Delay Discounting and Polydipsia in Spontaneously Hypertensive (SHR) and Lewis (LEW) Rats[1]

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Abstract

This study compared the performance of the Spontaneously Hypertensive rat (SHR) on a delay discounting task with the performance of the Lewis rat (LEW) to suggest that both strains of rats are potential models of Attention Deficit/Hyperactivity Disorder (ADHD). It measured choice in the initial link of a concurrent-chains procedure with presses on two levers arranging entries to two terminal links, one delivering 1-food pellet after a 0.1-s delay and the other 4-food pellets with delays of 0.1, 5, 10, 20, 40 or 80 seconds presented in random order during the session. A bottle with tap water could be available for the rats to drink during the session (B), or it was not available (A) according to an ABABA reversal design. The SHR and LEW rats made impulsive choices producing discounting functions showing discounting rates increasing with increasing training sessions. Early in training the SHR rats produced discounting rates greater than the LEW rats, but at the end of training both strains of rats produced comparable discounting rates. All rats developed polydipsia in condition B, but the SHR rats consumed more water and emitted more licks than the LEW rats. Polydipsia was not linked to discounting rate, nor polydipsia caused the rats' impulsive choices to decrease.

Keywords: *Impulsivity, polydipsia, ADHD, SHR, LEW, rats*

Resumen

Este estudio comparó la ejecución de la rata espontáneamente hipertensa (SHR) en una tarea de descuento temporal con la ejecución de la rata Lewis (LEW) para sugerir que las dos cepas de ratas son posibles modelos del trastorno por déficit de atención e hiperactividad (ADHD). La elección se midió en el eslabón inicial de un programa concurrente encadenado con presiones en dos palancas organizando entradas a dos eslabones terminales, uno entregó 1-pella de comida con una demora de 0.1 segundo y el otro entregó de 4-pellas de comida con demoras de 0.1, 5, 10, 20, 40, o 80 segundos presentadas en orden aleatorio durante la sesión. Una botella con agua podía estar disponible a las ratas para beber durante la sesión (B), o no estuvo disponible (A) de acuerdo con un diseño reversible ABABA. Las dos cepas de ratas hicieron elecciones impulsivas produciendo funciones de descuento temporal que mostraron tasas de descuento que

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[1] La referencia del artículo en la Web es: http://conductual.com/articulos/Delay Discounting and Polydipsia in Spontaneously Hypertensive (SHR) and Lewis (LEW) Rats.pdf

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aumentaron en las sesiones consecutivas de entrenamiento. Al inicio del estudio las ratas SHR hicieron más elecciones impulsivas que las ratas LEW, pero al finalizar este las dos cepas de ratas mostraron elecciones impulsivas equivalentes. Todas las ratas desarrollaron polidipsia en la condición B, pero las ratas SHR bebieron más emitiendo un mayor número de lengüetazos que las ratas LEW. La polidipsia no se vinculó con la tasa de descuento, ni la polidipsia redujo la elección impulsiva de las ratas.

Palabras clave*: Impulsividad, polidipsia, ADHD, SHR, LEW, ratas*

Everyday humans and nonhuman animals chose between consequences separated in time. The magnitude of the consequence, its quality, the delay to get it, the probability to obtain it, and the effort invested to produce it are factors affecting preference. Humans choose which foods to eat and when to do it, and nonhuman animals choose which preys to hunt and fruits or plants to eat. The price of the food, its taste, and the effort to get it (moving from one place to another) are factors affecting preference in humans. The amount of energy (cost) required to capture the prey, the density of prey (low vs. high) in the patch, the competence of resources by other predators, and the travel distance to find a new patch to deplete are factors affecting choices in nonhuman animals (Aparicio, 1999; 2001; Aparicio and Baum, 1997; Kono, 2019). Choice is effortless in situations where two alternatives differ from one another on one element only (e.g., the amount of food), and human and nonhuman animals develop a preference for the largest amount of food. But when two alternatives differ from one another on more than one element (e.g., amount of food and delay to get it), preference for the largest amount of food decreases with the increasing delay to get it. This process is termed delay discounting and indicates the largest amount of food loses value (efficacy) gradually with the increasing delay to obtain it (Vanderveldt et al., 2016).

Delay discounting plays a significant role in determining patterns of impulsive behavior receiving considerable attention in Psychology (Madden and Bickel, 2010). In studies arranging a choice between a smaller-immediate consequence (the smaller-sooner reinforcer, or SSR) and a larger-delayed consequence (the larger-later reinforcer, or LLR), choosing the SSR more often than choosing the LLR indicates impulsive choice (Ainslie, 1974; Rachlin & Green, 1972), and choosing the LLR over the SSR suggests self-controlled choice (Logue, 1988). Impulsive choice is related to pathologies, maladaptive behaviors, and behavioral traits (Odum, 2011). Behavioral biologists suggest that impulsive behavior might be adaptive to humans and nonhuman animals (Fawcett et al., 2012), and behavior analysts define impulsive behavior functionally instead of structurally improving our understanding of impulsiveness by keeping its interpretation open to empirical evidence (Winstanley et al., 2006). The behavior pattern labeled impulsivity increases as a function of increasing training in the choice situation (Aparicio et al., 2013; 2015; 2019).

Experimental efforts to describe and assess delay discounting developed mathematical models to estimate the shape of the discounting function (e.g., Killeen, 2009; Rachlin, 2006), generating research in psychology (Green and Myerson, 2004), cognitive neuroscience (Peters and Buchel, 2011; Sellitto et al., 2011), and economics (Frederick et al., 2002). Most models of intertemporal choice estimate the shape of the discounting function by relating the value of the consequence to the delay to obtain it (Killen, 2009; Rachlin, 2006), or connecting its value to the inter-reinforcement interval (Green et al., 2005; Kable and

Glimcher, 2010). One model of inter-temporal choice that suitably describes the degree to which the value of the LLR decays with the increasing delay to obtain it, is Mazur's (1987) hyperbolic-decay model.

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

Where V is value of the LLR, A its amount, D the delay to obtain it, and k a free parameter to estimate how fast the value of the LLR decays (its discounting rate) with the increasing delay to obtain it. The efficacy of the hyperbolic-decay model in describing delay discounting data from human (e.g., Myerson and Green, 1995; Rachlin et al., 1991) and nonhuman animals (Aparicio, 2015; Aparicio et al., 2013; 2015; 2019; Farrar et al., 2003; Green et al., 2007; Mazur, 2012; Stein et al., 2012), is remarkably general. Researchers assess changes in discounting rate (k) to estimate the effects of drugs, or other neurobiological agents, on impulsive choice (Richards et al., 1997) analyzed with adjusting-delay procedures (Mazur 1987), adjusting-amount titration procedures (e.g., Green et al., 2007), or the method developed by Evenden and Ryan (1996) to obtain a discounting function in each session. The advantages and disadvantages of each of these methods in generating graded discount functions warrant the use of alternative methods to study impulsive choice (Madden and Johnson, 2010). For instance, concurrent-chains methods varying the delay to the LLR within the session have been successfully used to analyze impulsive choices made by Spontaneously Hypertensive (SHR) and Lewis (LEW) rats (i.e., Aparicio et al., 2015; 2019). Inbred strains of SHR and LEW rats are used to examine impulsive choice because they experience irregularities of dopamine (DA) and serotonin (5-HT) activities related to symptoms of the Attention-Deficit Hyperactivity Disorder (ADHD) such as inattention, hyperactivity, and impulsivity (Aparicio et al., 2022).

Initially, animal models of ADHD prompted by the notion of minimal brain dysfunction administered hydroxydopamine (6-OHDA) to newborn rats to induce hyperactivity (Shaywitz et al., 1976a), and methylphenidate to reduce it (Shaywitz et al., 1978), or amphetamine, finding inconsistent results (Shaywitz et al., 1976b). Other models of ADHD emerged when experts left the notion of minimal brain dysfunction (i.e., DMS-III; American Psychiatry Association, 1980) to include the traits of impulsivity and inattention in the diagnostic of ADHD (American Psychiatry association, 1987), allowing the analysis of executive functions such as working memory and cognitive flexibility. With these changes, experts proposed three subtypes of ADHD: primarily inattentive (ADHD-IA), hyperactive-impulsive (ADHD-HI), and a combined subtype (ADHD-C) with incidence of 0.8, 3.4, and 5.9 %, respectively (i.e., American Psychiatry association, 2000). An appropriate model of ADHD should warrant the examination of clinical diagnostic criteria, executive functions, and treatments with drugs to reduce symptoms of ADHD such as inattention, hyperactivity, and impulsivity (Kantak, 2022). Because ADHD is a heterogeneous condition (Castellanos and Tannock, 2002; Nigg, 2006; Sonuga-Barke et al., 2010) linked to irregular activity of DA and 5-HT neurotransmitters and pathways in the brain (Sonuga-Barke, 2002; 2003; Wählstedt et al., 2009), the risk of drug use is higher in individuals diagnosed with ADHD than in control groups (Groenman et al., 2017; Lee et al., 2011), and drug use is a fitting phenotype to assess in models of ADHD (Sundquist et al., 2015).

