocks of sessions 1 to 3 show that the SHRs' sensitivity of choice to the immediacy of reinforcement ($s = 0.19, 0.12, \text{ and } 0.17; M = 0.16$) was like that the LEWs developed ($s = 0.12, 0.15, \text{ and } 0.18; M = 0.15$), confirming similar levels of impulsive choice in both strains early in training. In blocks 4 to 6 the SHRs developed higher sensitivity of choice to the immediacy of reinforcement ($s = 0.30, 0.30, \text{ and } 0.38; M = 0.33$) than that the LEWs developed ($s = 0.26, 0.21, \text{ and } 0.25; M = 0.24$), indicating that the SHRs made more impulsive choices than the LEWs. For the SHRs sensitivity of choice to the immediacy of reinforcement increased in blocks of sessions 7 to 9 ($s = 0.38, 0.44, \text{ and } 0.37; M = 0.39$), contrasting with a decrease in sensitivity of choice to the immediacy of reinforcement shown by the LEWs ($s = 0.22, 0.21, \text{ and } 0.21; M = 0.21$). While the choices of the LEWs displayed no further changes in sensitivity to reinforcement in blocks of

sessions 10 to 12 ($s = 0.20, 0.20, \text{ and } 0.21$; $M = 0.20$), the choices of the SHRs shown the highest sensitivity to the immediacy of reinforcement ($s = 0.46, 0.37, \text{ and } 0.41$; $M = 0.41$).

3.4 *Hyperbolic-decay Model and the Generalized Matching Law*

For both strains impulsive choice increased as a function of training in the choice situation (Figures 3 and 4). At the end of the training (block-12 of sessions), however, the group of the SHRs made more impulsive choices, producing higher discounting rates ($k = .035$) and showing more sensitivity to the immediacy of reinforcement ($s = 0.41$), than the group of the LEWs ($k = .016$ and $s = 0.21$, respectively). To confirm that the SHRs chose more impulsively than the LEWs, estimates of discounting rate (k in Eq. 1) and sensitivity of choice to the immediacy of reinforcement (s in Eq. 2) were computed with the data produced by the individual SHR and LEW rats and plotted in Figure 5 as a function of blocks of sessions. The top graphs show discounting rates produced by the individual SHR (left graph) and LEW (right graph) rats and the bottom graphs estimates of sensitivity of choice to the immediacy of reinforcement. The unfilled symbols stand for estimates of k and s for the data produced by the individuals and filled symbols estimates averaged for the group of SHRs (circles) and the group of LEWs (squares). The lines connecting the filled symbols are the best fitting lines generated by a 4-parameters logistic (4PL) nonlinear regression model formally expressed as follows:

$$y = \frac{A_1 - A_2}{1 + (x/x_0)^p} + A_2, \quad (3)$$

where A_1 is the minimum asymptote or initial value estimated for either k or s , p is the power or slope of the curve, x_0 the inflection point where the curvature changes direction, and A_2 the maximum asymptote or final value estimated for either k or s .

The top graphs of Figure 5 show that Eq. 3 nicely accounted for changes in estimates of the discounting rate (k) produced by the SHRs ($R^2 = .989$) and LEWs ($R^2 = .939$) that occurred as

a function of blocks of sessions. For the SHRs, estimates of the parameters A_1 and A_2 show that discounting rate increased from .004 in block-1 to .036 in block-12, respectively, and for the LEWs estimates of the parameters A_1 and A_2 showing that discounting rate increased from .008 in block-1 to .018 in block-12, respectively. The slope of the line fitting estimates of discounting rates for the LEWs is steeper ($p = 4.99$) than the slope of the line fitting estimates of discounting rates for the SHRs ($p = 4.35$), suggesting that the discounting rates produced by the LEWs increased faster than the discounting rates produced by the SHRs. The inflection point of the curve shows that the LEWs' discounting rates changed earlier ($x_0 = 3.02$) than the SHRs' discounting rates ($x_0 = 3.62$) to reach asymptotical level.

The bottom graphs of Figure 5 show that Eq. 3 also accounted for changes in sensitivity of choice to the immediacy of reinforcement that the SHRs ($R^2 = .974$) and LEWs ($R^2 = .957$) developed across blocks of sessions. Estimates of the parameters A_1 and A_2 for the choices the SHRs made across block of sessions, show that sensitivity to the immediacy of reinforcement increased from 0.09 in block-1 to 0.35 in block-12, respectively, contrasting with the choices made by the LEWs showing that sensitivity to the immediacy of the reinforcement increased from 0.13 to 0.22, respectively. The slope of the line fitting sensitivity to the immediacy of reinforcement for the choices made by SHRs, is steeper ($p = 3.65$) than the slope of the line fitting sensitivity to the immediacy of reinforcement for the choices made by the LEWs ($p = 2.62$); indicating that the SHRs' sensitivity to the immediacy of reinforcement increased faster than the LEWs' sensitivity to the immediacy of reinforcement. The inflection point of the curve fitting the data produced by the LEWs ($x_0 = 2.62$), shows that LEWs' sensitivity of choice to the immediacy of reinforcement reached maximum level earlier in training than that SHRs' sensitivity of choice to the immediacy of reinforcement ($x_0 = 3.65$).

The next analysis extended the generality of findings showing consistencies between the hyperbolic-decay model (Eq. 1) and the generalized matching law (Eq. 2). The discounting rates (k) produced by the individuals SHR and LEW rats were plotted in Figure 6 as a function of estimates of sensitivity of choice to the immediacy of reinforcement (s). The left graph shows data produced by the SHRs and the right graph data produced by the LEWs. Unfilled symbols stand for the data produced by the individual SHRs and LEWs and filled symbols for the mean of the group of SHRs (circles) and the mean of group of LEWs (squares). Results from linear regression and Pearson's r appear on the left-upper corner of each graph. Both graphs show a positive correlation between discounting rate and sensitivity of choice to the immediacy of reinforcement. The line fitting the data produced by the group of the SHRs, shows a steeper slope ($s = 1.58$) and higher correlation between s and k ($r = .991$) than the line fitting the data produced by the group of the LEWs, showing a slope of 1.56 and Pearson's r of .942. Linear regression accounted for the variability in the data produced by the group of SHRs ($R^2 = .980$) and the data produced by the group of LEWs ($R^2 = .976$). The lines fitting to the data produced by individual SHR and LEW rats (regression lines not shown), generated values of Pearson's r ranging from .856 to .987 ($M = .917$, $SD = .05$) for the former and from .685 to .975 ($M = .865$, $SD = .12$) for the latter strain of rats. The slopes of the lines fitting the data produced by the individual SHRs, ranged from 0.09 to 0.17 ($M = 0.14$, $SD = 0.06$), and the slopes fitting the data produced by the individual LEWs ranged from 0.05 to 0.22 ($M = 0.11$, $SD = 0.05$). Linear regression fitted the data well generating R^2 ranging from .706 to .971 ($M = .828$, $SD = .09$) for the data produced by the individual SHRs and from .706 to .971 ($M = .828$, $SD = .09$) for the data produced by the individual LEWs.

4. Discussion

4.1 Preference

The results revealed that the SHRs made more impulsive choices than the LEWs across blocks of sessions (Fig. 1) and food deliveries (Fig. 2), with the LEWs developing a stronger preference for the LLF than the SHR. The global analysis indicated that both strains developed a clear preference for pressing on the LL lever when its terminal link delivered the LLF after a slight delay (0.1 s). Their preference for pressing on the LL lever decreased when the LLF was delayed 5 and 10 s. Whereas the LEWs maintained a slight preference for pressing the LL lever when the LLF was delayed 40 s, the SHRs showed indifference for pressing either the SS or LL lever when the LLF was delayed 20 s. When the LLF was delayed either 40 or 80 s, the SHRs and LEWs pressed more on the SS lever than on the LL lever, producing mean proportions of LL choice indicating that their preference for pressing the SS lever slowly increased with increasing blocks of sessions. Results showing gradual changes in impulsive choice have been documented with Lewis and Fischer 344 rats responding to similar concurrent-chains procedures (Aparicio, Hughes, & Pitts, 2013), and the present study extended the generality of these findings to SHR and LEW rats. Even though the choices of the LEWs show indifference for pressing either the SS or LL lever in the first block of sessions (Fig. 1), it can be said that the LEWs tolerated longer delays to receive the LLF across blocks of sessions than the SHRs.

The analysis of the proportion of LL choice block by block of sessions provided a global view of changes in preference across delay components. It is important to support the idea that naïve rats learn to choose impulsively with their experience in the choice situation, regardless of their genetic or neurophysiological conditions at the beginning of training (Aparicio et al., 2019). The local analysis of choice food by food delivery, however, was remarkable in demonstrating that both strains of rats can track with their responses the lever producing the largest amount of food (Fig. 2). It was found that the SHRs and LEWs pressed on both levers indicating indifference to

get the first food that each delay component delivered. This result was caused by the procedure presenting delay components in random order during the session, making difficult for the rats to anticipate the amount of food (SSF or LLF) delivered by each delay component. Consequently, the local analysis of choice showed that two or more foods delivered by the same component were required for the rats to discriminate the amount of food being produced by pressing on the SS or LL lever (Aparicio, Malonson, & Hensley, 2020). When the delay to obtain the LLF was 0.1 s, both strains pressed more on the LL lever than on the SS lever. When choosing between the SSF and the LLF delivered by the 5 s delay component, the SHRs and LEWs produced proportions of LL choice like those they produced to obtain the foods delivered by the 0.1 s delay component. For both strains a small decrease in their preference for pressing more on the LL lever than on the SS lever was observed with consecutive foods delivered by the 10 s delay component. Nonetheless, most SHRs and LEWs produced proportions of LL choice showing indifference with consecutive foods delivered by the 20 s delay component. The rats' preference to press more on the SS lever than on the LL lever, emerged with foods delivered by the 40 s delay component and was further strengthened with consecutive foods delivered by the 80 s delay component. These findings are consistent with those showing that impulsive choice in non-human animals is controlled by each food produced in choice situations varying the delay to the LLF (Aparicio, et al., 2019; 2020).