The SHR is a validated rodent model of ADHD (Sagvolden, 2000) originated by breeding selectively an outbred strain of Wistar Kyoto (WKY) rats experiencing elevated systolic blood pressure (Okamoto and Aoki, 1963). The SHR was reselected at each generation and sent to the National Institute of Health (NIH). The NIH distributed two innovative cohorts of SHR(SHR/N) rats, Charles River Laboratories acquired one cohort (SHR/NCrl) and Harlan Sprague-Dawley the other cohort (SHR/NHsd). Studies on genomic landscape of rat strain and sub-strain variation in elevated blood pressure confirmed equivalence between SHR/NCrl rats and SHR/NHsd rats at seven weeks of age (Hersem et al., 2015). Research on ADHD compares the SHR rat (NCrl or NHsd) to inbred WKY and outbred Wistar (WIS) rats, because the WKY is the source strain of the SHR and its normotensive control (Okamoto, 1969), and the WIS is the source strain of the WKY. The SHR possesses three traits of the combined subtype of ADHD-C: (1) Hyperactivity (Kim et al., 2012; Fasmer and Johansen, 2016; Somkuwar et al., 2016); (2) Impulsivity (Hand et al., 2009; Aparicio et al., 2019); And (3) inattention (De Bruin et al., 2003; Sagvolden, 2011).

While SHR/NHsd rats and SHR/NCrl rats are highly genetically related (Hersem et al., 2015), their genetic architecture suggest that they are sub-strains of rats from dissimilar sources (Zhang-James et al., 2013), with the ADHD-like phenotype of the SHR/NHsd rat indicating less consistency than that of the SHR/NCrl rat (Kantak, 2022). For example, the SHR/NHsd does not differ from control strains in hyperactivity (e.g., Ferguson and Cada, 2003), impulsiveness, and inattention (van den Bergh et al., 2006). Also, the SHR/NHsd's attention does not improve with methylphenidate and guanfacine (Jentsch, 2005), nor its impulsivity decreases with low doses of methylphenidate and d-amphetamine (i.e., Ferguson et al., 2007; Wooters and Bardo, 2011). In contrast, the SHR/NCrl rat shows more impulsive action (e.g., deficient performance on DRL schedules) and more compulsive behavior (e.g., consumes more water in situations inducing polydipsia) than the SHR/NHsd rat (e.g., Leffa et al., 2019; van der Kooij and Glennon, 2007; Wickens et al., 2011). Thus, studies questioning the predictive validity of the SHR as a model of ADHD should address the source accounting for phenotypic differences between SHR/NHsd and SHR/NCrl rats (Leffa et al., 2019; van der Kooij and Glennon, 2007; Wickens et al., 2011).

Research supporting the SHR as a suitable model of ADHD (Sagvolden, 2000) indicates that the SHR rat displays behaviors characterizing ADHD such as impulsivity (Fox et al., 2008), hyperactivity (Knardahl and Sagvolden, 1979), poor sustained attention (Diana, 2002), learning insufficiencies (Meneses and Hong, 1998), hypersensitivity to delayed consequences (Johansen et al., 2005), resistance to extinction (Brackney et al., 2012; Johansen and Sagvolden, 2004), and impulsive action (Orduña, 2015). While hyperactivity in the SHR is comparable to that displayed by children diagnosed with ADHD (Sagvolden et al., 1992), the experimental setting and control strain are crucial factors to assess the SHR's hyperactivity. For example, the SHR is more active in the eight-arm maze than the WKY rat. Yet, the SHR rat is less activity in the running wheel and open field than Sprague Dawley and WKY rats (Ferguson and Cada, 2003). Also, the SHR's activity decreases faster in open fields and home cages than the activity displayed by WIS and Sprague Dawley rats (Sagvolden et al., 1993). Still, the SHR makes more errors in operant tasks testing impulsivity than the WKY rat (Sagvolden, 2000; Sagvolden et al., 2005; Wiersema et al., 2005), it chooses more impulsively on delay discounting tasks than the WKY (Hand et al., 2009; Aparicio et al., 2019), and it produces greater burst of responses on a differential reinforcement of low rate (DRL) schedule than the WKY (Somkuwar et al., 2016). Regarding inattention, the SHR shows less accurate nose poking behavior in a five-choice serial reaction time test than the WKY (De Bruin et al., 2003), and it produces lower proportion of correct responses in a visual discrimination task than the WKY (Sagvolden, 2011). Thus, face validity in the SHR is not an issue, but it is difficult to explain why its predicted behavioral deviations sometimes do not occur (Regan et al., 2022). For example, studies that found no differences in impulsive choice between the SHR and WKY rat (Garcia and Kirkpatrick, 2013) claim that the WKY is not an appropriate control to the SHR (van den Bergh et al., 2006; Aslop, 2007). But research shows that the SHR chooses more impulsively than the WKY on discrete trials, multiple two-component concurrent-chains schedules, and concurrent-chains procedures (e.g., Adriani et al., 2003; Fox et al., 2008; Orduña, 2015;

Orduña and Mercado, 2017; Aparicio et al., 2019) supporting the WKY rat as an appropriate control to the SHR to examine impulsivity and cognitive deterioration characterizing ADHD (e.g., Adriani et al., 2003; Barkley and Peters, 2012; Russell, 2007; Sagvolden, 2000; Solanato et al., 2001; Sonuga-Barke et al., 1992; Sonuga-Barke, 2002). Hypertension, however, is not the only factor causing cognitive deterioration in the SHR rat (Diana, 2002). It experiences irregularities in glutamate, dopamine, and norepinephrine activities like those disturbing neural circuits controlling receptiveness in humans diagnosed with ADHD (Oades et al., 2005, Heal et al., 2008), and irregular activity of those neurotransmitters might cause differences between the SHR and WKY rats in the expression of genes connected to ADHD (DasBanerjee et al., 2008), warranting further research to determine the use of the WKY as a suitable control to the SHR.

Research on delay discounting has examined alternative models of ADHD like the Lewis (LEW) rat, an inbred derived from the source strain the WIS rat, and its control the Fischer 344 rat (e.g., Aparicio et al., 2015; 2013). Genetic differences between LEW and F344 rats are well documented in addictions to alcohol (Suzuki, George, and Meisch, 1988), nicotine (Brower et al., 2002), cocaine (Kosten et al., 1997), etonitazene (Suzuki et al., 1992), and morphine (Martin et al., 2003) showing that the self-administration of these substances is more readily in the LEW rat than in the F344 rat. This is important because impulsivity facilitates drug addiction and the LEW rat possess a phenotype highly susceptible to drug addiction (i.e., Garcia-Lecumberri et al., 2011), representing a genetic model of human drug abuse (Kosten and Ambrosio, 2002). Also, the LEW rat endures lower levels of dopamine (DA) and serotonin (5-HT) activity in the brain than the F344 rat (Burnet et al., 1996), accounting for differences in impulsive choice between the LEW rat and the F344 rat. However, the length of training is a crucial factor to assess when looking for differences in impulsive choice between LEW and F344 rats. In studies on delay discounting where the amount of the larger-later food (LLF) and the delay to obtain it remained constant for a minimum ten baseline sessions, LEW rats produced steeper discounting functions than F344 rats (Anderson and Diller, 2010; Anderson and Woolverton, 2005; Huskinson et al., 2012; Madden et al., 2008). However, studies that used a maximum of five sessions to vary the amount of the LLF and the delay to it found no differences in impulsive choice between LEW and F344 rats (Stein et al., 2012; Wilhelm and Mitchell, 2009). Later research using concurrent-chains procedures to vary the delay to the LLF in the session found no differences in discounting rate between LEW and F344 rats (Aparicio et al., 2013), the F344 developed patterns of impulsive choice like those developed by the LEW, indicating that the F344 rat required more sessions of training to detect dynamic changes in the delay to obtain the LLF than the LEW rat (Aparicio et al., 2013). Also, the impulsive choices made by LEW and F344 rats were differentially affected by the order in which the delay to the LLF presented in the session (i.e., ascending, descending, or random order), with both strains producing the steepest discounting functions with delays to LLF presented in random order. These studies showed that initial differences in discounting rate between LEW and F344 rats decrease with extended training in the choice situation, indicating that impulsivity is not a static property of behavior only governed by genetic and neurochemical mechanisms, impulsivity in rats increases with their experience in the choice situation (Aparicio et al., 2013; 2015; 2019).

The aim of the present study was to compare the performance of the SHR rat on a delay discounting task with that of the LEW rat to propose that both strains are potential models of ADHD. One objective was to examine Grosch's and Neuringer notion (1981) that impulsivity decreases in situations where the organism can engage in an activity (e.g., drinking water) during the delay to get the LLF. Another objective was to show that drinking water excessively, initially called polydipsia (Falk, 1961; 1966; 1969) and later schedule-induced drinking (e.g., Ruiz et al., 2016; Wetherington, 1979), does not cause discounting rate to increase (Íbias and Pellón, 2011) questioning a positive relation between polydipsia and discounting rate (Íbias and Pellón, 2014). These objectives are important because compulsive behaviors like polydipsia and impulsivity are linked to irregularities of DA activity in the SHR rat (e.g., Leffa et al., 2019; van der Kooij and Glennon, 2007; Wickens et al., 2011), and the LEW rat also endures irregular activity of DA and 5-HT linked symptoms of ADHD such as inattention, hyperactivity, and impulsivity. Lastly, the present study used a 4-parameter logistic (4PL) nonlinear regression model (Elcoro et al., 2016; Aparicio et al., 2020; 2022) fitting discounting rates produced, milliliters of water consumed, and licks emitted by the rats to the spout of the bottle across blocks of sessions of water conditions.

$$y = \frac{A_1 - A_2}{1 + \left(\frac{x}{x_0}\right)^p} + A_2. \qquad (2)$$

Where y is the dependent variable, A_1 its minimum asymptote or initial value, A_2 its maximum asymptote or final value, p is the power or slope of the curve, x_0 is the inflection point where the curvature changes direction, and x is the independent variable.