4.2 Discounting Rate

Choosing between the SSF and the LLF, the SHRs and LEWs produced discounting functions indicating that the LLF was discounted as a function of the delay to obtain it (Fig. 3). Mazur's (1987) hyperbolic-decay model fitted the data produced by the SHRs and LEWs well, accounting for most of the variability in the proportion of LL choice that occurred as a function of the delay to deliver the LLF. For the discounting functions produced by the SHRs and WKYs,

estimates of y-intercept (A in Eq. 1) increasing from .56 to .74 ($M = .68$) and from .54 to .72 ($M = .68$), respectively, indicated that for both strains sensitivity of choice to the magnitude of the LLF increased as a function of training. The slopes of the discounting functions produced by the SHRs and LEWs, revealed that discounting rate (k in Eq. 1) also increased as a function of training in the choice situation. In the first block of sessions the slope of the discounting function produced by the LEWs was steeper than that produced by the SHRs, indicating that the LEWs made more impulsive choices at the beginning of the study than the SHRs. In the second block of sessions, however, the slope of the discounting functions produced by SHRs was like that produced by the WKYs showing minor differences in discounting rates. As training progressed, impulsive choice increased extremely in the SHRs producing discounting functions with slopes that were steeper than the slopes of the discounting functions produced by LEWs. These findings add to the cumulative body of evidence showing that impulsive choice in non-human animal's changes as a function of extended training (Aparicio, 2015; Aparicio et al, 2013; 2019; 2020).

4.3 *Sensitivity of Choice to Immediacy of Reinforcement*

A modified version of Baum's (1974) Generalized Matching Law (GML) was used to estimate sensitivity of choice to the immediacy of reinforcement (s) and a bias for pressing one lever more than on the other (b). The GML (Eq. 2) fitted discounting data produced by the SHRs and LEWs well (Fig. 4), accounting for the variability in response ratios that occurred as a function of dynamic changes in delay ratios. Both strains developed a bias for pressing the LL lever more than the SS lever, causing choice to deviate from matching to undermatching (Baum, 1974) and suggesting that changes in the response ratios produced by the SHRs and LEWs were slower than those predicted by the GML varying the delay ratio. Consistent with the discounting rates (k in Eq. 1) produced by the SHRs and LEWs in blocks of sessions 1 to 3, sensitivity of choice to the

immediacy of reinforcement (s in Eq. 2) suggested no between strains differences in impulsive choice early in training. In blocks 4 to 6, however, the SHRs made more impulsive choices than the LEWs indicating that the SHR's sensitivity of choice to the immediacy of reinforcement increased. Contrasting with the choices that the LEWs made in blocks of sessions 7 to 12 indicating no further changes in sensitivity to reinforcement, the choices made by the SHRs indicated the highest level of sensitivity to the immediacy of reinforcement. These results extend the generality of conclusions indicating that the GML fits discounting data produced by nonhuman animals well (Aparicio, 2015; Aparicio et al., 2019). This finding is important because the original Matching Law (Herrnstein, 1961) did not describe the data from concurrent-chains procedures well, and the present study shows that the Generalized Matching Law (Baum & Rachlin, 1969; Staddon, 1968) does describe data from concurrent-chains procedures well, identifying sources of undermatching such as asymmetrical pausing, inconsistency in preference through time, patterns of changeover, and brief bouts of responding (Baum, 1979).

4.4 Hyperbolic decay model and the generalized matching law

At the beginning of training (blocks of sessions 1 and 2) the group of LEW rats made more impulsive choices than the group of SHR rats. For both groups impulsive choice increased as a function of increasing blocks of sessions. At the end of training (blocks of sessions 9 to 12), however, the SHRs produced higher discounting rates (Fig. 3) and developed more sensitivity to the immediacy of reinforcement (Fig. 4) than the LEWs. More evidence supporting this finding came from estimates of discounting rate (k in Eq. 1) and sensitivity of choice to the immediacy of reinforcement (s in Eq. 2) computed with the data produced by the individual SHR and LEW rats, showing values of k and s that increased as a function of increasing blocks of sessions (Fig. 5). A 4 -parameters logistic (4PL) nonlinear regression model (Eq. 3) fitted estimates of k and s well,

accounting for changes in values of k and s that occurred with increasing blocks of sessions. The slope of the curve (p) fitting the discounting rates (k values) produced by the LEWs was steeper than the slope of the curve fitting estimates of k computed for the SHRs, indicating faster changes in discounting rate for the LEWs than for the SHRs. Yet, the slope of the curve (p) fitting estimates of k for the choices made by the SHRs was steeper than that fitting the choices made by the LEWs, suggesting that the SHRs' sensitivity to the immediacy of reinforcement increased faster than that the LEWs shown across blocks of sessions. In all cases, the inflection points of the curves (x_0) fitting estimates of k and s for the data produced by the LEWs, showed lower values than those corresponding to the data produced by the SHRs, indicating that the choices made by the LEWs moved to asymptotical level faster than choices made by the SHRs. Lastly, estimates of initial values of k and s (A_1) for the choices made by individual LEWs were higher than those estimated for the choices made by the SHRs, confirming the LEWs made more impulsive choices at the beginning of training than the SHRs. The claim that the SHRs developed more impulsivity across blocks of sessions than the LEWs was nicely supported with estimates of final values of k and s (A_2), confirming that at the end of training the SHRs produced higher discounting rates and developed more sensitivity to the immediacy of reinforcement than the LEWs.

It is concluded that the 4-parameters logistic (4PL) nonlinear regression model has been successfully used to estimate the inhibition of responses in nonhuman animals (Elcoro, Aparicio, Kelly, & Thompson, 2016) and analyze the acquisition, behavioral inhibition, and restoration of responses in SHRs and LEWs (Aparicio et al, 2020). And the present study extends its generality to assess changes in discounting rate and sensitivity of choice to the immediacy of reinforcement occurring as a function of extended training in choice situations varying the delay to the LLF. Future research using concurrent-chains procedures to analyze impulsive choice in inbred strains

of SHR and LEW rats, might find the empirical parameters from a logistic nonlinear regression model (4PL) useful to evaluate environmental and neuropharmacological variables affecting impulsive behavior in non-human animals.

Lastly, the present study looked for possible consistencies between the hyperbolic-decay model (Eq. 1) and the generalized matching law (Eq. 2) predicting choice. Discounting rates (k) produced by the SHRs and LEWs were plotted as a function of estimates of sensitivity of choice (s) to the immediacy of reinforcement (Fig. 6). Positive correlations between k and s were found, with the regression line fitting estimates of k and s for the choices made by the SHRs showing a steeper slope ($s = 1.58$) and higher correlation between s and k (Pearson' $r = .991$), than the line fitting estimates of k and s for the choices made by LEWs showing a slope of 1.56 and Pearson' r of .942. This finding is consistent with the idea suggesting some compatibility between Mazur's (1987) hyperbolic-decay model and Baum's (1974) Generalized Matching Law (Aparicio et al., 2015, 2019, 2020).

4.5 Conclusions

Both strains learned to choose impulsively with their experience in the choice situation, regardless of their genetic or neurophysiological conditions at the beginning of the study. Early in training the LEWs made more impulsive choices than the SHRs, but late in training the SHRs developed more impulsive choice than the LEWs. The analysis of the proportion of LL choice block by block of sessions provided a global view of gradual changes in preference across delay components, and the analysis of the proportion of LL choice food by food delivery a local view of changes in preference within delay components indicating that the SHRs and LEWs tracked with their responses the lever producing the largest amount of food (LLF). Both strains produced discounting functions indicating that the LLF was discounted as a function of the delay to obtain

it. Mazur's (1987) hyperbolic-decay model fitted the data produced by the SHRs and LEWs well. The y-intercept (A) and slopes (s) of the discounting functions produced by the SHRs and LEWs indicated that sensitivity of choice to the magnitude of the LLF and discounting rate increased as a function of training in the choice situation. As training progressed, impulsive choice increased extremely in the SHRs producing discounting functions with slopes that were steeper than the slopes of the discounting functions produced by LEWs. A modified version of Baum's (1974) Generalized Matching Law (GML) also fitted discounting data produced by the SHRs and LEWs well. Both strains developed a bias for pressing the LL lever more than the SS lever with choice showing undermatching. Early in training estimates of sensitivity of choice to the immediacy of reinforcement (s) indicated no between strains differences in impulsive choice. Late in training, however, the SHRs shown higher sensitivity to the immediacy of reinforcement than the LEWs. For the choices made by individual SHR and LEW rats, a 4-parameters logistic (4PL) nonlinear regression model (Eq. 3) fitted estimates of k and s well, showing that both discounting rate and sensitivity of choice to the immediacy of reinforcement, respectively, increased as a function of increasing blocks of sessions. Positive correlations between k and s suggested some regularities between the hyperbolic-decay model and the generalized matching law fitting delay discounting data. Overall, the present study supports the claim that the LEW rat is an appropriate control for the SHR. Future research using concurrent-chains procedures to analyze impulsive choice in inbred strains of SHR and LEW rats, might find the empirical parameters from a logistic nonlinear regression model (4PL) useful to evaluate environmental and neuropharmacological variables affecting impulsive behavior in non-human animals.

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Figure Captions

Figure 1.

Proportion of LL choice ($(LL/(LL+SS))$) as a function of block of sessions. The left graphs show data produced by the SHRs and the right graphs data produced by the LEWs. From top to bottom the graphs are organized by delay component (0.1, 5, 10, 20, 40, and 80 s). The unfilled symbols represent data from individuals and filled symbols joined by the solid line data from the group. The dotted line intercepting the y-axis at .5 is the indifference line.

Figure 2.

Proportion of LL choice as a function of foods delivered by each delay component. Other details as in Fig. 1.