Method

Subjects

Sixteen experimental naïve SHR (n = 8) and LEW (n = 8) male rats (Charles River, Wilmington, MA), between 90-120 days old at the start of training, were the subjects. Animals were placed on an ad-libitum feeding regimen of Purina Lab Chow to allow habituation to the laboratory. On the day before training the feeders of all cages were emptied and the rats were placed on a regimen of food restriction, but there were no attempts to reduce their weights. The rats were fed with 10 g (+/- 2 g) of Purina Chow (Mazuri®) twenty minutes after the end of each session, such that the weights of the SHR and LEW rats at the start of the training ranged from 241 to 286 g (M = 260 g) and from 262 to 298 g (M = 283 g), respectively, and at the end of the study their weights ranged from 294 to 386 g (M = 351 g) and from 392 to 417 g (M = 406 g), respectively. Between sessions, the rats were individually housed in plastic cages, measuring 45 cm x 24 cm x 20 cm, with water permanently available in a temperature-controlled colony room (68º to 72º F) preserving a 12:12h light/dark cycle (lights on at 07:00). Sessions were conducted daily at same time (12:00 PM). Salem State University's Institutional Animal Care and Use of Laboratory Animals (IACUC) approved the research protocol (IACUC 011817-2) according to guidelines of NIH (No. 8023); a veterinary (DVM, MS, DACLAM) supervised the health of the rats. The present research had no conflict of interest, nor did it receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

Apparatus

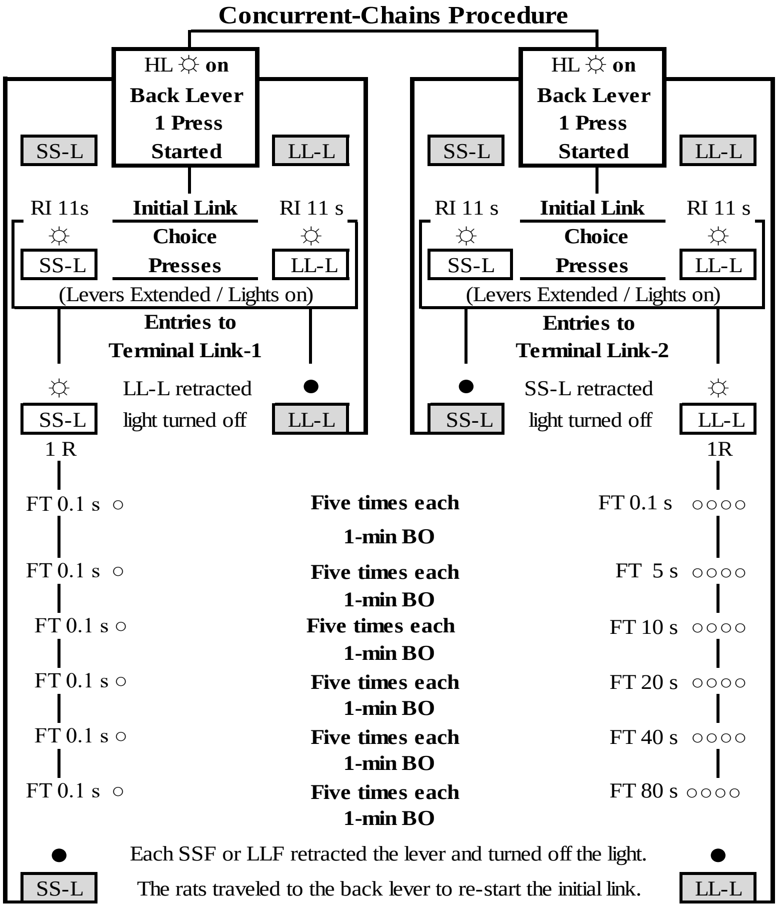
Eight modular chambers for rats (Colbourn Instruments®), each measuring 30 cm x 33 cm x 25 cm, were enclosed in isolation cubicles that from the outside measured 79 cm x 53 cm x 51 cm. The sidewalls of each chamber were of Plexiglas and front and rear walls of stainless steel. The floor of each chamber was a square metal grid. Two retractable levers 3.3 cm x 1.5 cm were located on the front wall of each chamber 6 cm above the floor, the edge of each lever was 2.5 cm from its respective left and right sidewalls. The extension and retraction mechanisms of the levers took approximately 0.1 s. A 24-V DC stimulus light was positioned 3.5 cm above each retractable lever. A food dispenser positioned behind the front wall of each chamber delivered 45-mg grain-based pellets (BioServ®, F0165) into a food cup, 3 cm x 4 cm, centered between the left and right retractable levers 2 cm from the floor, 4.5 cm from the left lever, and 4.5 cm from the right lever. A third nonretractable lever was centered on the rear wall of each chamber 6 cm above the floor. All levers required a force of 0.2 N to operate. One 24-V DC house light, centered on the rear wall 19 cm above the nonretractable lever and 2 cm below the ceiling, provided the illumination of the chamber. A photo-operandum buffer attached to a hopper located on the rear wall of each chamber, 2.6 cm above the floor and 7 cm from the center of the nonretractable lever, recorded licks (contacts) to the metal spout of a bottle containing 100 ml of tap water. A white noise generator connected to a 2.6 cm x 4.0 cm speaker placed on the rear wall of each chamber, at 20 cm from the floor, 1 cm from the left sidewall, and 1 cm below the ceiling, provided a constant white noise at 20 kHz (+/- 3 dB). Two computers each linked to four chambers using Habitest Lincs, delivered the stimuli and recorded the data executing Colbourn Instruments® software (Graphic State Notation, V 3.03) operating at a 0.01-s resolution.

Procedure

Training. An auto-shaping procedure developed in our laboratory (Aparicio et al., 2020) trained the rats to press on the levers. It consisted of two variable time 50 s schedules operating concurrently (Conc VT 50 s VT 50 s) to arrange sixty trials, thirty trials with the left lever and thirty trials with the right lever. Each trial started by extending one lever (the left lever, or right lever) into the chamber and turning on the light above it, the opposite lever remained retracted from the chamber with the light above it turned off. Trials lasted 15 s each regardless of whether the rat pressed on the extended lever, lever presses during the 15 s did not end the trial, nor did lever presses produce food immediately. At the end of 15-s trial, one food-pellet was delivered into the food cup, the lever was retracted from the chamber, and the light above it turned off to start an inter-trial interval ($M = 50$ s, range 2 to 120 s) set up by a constant-probability algorithm (Catania and Reynolds, 1968). During the inter-trial interval, the program randomly selected the same left lever, or the other right lever to be extended into the chamber for the next 15-s trial. A nonretractable lever was continually available in the rear wall of the chamber with no scheduled consequences but presses on it were recorded in the session. Sessions lasted 60 minutes each, or ended after 60 trials occurred, whichever occurred first. The procedure remained on effect until all rats pressed consistently the levers in all sixty trials.

General Procedure. It was a concurrent chains-procedure (Aparicio et al., 2015; 2019). The session started with the house light illuminated, the front levers retracted from the chamber, and the lights above them turned off (see Figure 1). One press on the back-nonretractable lever turned off the house light, extended two front levers into the chamber, and turned on the lights above the levers starting the initial link. Two non-independent random interval (RI) schedules averaging 11 s each, one linked to the left lever or SS-lever, and the other linked to right lever or LL-lever, operated concurrently in the initial link (conc RI 11 s RI 11 s) arranging entries to two terminal links, one to deliver 1-food pellet (the SSF) and the other terminal link to deliver 4-food pellets (the LLF). The random intervals were generated by a probability generator set to .05 and queried every second. Choice was measured in the initial link with the distribution of presses on the levers (Grace, 1999), and the RI schedules arranging an equal number of terminal link entries keeping constant the relative rate of reinforcement (i.e., Stubbs and Pliskoff, 1969). When the RI schedule linked to the SS-lever arranged a terminal-link entry, one press on the SS-lever started one terminal link retracting the LL-lever from the chamber and turning off the light above it. Another press on the SS-lever started a 0.1-s fixed time (FT 0.1 s) to deliver 1-food pellet. Food delivery (SSF) retracted the SS-lever from the chamber and turned off the light above it. The rat moved from the front wall to the back wall of the chamber to press the back-nonretractable lever re-starting the initial link. Once the RI linked to the LL-lever arranged a terminal link entry, one press on the LL-lever started the other terminal link retracting the SS-lever from the chamber and turning off the light above it. Another press on the LL-lever started the FT (0.1, 5, 10, 20, 40, or 80 s) delaying the delivery of 4-food pellets (i.e., the LLF). The FT was selected from a list and presented in random order during the session. The LL-lever was not retracted from the chamber during the FT to prevent its retraction to signal the delay to the LLF, presses on the extended LL-lever during the FT, or at the end of it, had no scheduled consequences. The delivery of the LLF retracted the LL-lever from the chamber and turned off the light above it. Again, the rat moved to the back wall of the chamber to press the back-nonretractable lever re-starting the initial link. Pressing on the nonretractable lever during the initial link, or pressing on it during the terminal link, had no scheduled consequences. To prevent the rats' bias for one lever over the other lever, for four rats of each strain the left lever was the LL-lever and the right lever the SS-lever. These conditions were reversed for the other four rats of each strain, the left lever was the SS-lever and the right lever the LL-lever. After ten food deliveries, 5-SSF with the SS-lever and 5-LLF with the LL-lever, a 1-min blackout started with all lights turned off and both levers retracted from the chamber. At the end of the blackout, the procedure selected a different FT to delivery another 5-LLF with the LL-lever and 5-SSF with the SS-lever using the same FT 0.1 s. The house light was illuminated, the front levers retracted from the chamber, the lights above them turned off, and the above procedure was repeated for another ten food deliveries. The session ended when the rats obtained sixty foods, thirty SSF in one terminal link using the same FT 0.1 s and thirty LLF in the other terminal link using six FT schedules to delay the LLF, or it ended when 60 min elapsed, whichever happened first. Most sessions, however, ended with the rats obtaining all sixty foods.