Figure 3.

Proportion of LL choice as a function of the delay (s) to deliver the LLF. From left to right and top to bottom, the graphs show discounting functions produced in 12 blocks of 15 sessions each. The unfilled circles represent mean proportions LL choice computed for the group of SHRs and unfilled squares mean proportions of LLL choice computed for the group of LEWs. Estimates of discounting rate for the data produced by the SHRs (k_{SHR}) and LEWs (k_{LEW}) appear on the upper right corner of each graph. The line is the best fits of Eq. 1 to the data produced by the group.

Figure 4.

\log_2 of response ratio (LL/SS) as a function of the \log_2 of the delay ratio (SS/LL). The dotted line intercepting the y-axis at zero is the indifference line and the solid line the best fit of Eq. 2 to the mean data produced by the groups of SHRs and LEWs. Other details as in Fig. 3.

Figure 5.

For the data produced by the individual SHRs (left graphs) and LEWs (right graphs), estimates of discounting rate (top) and sensitivity of choice to the immediacy of reinforcement (bottom) as a function of blocks of sessions. Unfilled symbols are the data from the individuals and filled symbols with error bars the mean of the group.

Figure 6.

Estimates of k as a function of estimates of s . The left graph shows the data from the SHRs and the right graph shows the data from the LEWs. The unfilled symbols represent the estimates for the data of the individual SHR and WKYs and filled symbols with regressions lines the mean for the group data. Regression results and Pearson's r appear on the left-upper corner of each graph. Note the \log_{10} base scales on the x- and y-axis.

Table 1.
Hyperbolic-decay model, resulting parameters (Eq. 1).

Block	A		k		R^2	
	SHR	LEW	SHR	LEW	SHR	LEW
1	0.564	0.535	0.004	0.008	0.819	0.872
2	0.609	0.654	0.005	0.007	0.983	0.966
3	0.619	0.692	0.013	0.008	0.962	0.915
4	0.673	0.720	0.027	0.013	0.984	0.990
5	0.679	0.708	0.028	0.013	0.968	0.995
6	0.703	0.705	0.034	0.015	0.966	0.995
7	0.693	0.695	0.036	0.013	0.971	0.989
8	0.700	0.680	0.041	0.013	0.972	0.977
9	0.709	0.683	0.032	0.014	0.976	0.996
10	0.742	0.689	0.046	0.014	0.956	0.984
11	0.737	0.678	0.036	0.015	0.938	0.990
12	0.737	0.702	0.035	0.016	0.942	0.994
Mean	0.680	0.678	0.028	0.012	0.953	0.972

Table 2.
Generalized matching law, resulting parameters (Eq. 2).

Block	b		s		R^2	
	SHR	LEW	SHR	LEW	SHR	LEW
1	0.591	0.536	0.190	0.125	0.990	0.840
2	1.035	1.390	0.124	0.152	0.597	0.708
3	1.020	1.711	0.173	0.176	0.433	0.788
4	1.506	2.054	0.299	0.257	0.623	0.617
5	1.632	1.700	0.298	0.209	0.510	0.608
6	1.939	1.796	0.381	0.252	0.607	0.656
7	1.837	1.627	0.380	0.218	0.619	0.679
8	2.052	1.529	0.436	0.205	0.698	0.670
9	2.028	1.513	0.366	0.214	0.596	0.644
10	2.381	1.558	0.463	0.198	0.629	0.593
11	1.914	1.388	0.368	0.198	0.557	0.644
12	2.319	1.599	0.409	0.215	0.548	0.664
Mean	1.688	1.533	0.324	0.202	0.617	0.676

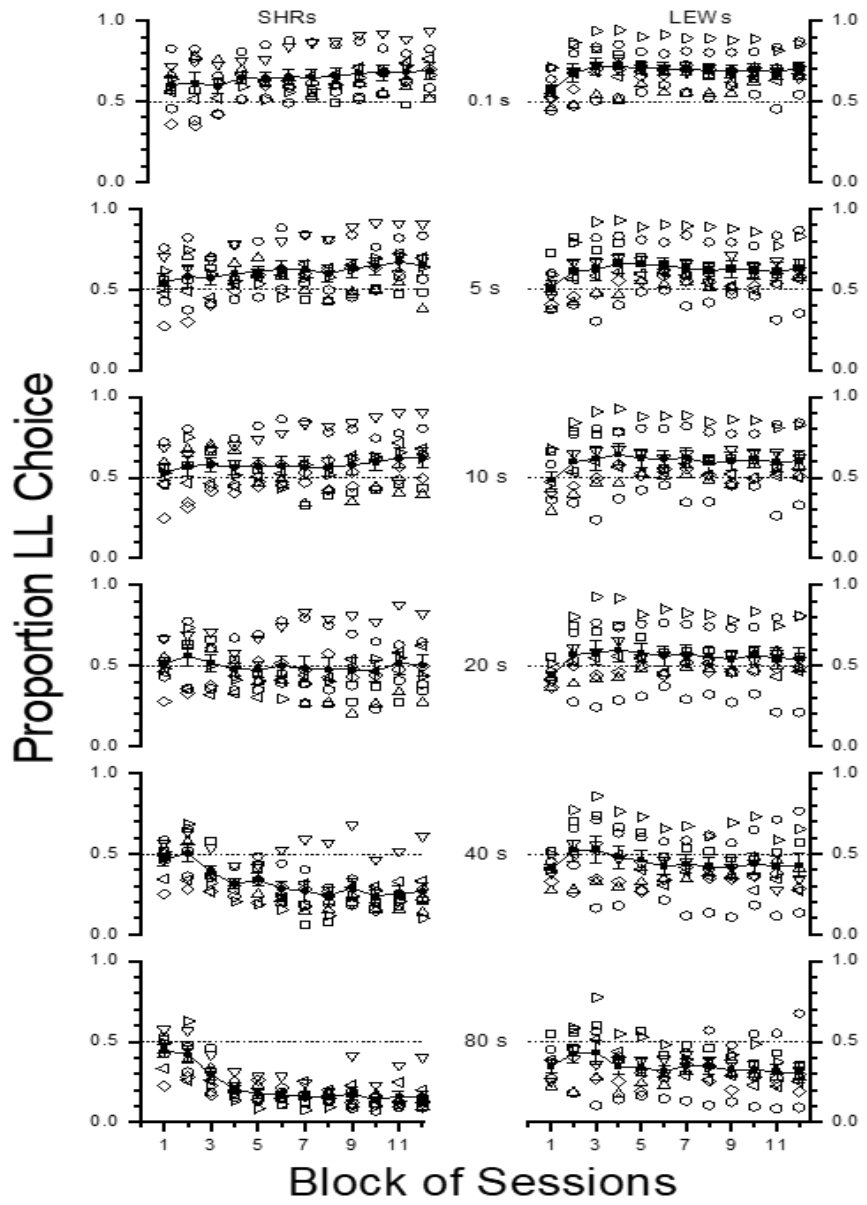


Fig 1.