Experimental design. An *ABABA* reversal design manipulated the availability of a bottle with water for the rats to drink during the session, where A was a no water condition (A_1, A_2, and A_3), and B was a water condition (B_1 and B_2). In condition A the bottle with the water, the photo-operandum buffer, and the hopper attached to it were removed from the chamber. In condition B the bottle contained 100 ml of tap water, the photo-operandum buffer, and the hopper attached to it were accessible in the chamber for the rat to drink water during the session. At the end of each session, the bottle was removed from the chamber to measure the volume of water consumed by the rat in the session, computing the difference between 100 ml of water at the beginning of the session and the volume (ml) of water remaining in the bottle at the end of the session. Condition A_1 was studied for 180 consecutive sessions allowing discounting rate to reach asymptotic value showing no increasing or decreasing trend. Conditions B_1, A_2, B_2, and A_3 lasted sixty sessions each that were enough for discounting rate to show stability (no increasing or decreasing trend).



Note. Blackout (BO), 1-food pellet ○, 4-food pellets ○○○○ (45 mg each).

Figure 1. Concurrent-chains procedure. One press on the back-nonretractable lever turned off the house light, extended two front levers into the chamber, and turned on the lights above the levers starting the initial link. Choice was measured in the initial link with presses on two levers (SS-L and LL-L) linked to non-independent random interval schedules (conc RI 11 s RI 11 s) arranging entries to two terminal links, one delivered 1-food pellet (SSF) after a 0.1-s delay and the other 4-food pellets (LLF) after a delay of 0.1, 5, 10, 20, 40, or 80 s presented in random order in the session. Each food (SSF or LLF) retracted the active lever from the chamber and turned off the light above it. The rat traveled to the back lever to press on it re-starting the initial link. After ten foods, 5-SSF and 5-LLF, both levers were retracted from the chamber starting a 1-min blackout (BO). At the end of the BO another delay to the LLF was selected. The rat pressed the back lever to start the initial link arranging another ten foods in the terminal links.

Data analysis

The data from all sessions of each condition were grouped in blocks of fifteen sessions each and analyzed. The data were sorted and separated by delay component counting the total number of presses (responses) on the SS-lever and LL-lever emitted by the rats in the initial link. With the computations obtained with fifteen session of each block, medians of responses on the SS-lever and LL-lever were computed for individuals of the same strain and the group of rats. Medians of responses were computed for each block of sessions instead of means of responses, because the data in delay discounting are not normally distributed (Myerson & Green, 1995). For each rat and the group of rats, the medians of responses were used to compute proportions of LL choice ((LL-responses / (LL-responses + SS-responses)). Eq. 1 provided nonlinear curve fitting to proportions of LL choice where the parameter A was free to vary (A was not assumed to be 1.0 LL choice at the y-intercept). For sessions of condition B, the number of licks emitted by each rat to the spout of the bottle were recorded and averaged across rats of the same strain computing the mean of licks emitted by each group of rats. The least-squares method generated fitting lines to licks during blackouts, licks before starting the initial link, licks in the initial link, and licks in the terminal link. Eq. 2 provided nonlinear curve fitting to changes in estimates of *A* and *k* from Eq. 1, and it fitted changes in the milliliters of water consumed by the rats and their licks to the spout of the bottle that occurred with increasing sessions of condition B. Because normality and equal error variance, two main requirements of the analysis of variance, were not fulfilled and the small size of the samples did not allow for confident assertions of the main assumptions, nonparametric Wilcoxon-paired test examined differences in discounting rate and licks emitted to the spout of the bottle between the SHR and LEW rats. Origin® provided curvilinear fitting, linear fitting, and nonparametric tests at the alpha level of 0.05.

Results

The first analysis focused on the acquisition of impulsive choice. Figure 2 shows the discounting functions produced by the SHR and LEW rats in the baseline-no-water condition A_1, with proportions of LL choice plotted as a function of the delay in seconds to obtain the LLF. The top, middle, and bottom rows of graphs show proportions of LL choice computed in blocks of sessions 1 to 4, 5 to 8, and 9 to 12 representing early, intermediate, and advanced stages of training. The left column shows medians of proportions of LL choice computed for the group (LEW squares and SHR circles), and the central and right columns show with multiple symbols proportions of LL choice produced by individual SHR and LEW rats, respectively. The graphs show discounting functions with hyperbolic shape. All rats made impulsive choices producing proportions of LL choice decreasing with the increasing delay to the LLF, showing that their preference for the LLF switched to the SSF. Eq. 1 suitable fitted group proportions of LL choice produced by the SHR and LEW rats in blocks of sessions 1 to 4 ($R^2 = .990$ and .975), 5 to 8 ($R^2 = .973$ and .993), and 9 to 12 ($R^2 = .955$ and .993). The discounting functions produced by the group of SHR rats show estimates of *A* (.612, .697, and .730) comparable those computed for the discounting functions produced by the group of LEW rats (.651, .697, and .688), indicating that both strains developed similar levels of sensitivity to the magnitude of the LLF in condition A_1. Blocks 1 to 4 show a discounting rate estimated for the group of SHR rats ($k = .010$) comparable to that estimated for the group of LEW rats ($k = .009$), indicating that both strains of rats made similar impulsive choices early in training. In blocks 5 to 8 the discounting rate estimated for the group of SHR rats ($k = .036$) was greater than that estimated for the group of the LEW rats ($k = .014$). The SHR and LEW rats produced the highest discounting rates in blocks 9 to 12, but the discounting rate estimated for the group of SHRs ($k = .037$) was greater than that estimated for the group of LEWs ($k = 0.15$). Table 1 shows resulting parameters from Eq. 1 fitting proportions of LL choice produced by individual SHR and LEW rats. Eq.1 fitted proportions of LL choice produced by individual SHR and LEW rats well in blocks of sessions 1 to 4, 5 to 8, and 9 to 12. Estimates of R^2 show medians of .945, .929, and .972 for the discounting functions produced by the SHR rats, and medians of .857, .953, and .924 for the discounting functions produced by the LEW rats. Estimates of *A* for the discounting functions produced by individual SHR rats in blocks 1 to 4 (Mdn = .636, range from .405 to .819) are like ($W = 14$, $p = .624$) those for the discounting functions produced by individual LEW rats (Mdn = .630, range from .447 to .865). Also, estimates of *A* for the discounting functions produced by the individual SHR rats in blocks 5 to 8 (Mdn = .640, range from .550 to .945) are equivalent ($W = 21$, $p = .726$) to estimates of *A* for the discounting functions produced by the individual LEW rats (Mdn = .666, range .559 to .947). Consistently, estimates of *A* for the discounting functions produced by the individual SHR rats in blocks 9 to 12 (Mdn = .737, range from .544 to .979) are comparable ($W = 23$, $p = .529$) to estimates of *A* for the discounting functions produced by the individual LEW rats (Mdn = .662, range from .539 to .902). The discounting rates produced by the individual SHR rats in blocks 1 to 4 (Mdn = .011, range .004 to .018) are like (W = 19, p = .472) the discounting rates produced by the individual LEW rats (Mdn = .009, range .005 to .023). But the discounting rates produced by the individual SHR rats in blocks 5 to 8 (Mdn = .031, range from .018 to .043) are greater (W = 33, p = .021) than the discounting rates produced by the individual LEW rats (Mdn = .012, range from .005 to .042). Equally, the discounting rates produced by the individual SHR rats in blocks 9 to 12 (Mdn = .037, range from .017 to .053) are greater (W = 31, p = .040) than the discounting rates produced by the individual LEW rats (Mdn = .015 range from .006 to .058).