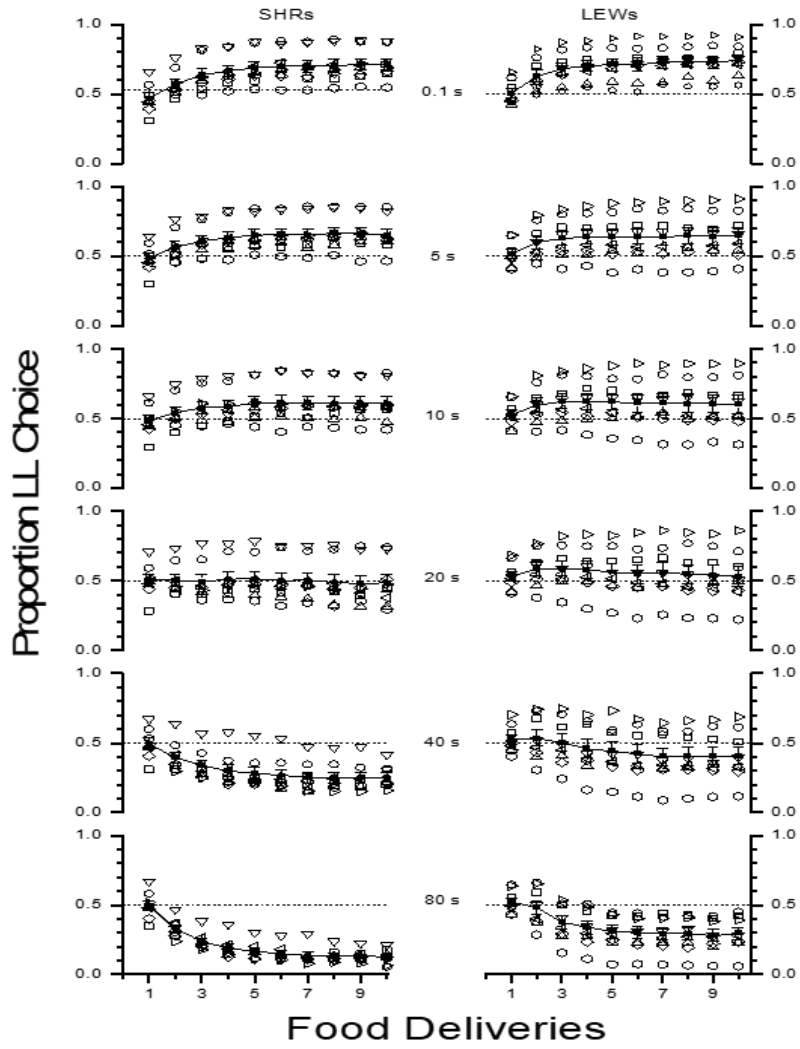


Fig. 2

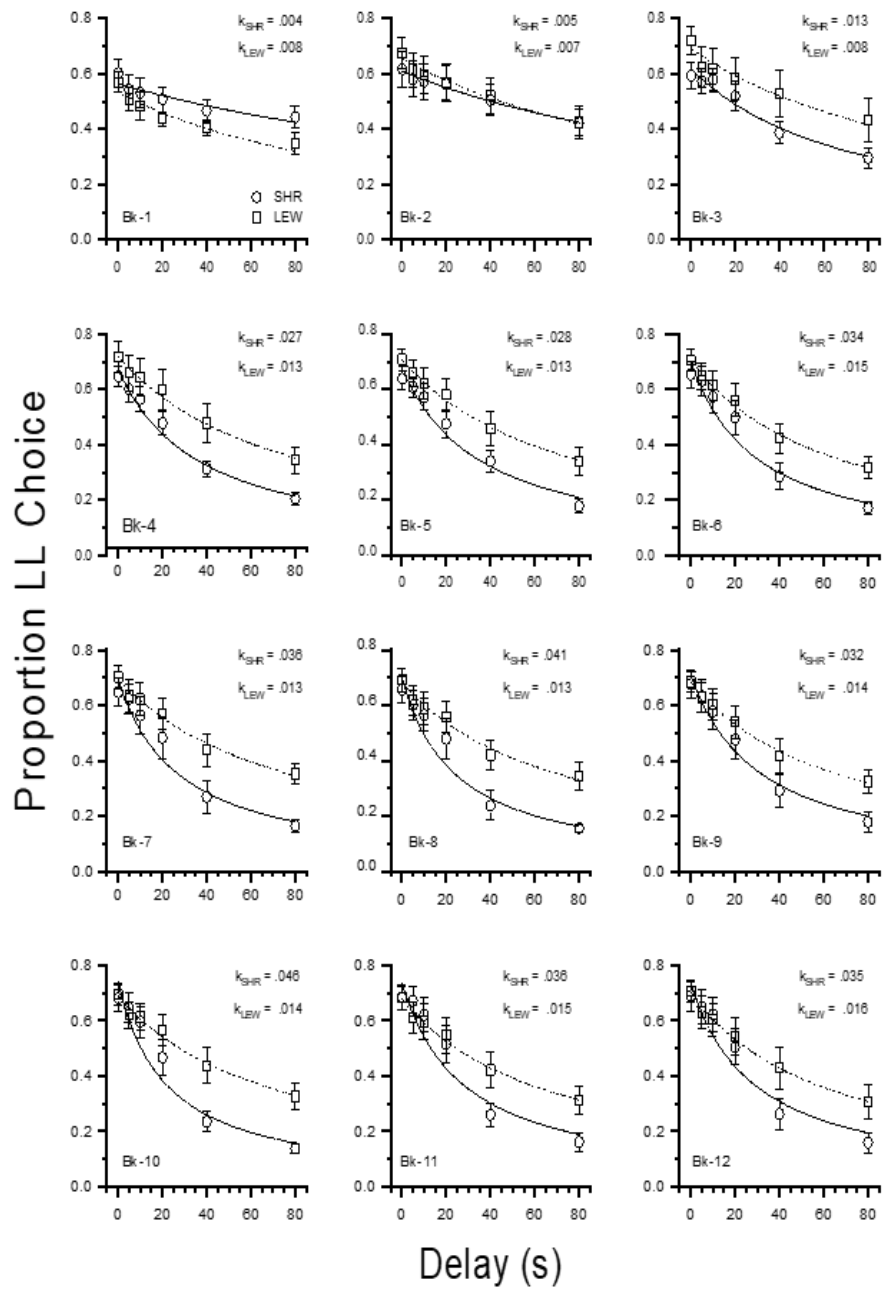


Fig. 3