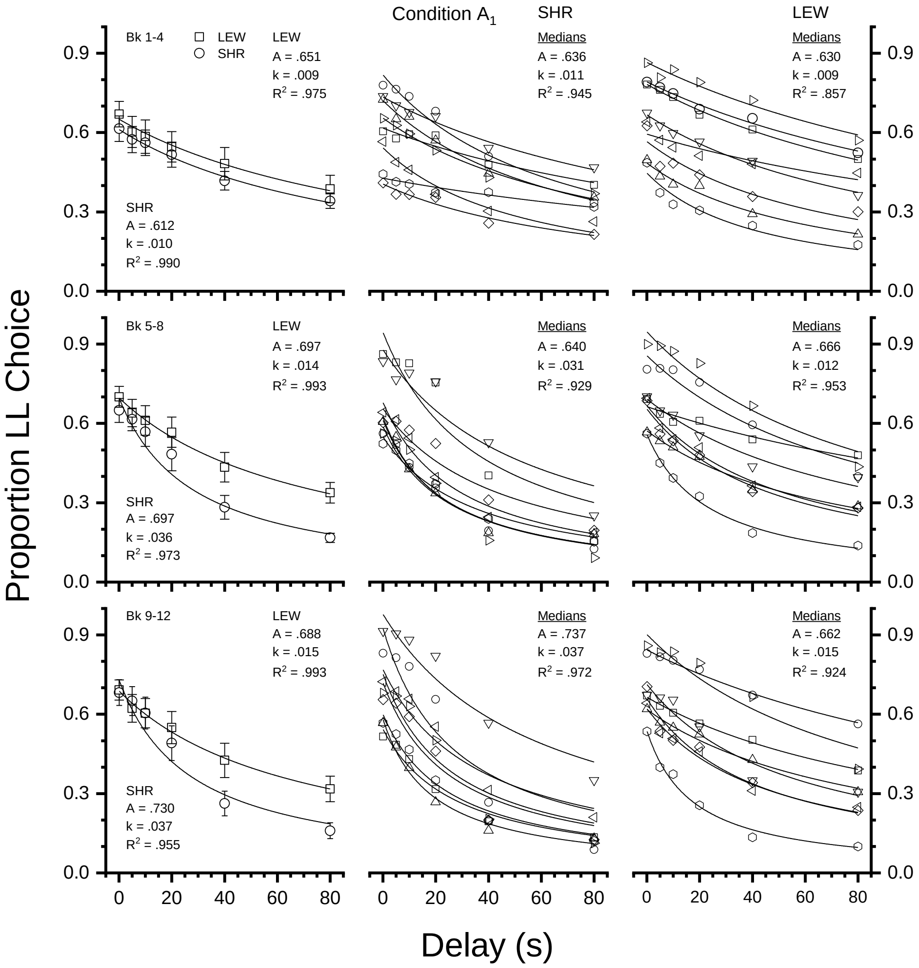


Figure 2. Discounting functions produced by the SHR and LEW in baseline-no-water condition A_1. Proportions of LL choice produced in blocks of sessions 1 to 4 (Bk 1-4), 5 to 8 (Bk 5-8), and 9 to 12 (Bk 9-12) are plotted as a function of the delay in seconds to obtain the LLF. The left column of graphs shows medians of proportions of LL choice computed for the group (LEWs squares and SHRs circles). Estimates of *A*, *k*, and R^2 appear near to lines of best fit from Eq. 1. The central and right columns of graphs show proportions of LL choice produced by individual SHR and LEW rats (multiple symbols), respectively, and the medians of empirical parameters *A, k,* and R^2 from fits of Eq. 1 to proportions of LL choice produced by the individuals.

Table 1.

Hyperbolic-decay model, resulting parameters (condition A_1).

		A		k		R^2	
Blocks	Rat	SHR	LEW	SHR	LEW	SHR	LEW
1-4	1	0.617	0.792	0.006	0.006	0.899	0.983
	2	0.819	0.783	0.015	0.007	0.951	0.992
	3	0.721	0.485	0.014	0.015	0.977	0.964
	4	0.735	0.667	0.007	0.010	0.971	0.988
	5	0.405	0.566	0.012	0.014	0.938	0.840
	6	0.543	0.594	0.018	0.005	0.935	0.779
	7	0.655	0.865	0.011	0.006	0.978	0.945
	8	0.428	0.447	0.004	0.023	0.893	0.910
	Median	**0.636**	**0.631**	**0.011**	**0.009**	**0.945**	**0.954**
5-8	1	0.589	0.664	0.039	0.005	0.970	0.917
	2	0.945	0.856	0.027	0.011	0.834	0.913
	3	0.624	0.572	0.043	0.013	0.959	0.973
	4	0.879	0.692	0.018	0.011	0.850	0.950
	5	0.656	0.655	0.022	0.020	0.899	0.956
	6	0.680	0.668	0.034	0.019	0.962	0.964
	7	0.614	0.947	0.041	0.011	0.896	0.928
	8	0.550	0.559	0.028	0.042	0.974	0.988
	Median	**0.640**	**0.666**	**0.031**	**0.012**	**0.929**	**0.953**
9-12	1	0.544	0.665	0.036	0.009	0.969	0.994
	2	0.926	0.843	0.037	0.006	0.830	0.987
	3	0.582	0.618	0.053	0.012	0.984	0.981
	4	0.979	0.713	0.017	0.018	0.914	0.915
	5	0.720	0.659	0.038	0.024	0.894	0.934
	6	0.770	0.621	0.027	0.021	0.935	0.964
	7	0.753	0.902	0.037	0.011	0.865	0.886
	8	0.601	0.539	0.039	0.058	0.963	0.980
	Median	**0.737**	**0.662**	**0.037**	**0.015**	**0.924**	**0.972**

The next analysis capitalized on results indicating that discounting rate (*k*) and sensitivity of choice to the magnitude of the LLF (*A*) increased with increasing block of sessions. Figure 3 shows values of *K* (top row) and *A* (bottom row) plotted against 12 blocks of fifteen days each. The open symbols are estimates of *K* and *A* for the individuals, and the filled circles (SHR) and squares (LEW) the mean values of *K* and *A* computed for the group of rats. The upper-left graph shows discounting rates produced by the group of SHRs increasing from .005 in block one to .035 in block twelve, and the upper-right graph shows discounting rates produced by the group of LEWs increasing from .008 to .024, respectively. Eq. 2 fitted the discounting rates produced by the SHR (R^2 = .988) and LEW rats (R^2 = .943) well, showing that discounting rates increased hyperbolically with increasing block of sessions. The estimate of the starting point for the curve fitting discounting rates produced by the LEWs (A_1 = .008) is greater than that corresponding to the curve fitting discounting rates produced by the SHRs (A_1 = .004), indicating that LEWs made more impulsive choices early in training than SHRs. But the estimate of the ending point for the curve fitting the discounting rates produced by the LEWs (A_2 = .018) is smaller than that for the curve fitting the discounting rates produced by the SHRs (A_2 = .036), indicating that the SHRs made more impulsive choices late in training than the LEWs. The inflection points of the curves indicate that the LEWs' discounting rates moved to asymptotic level sooner (x_0 = 3.08) than the SHRs' discounting rates (x_0 = 3.61). But the slope of curve fitting the LEWs' discounting rates (*p* = 4.65) is steeper than the slope of the curve fitting the SHRs' discounting rates (*p* = 4.51), indicating that discounting rates increased faster in the former than in the latter strain of rats. Empirical parameters from Eq. 2 fitting discounting rates produced by the individuals indicated no differences between the SHR and LEW rats in estimates of A_1 (W = 12, p = .441), A_2 (W = 28, p = .183), x_0 (W = 13, p = .528), and *p* (W = 6, p = .107).

The lower-left graph shows estimates of sensitivity of choice to the magnitude of the LL food (*A* in Eq. 1) for the discounting functions produced by the group of SHR rats increasing from .569 in block one to .741 in block twelve, and the lower-right graph shows estimates for the discounting functions produced by the group of LEWs increasing from .537 to .711, respectively. Eq. 2 fitted these data well ($R^2 = .953$ and .941, respectively) accounting for changes in estimates of *A* that occurred with increasing block of sessions. The curve fitting estimates for the LEW rats has a starting point ($A_1 = .535$) higher than that of the curve fitting estimates for the SHR rats ($A_1 = .502$), indicating that the LEWs' choices showed more sensitivity to the magnitude of the LLF early in training than the SHRs' choices. Yet, the ending point of the curve fitting estimates for the SHRs ($A_2 = .859$) is greater than that of the curve fitting estimates for the LEWs ($A_2 = .701$), indicating that the SHRs' choices showed more sensitivity to the magnitude of the LLF late in training than the LEWs' choices. Sensitivity of choice to the magnitude of the LLF moved to asymptotic level sooner in the LEWs ($x_0 = 1.79$) than in the SHRs ($x_0 = 5.27$), and it increased faster in the LEWs (p = 8.32) than in the SHRs (p = 0.90). Eq. 2 fitted estimates of *A* for the discounting functions produced by the individuals showing no differences between the SHR and LEW rats in parameters A_1 (W = 21, p = .726), A_2 (W = 19, p = .944), and *p* (W = 19, p = .944). However, the inflexion points (x_0) of the curves fitting estimates of *A* for the SHRs (*Mdn* = 5.92, range from 3.65 to 8.75) were greater (*W* = 36, p = .014) than the inflection points of the curves fitting estimates of *A* for the LEWs (*Mdn* = 1.81, range .001 to 3.36), confirming that sensitivity to the magnitude of the LLF moved to asymptotic level sooner in the LEW than in the SHR rats.

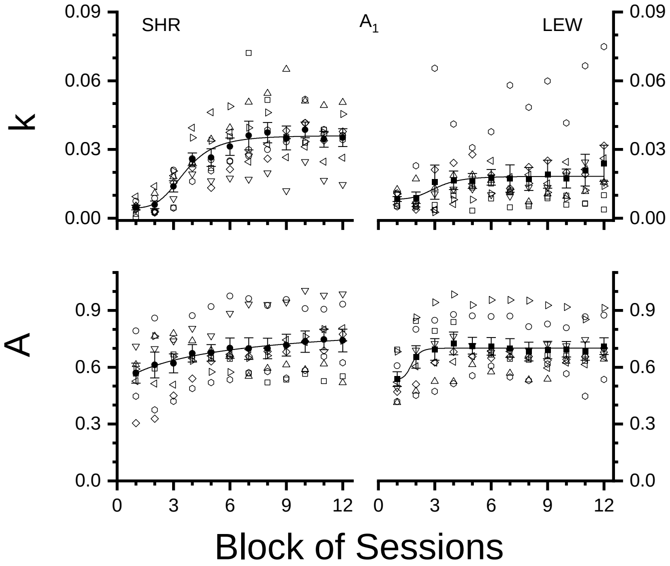


Figure 3. Estimates of discounting rate (*k*) and sensitivity of choice to the magnitude of the LLF (*A*) for discounting functions produced by the SHR (left graphs) and LEW rats (right graphs) in condition A_1 plotted against blocks of sessions. The open symbols are estimates of *K* and *A* for the discounting functions produced by the individuals, and the filled circles (SHR) and squares (LEW) the mean values of K and A computed for the group of rats. The line is the best fit from Eq. 2 to estimates of *k* and *A*.

The next analysis looked at the discounting functions produced by SHR and LEW rats in postbaseline conditions differing from one another in whether a bottle containing 100 ml of plain water was available in the choice situation for the rats to drink during the session (conditions B_1 and B_2), or it was not available at all (conditions A_2 and A_3). Figure 4 shows group proportions of LL choice produced by the SHR (circles), and LEW (squares) rats plotted as a function of the delay in seconds to the LLF. The graphs show discounting functions with hyperbolic shape, the SHR and LEW rats produced proportions of LL choice decreasing as a function of the increasing delay to the LLF. Within a condition and among conditions, the discounting functions produced by the SHR rats have slopes steeper than the slopes of the discounting functions produced by the LEW rats. All graphs show estimates of discounting rate for the impulsive choices made by the SHRs rats (k_{SHR}) with values greater than those corresponding to impulsive choices made by the LEWs (k_{LEW}), confirming that the group of SHR rats discounted the LLF steeper than the group of the LEW rats. Table 2 shows parameters from Eq. 1 fitting group proportions of LL choice. Estimates of R^2 for the discounting functions produced by the LEW rats in conditions B_1 (*Mdn* = .988), A_2 (*Mdn* = .983), B_2 (Mdn = .984), and A_3 (*Mdn* = .976) have values greater than those corresponding to R^2 for the discounting functions produced by the SHR rats (*Mdn* = .937, .944, .973, and .962, respectively). Estimates of sensitivity of choice to the magnitude of the LLF (*A*) for the discounting functions produced by the SHRs (*Mdn* = .708 and .723) and LEWs (*Mdn* = .706 and .681) in conditions B_1 and B_2, have values smaller than estimates corresponding to the discounting functions produced by the SHRs (*Mdn* = .754 and .727) and LEWs (*Mdn* = .737 and .682) in conditions A_2 and A_3, suggesting that sensitivity of their choices to the magnitude of the LLF was greater when the water was not available in the choice situation (A_2 and A_3) than when it was available (B_1 and B_2). Discounting rates produced by the SHRs in conditions B_1 and B_2 (*Mdn* = .034 and .028) have values smaller than discounting rates produced conditions A_2 and A_3 (Mdn = .042 and .033), indicating that the SHRs made more impulsive choices when the water was not available in the choice situation (A_2 and A_3) than when it was available (B_1 and B_2). In contrast, discounting rates produced by the LEWs in conditions B_1 and B_2 (*Mdn* = .017 and .016) were equivalent to discounting rates produced in condition A_2 (Mdn = .015). However, the LEWs produced the highest discounting rates (Mdn = .022) in condition A_3 showing that their impulsive choices increased in the last no water condition.

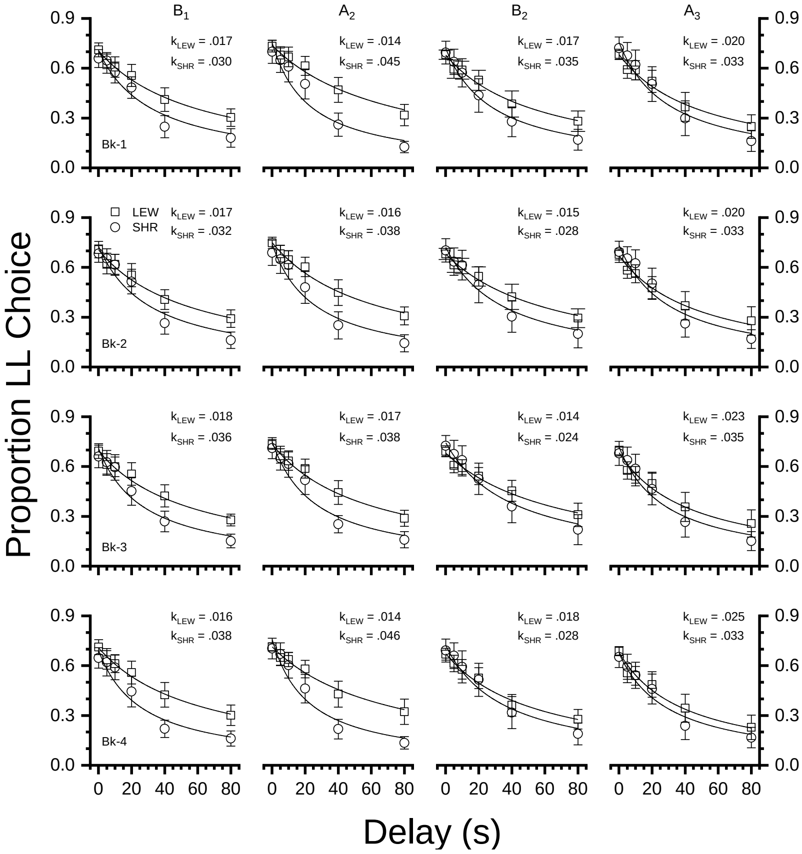


Figure 4. Discounting functions produced by SHR and LEW rats in postbaseline conditions with water available to drink (conditions B_1 and B_2), or not available at all (conditions A_2 and A_3). It shows mean proportions of LL choice produced by the group of SHR rats (circles) and LEW rats (squares) in blocks of sessions 1 to 4 (Bk-1, Bk-2, Bk-3, and Bk-4) plotted as a function of the delay in seconds to the LLF. Estimates of discounting rate (*k*) from fits of Eq. 1 to proportions of LL choice produced by the group of SHRs (k_{SHR}) and LEWs (k_{LEW}) appear near to fitting lines.

Table 2.

Hyperbolic-decay model, resulting parameters for post-baseline conditions.

		A		*k*		R^2	
Cond.	Block	SHR	LEW	SHR	LEW	SHR	LEW
B_1	1	0.707	0.706	0.030	0.017	0.938	0.989
	2	0.728	0.706	0.032	0.017	0.935	0.986
	3	0.710	0.695	0.036	0.018	0.958	0.987
	4	0.692	0.708	0.038	0.016	0.934	0.990
	Median	**0.708**	**0.706**	**0.034**	**0.017**	**0.937**	**0.988**
A_2	1	0.755	0.740	0.045	0.014	0.943	0.973
	2	0.741	0.750	0.038	0.016	0.944	0.986
	3	0.752	0.735	0.038	0.017	0.945	0.985
	4	0.760	0.714	0.046	0.014	0.948	0.980
	Median	**0.754**	**0.737**	**0.042**	**0.015**	**0.944**	**0.983**
B_2	1	0.721	0.680	0.035	0.017	0.983	0.984
	2	0.723	0.681	0.028	0.015	0.971	0.984
	3	0.745	0.681	0.024	0.014	0.976	0.971
	4	0.723	0.673	0.028	0.018	0.968	0.986
	Median	**0.723**	**0.681**	**0.028**	**0.016**	**0.973**	**0.984**
A_3	1	0.757	0.682	0.033	0.020	0.962	0.977
	2	0.735	0.671	0.033	0.020	0.946	0.982
	3	0.719	0.685	0.035	0.023	0.961	0.970
	4	0.676	0.682	0.033	0.025	0.965	0.974
	Median	**0.727**	**0.682**	**0.033**	**0.022**	**0.962**	**0.976**

Figure 5 shows the discounting rates produced by the SHR (left graphs) and LEW (right graphs) rats in postbaseline conditions plotted against 4 blocks of sessions. The open symbols are discounting rates produced by the individuals, and the filled circles (SHR) and squares (LEW) are mean values of K computed for each group of rats. It includes computations of discounting rates for the last 4 blocks of condition A_1 to allow comparisons with computations of discounting rates for 4 blocks of each postbaseline condition B_1, A_2, B_2, and A_3. Discounting rates produced by the SHR rats were greater than those produced by the LEW rats in conditions A_1 ($W = 445$, $p < .001$), B_1 ($W = 407$, $p = .004$), A_2 ($W = 459$, $p < .001$), and B_2 ($W = 279$, $p = .042$). Nonetheless, discounting rates produced by the SHR rats in condition A_3 (Mdn = .043, range from .009 to .012) were like those ($W = 183$, $p = .657$) produced by the LEW rats (Mdn = .032, range from 0 to .138).