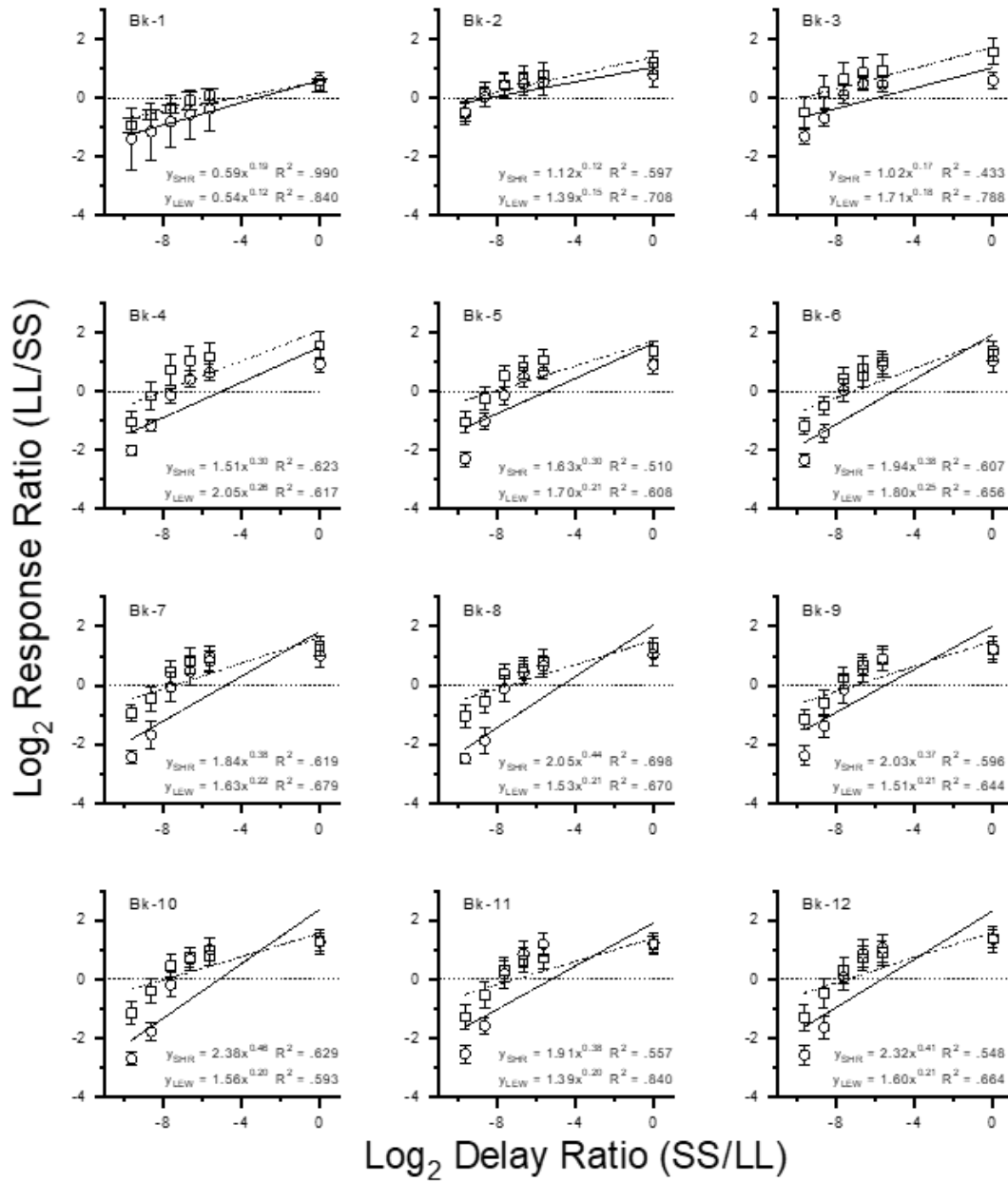


Fig. 4



Fig. 5

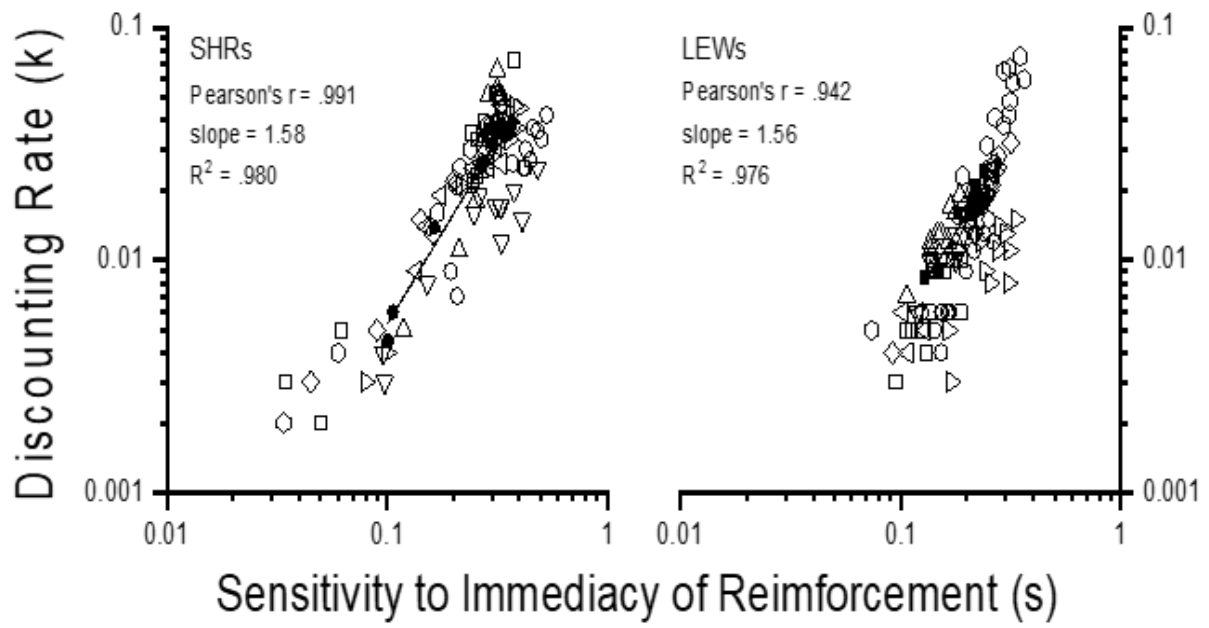


Fig. 6