Further comparisons of the discounting rates produced by the SHR rats among conditions indicated that: (1) Discounting rates in condition A_1 (Mdn = .036, range from .012 to .065) were like ($W = 232$, $p = .556$) discounting rates in condition B_1 (Mdn = .039, range from .007 to .114), as well as, discounting rates in condition A_1 were comparable to discounting rates ($W = 173$, $p = .501$) in condition B_2 (Mdn = .036, range from .003 to .108). (2) Discounting rates in condition A_2 (Mdn = .040, range from .009 to .139) were greater ($W = 382$, $p = .028$) than discounting rates in condition B_1; (3) Discounting rates in condition B_2 were equivalent ($W = 224$, $p = .649$) to discounting rates in condition A_2; (4) Discounting rates in condition A_3 (Mdn = .043, range from .009 to .116) were greater ($W = 301$, $p = .026$) than discounting rates in condition B_1. (5) Discounting rates in condition B_2 were like ($W = 242$, $p = .381$) discounting rates in condition A_3; (6) Discounting rates in condition A_1 were greater ($W = 134$, $p = .015$) than discounting rate in condition A_2. (7) Discounting rates in condition A_3 were comparable to discounting rates in conditions A_1 ($W = 125$, $p = .078$) and A_2 ($W = 201$, $p = .973$); And (8) Discounting rates in condition B_1 were like ($W = 189$, $p = .762$) discounting rates in condition B_2.

Comparisons of discounting rates produced by the LEW rats among conditions showed that: (1) Discounting rates in condition A_1 (*Mdn* = .015, range from .004 to .075) were greater (*W* = 133, *p* = .015) than discounting rates in condition B_1 (*Mdn* = .014, range from .005 to .091); (2) Discounting rates in condition B_2 (*Mdn* = .016, range from .001 to .075) were equivalent (*W* = 195, *p* = .200) to discounting rates in condition A_1; (3) Discounting rates in condition A_2 (*Mdn* = .018, range from .003 to .047) were like discounting rates in conditions B_1 (*W* = 254, *p* = .859) and B_2 (*W* = 195, *p* = .200); (4) Discounting rates in condition A_3 (*Mdn* = .025, range from 0 to .138) were greater than discounting rates in conditions B_1 (*W* = 413, *p* = .005) and B_2 (W = 451, p < .001); (5) Discounting rates in condition A_1 were like (*W* = 228, *p* = .500) discounting rates in condition A_2; (6) Discounting rates in condition A_3 were greater than discounting rates in conditions A_1 (*W* = 85, *p* < .001) and A_2 (*W* = 77, *p* < .001); And (7) discounting rates in condition B_1 were equivalent (*W* = 212, *p* = .331) to discounting rates in condition B_2.

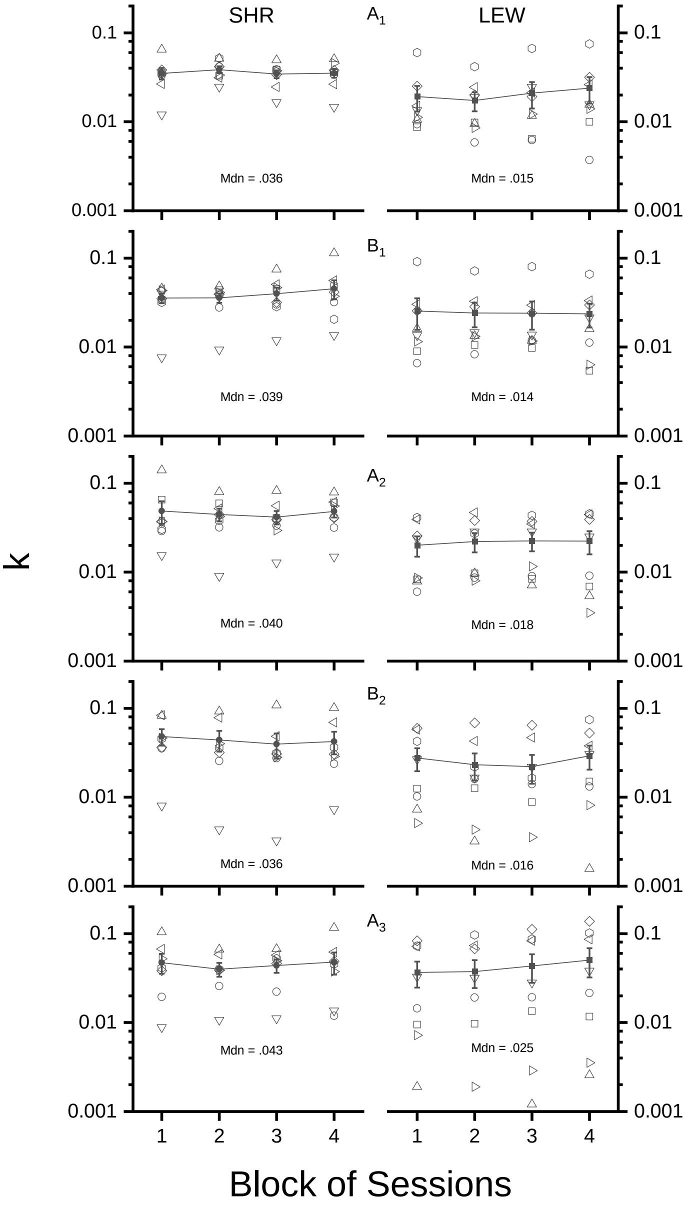


Figure 5. Discounting rates produced by the SHR (left graphs) and LEW (right graphs) rats in postbaseline conditions plotted against blocks of sessions. The open symbols are discounting rates (*k* values) produced by the individuals, and the filled circles (SHR) and squares (LEW) are mean values of *k* computed for each group of rats. Discounting rates produced in the last four blocks

of condition A_1 (upper graphs) are included allowing comparisons with discounting rates produced in four blocks of each postbaseline condition B_1, A_2, B_2, and A_3. Medians of *k* from fits of Eq.1 to proportions of LL choice produced by the individuals appear below the data points. Note logarithmic scale base-10 on the y-axis.

Figure 6 shows milliliters of the water consumed (top graphs), and licks emitted (bottom graphs) by the group of SHR rats (circles) and the group of LEW rats (squares) plotted against sessions of conditions B_1 (left graphs) and B_2 (right graphs). The milliliters of water consumed by the group of SHR rats in condition B_1 (*Mdn* = 18.6, range from 7.3 to 22.3) were significantly greater ($W = 1770$, $p < .001$) than the milliliters of water consumed by the group of LEW rats (*Mdn* = 8.6, range from 4.4 to 11.5). Similarly, the licks emitted by the group of SHR rats (*Mdn* = 3190, range from 1018 to 3594) were significantly greater ($W = 1770$, $p < .001$) than the licks emitted by the group of LEW rats (*Mdn* = 1242, range from 394 to 1786). A linear regression generated the lines fitting milliliters of water consumed ($R^2 = .546$) and licks emitted ($R^2 = .634$) by the group of LEW rats, showing positive correlations between milliliters of water consumed and number of sessions (r = .745) and between licks emitted and number of session (r = .800). In contrast, Eq. 2 fitted the milliliters of water consumed ($R^2 = .514$) and licks emitted ($R^2 = .874$) by the group of SHR rats well, showing that milliliters of water consumed, and licks emitted by the SHR rats increased hyperbolically with the increasing number of sessions. Eq. 2 estimated the starting and ending points of the curves fitting milliliters of water consumed ($A_1 = 7.8$ and $A_2 = 19.7$, respectively), and licks emitted ($A_1 = 1073$ and $A_2 = 3246$, respectively) by the group of SHR rats. The inflection points of the curves ($x_0 = 5.4$ and 3.5, respectively) show that milliliters of water consumed, and licks emitted by the group of SHR rats moved to asymptotic level early in training. The slope of the line fitting the milliliters of water consumed by the group of SHR rats is steeper (p = 2.1) than the slope of the line fitting the milliliters of water consumed by the group of LEW rats (0.07x), indicating that the milliliters of water consumed by the group of SHR rats increased faster in condition B_1 than the milliliters of water consumed by the group of LEW rats. Yet, the licks emitted by the group of LEW rats (14.0x) increased faster in condition B_1 than the licks emitted by the group of SHR rats (p = 2.4).

The upper-right graph shows that the milliliters of water consumed by the group of SHR rats in condition B_2 (*Mdn* = 13.8, range from 12.0 to 16.9) were greater (W = 1816, $p < .001$) than the milliliters of water consumed by the group of LEW rats (*Mdn* = 12.4, range from 9.9 to 14.6). Also, the lower-right graph shows that the licks emitted by the group of LEW rats (Mdn = 2383, range from 2217 to 2815) were greater (W = 1518, p < .001) than the licks emitted by the group of SHR rats (Mdn = 2268, range from 1717 to 2744). The milliliters of water consumed, and licks emitted by the group of LEWs showed negative correlations with sessions of condition B_2 (r = - .380 and - .277 respectively), but the milliliters of water consumed, and licks emitted by the group of SHRs showed positive correlations with sessions of condition B_2 (r = .295 and .688, respectively). Poor fits of linear regression to milliliters of water consumed by the SHRs ($R^2 = .072$) and LEWs ($R^2 = .130$) revealed negligible changes in milliliters of water consumed by the SHR and LEW rats across sessions of condition B_2. A linear regression fitting licks emitted by the group of SHR rats ($R^2 = .465$) did better than fitting licks emitted by the group of LEW rats ($R^2 = .061$). The y-intercepts of the lines fitting the milliliters of water consumed (14.5) and the licks emitted (2457) by the group of LEW rats, are greater than the y-intercepts of the lines fitting the milliliters of water consumed (11.7) and the licks emitted (2006) by the group of the SHR rats indicating that at the beginning of condition B_2 the group of LEW rats consumed more water and emitted more licks than the group of SHR rats. The slopes of the lines fitting milliliters of water consumed, and licks emitted by the group of SHR rats (.02x and 7.67x, respectively), indicate that both dependent variables increased with increasing number of sessions of condition B_2. In contrast, the slopes of the lines fitting milliliters of water consumed, and licks emitted by the group of LEW rats (- 0.02x and – 1.91x, respectively), indicate that both dependent variables decreased with increasing number of sessions of condition B_2.

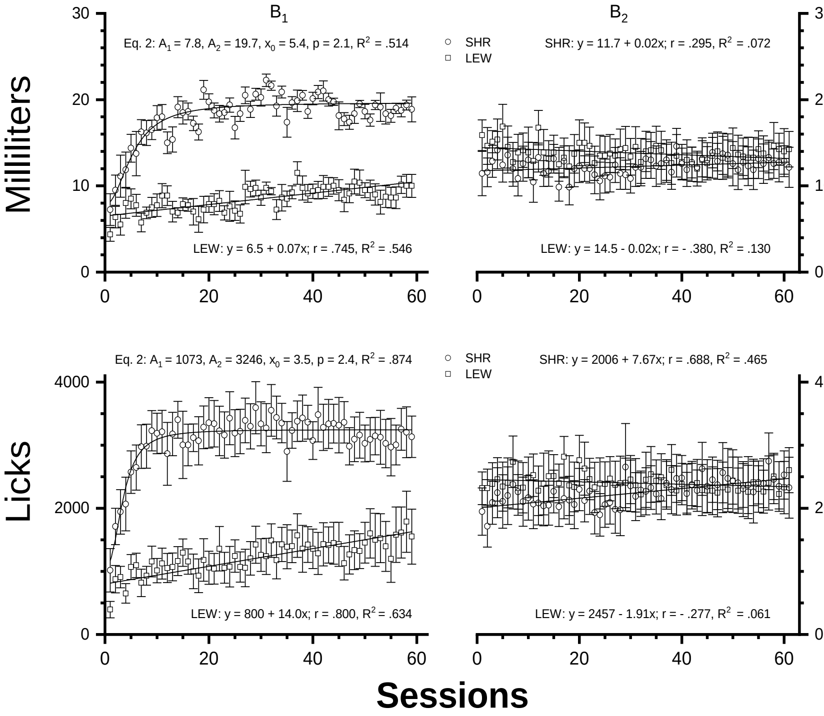


Figure 6. Milliliters of the water consumed (top graphs), and licks emitted (bottom graphs) by the group of SHR rats (circles) and the group of LEW rats (squares) plotted against sessions of conditions B_1 (left graphs) and B_2 (right graphs). Eq. 2 generated curvilinear fits, and the least square method generated linear fits to milliliters of water consumed and licks emitted by the rats. Empirical parameters from Eq. 2 and linear regression appear near to best fitting lines.

Figure 7 shows licks to the spout of the bottle emitted by the SHR and LEW rats during blackout periods, plotted against blocks of sessions of conditions B_1 (top graphs) and B_2 (bottom graphs). The left graphs show means of licks computed for the group of SHR rats (circles) and the group of LEW rats (squares), and the middle and right graphs show licks emitted by the individual SHR and LEW rats (the different symbols), respectively. All graphs show positive correlations between licks emitted during blackout periods and blocks of sessions. In condition B_1 the licks emitted by the group of LEW rats increased from 4593 in block 1 to 9077 in block 4 (M = 7717), and the licks emitted by the group of SHR rats increased from 5222 to 5966 (M = 5949). A linear regression fitting the licks emitted by the LEW rats did better (R^2 = .638) than fitting the licks emitted by the SHR rats (R^2 = - .439). The correlation between the licks emitted by the LEW rats and block of sessions (r = .871), is higher than the correlation between the licks emitted by the SHR rats and block of sessions (r = .201). The slope of the line fitting the licks emitted by the LEW rats (.30x) is steeper than the slope of the line fitting the licks emitted by the SHR rats (.02x), indicating that the licks emitted by the LEW rats increased faster across blocks of condition B_1 than the licks emitted by the SHR rats. The y-intercept of the line fitting the licks emitted by the LEW rats (12.1) is like the y-intercept of the line fitting the licks emitted by the SHR rats (12.5), showing that both strains emitted a similar number of licks in blocks of sessions 1 and 2 of condition B_1.

The middle and right graphs show that the licks emitted by the individual SHR rats (Mdn = 6587, range from 1308 to 9979) were equivalent (W = 175, p = .098) to the licks emitted by the individual LEW rats (Mdn = 6370, range from 376 to 20563). The analyses of the parameters from linear fits to licks emitted by the individual SHR and LEW rats indicate that: (1) The y-intercepts of the lines fitting the licks emitted by the SHR rats (*Mdn* = 12.5, range from 10.1 to 13.4) are equivalent (*W* = 30, *p* = .406) to y-intercepts of the lines fitting the licks emitted by the LEW rats (*Mdn* = 12.1, range from 7.7 to 13.3); (2) The slopes of the lines fitting the licks emitted by the SHR rats (*Mdn* = .08, range from .03 to .25) are like (*W* = 12, *p* = .236) the slopes of the lines fitting the licks emitted by the LEW rats (*Mdn* = .12, range from .03 to .39); And (3) Correlations between the licks emitted by the LEW rats and blocks of sessions (Mdn = .845, range from .285 to .990) are greater (W = 3, p = .024) than correlations between the licks emitted by the SHR rats and blocks of sessions (Mdn = .201, range from - .840 to .890).

The left-bottom graph shows licks emitted by the group of LEW rats increasing from 9302 in block 1 to 10097 in block 4 (M = 10371) of condition B_2, and licks emitted by the group of SHR rats increasing from 6932 to 7461 (M = 7248), respectively. The positive correlation between licks emitted by the SHR rats and blocks of sessions (r = .947) is greater than that between licks emitted by the LEW rats and blocks of sessions (r = .439). A linear regression fitting licks emitted by the SHR rats did better (R^2 = .843) than fitting licks emitted by the LEW rats (R^2 = - .211). The y-intercept of the line fitting licks emitted by the LEW rats (13.2) is like the y-intercept of the line fitting licks emitted by the SHR rats (12.7). But the slope of the line fitting licks emitted by the LEW rats (.04x) is steeper than the slope of the line fitting licks emitted by the SHR rats (.03x), indicating that licks emitted by the LEW rats increased faster across blocks of condition B_2 than licks emitted by the SHR rats.

The middle-lower and right-lower graphs show that the licks emitted by the individual LEW rats (*Mdn* = 11171, range from 781 to 23288) were greater (*W* = 294, *p* = .019) than the licks emitted by the individual SHR rats (*Mdn* = 7369, range from 3830 to 9083), respectively. Remarkably, the SHR rats show less between subjects variability in the licks emitted during blackouts of condition B_2 than the LEW rats. The analyses of parameters from linear regression showed that: (1) Correlations between the licks emitted by the SHR rats and blocks of sessions (Mdn = .776, range - .901 to .984), are comparable (W = 29, p = .141) to correlations between the licks emitted by the LEW rats and blocks of sessions (Mdn = .167, range - .986 to .725); (2) The y-intercepts of the lines fitting the licks emitted by the SHR rats (*Mdn* = 12.8, range from 11.5 to 13.3*),* are like (*W* = 12, *p* = .441) the y-intercepts of the lines fitting the licks emitted by the LEW rats (*Mdn* = 13.1, range from 11.6 to 14.3); And (3) the slopes of the lines fitting the licks emitted by the SHR rats (*Mdn* = .05, range - .14 to .31) are not different (*W* = 21, *p* = .726) from the slopes of the lines fitting the licks emitted by the LEW rats (*Mdn* = .02, range from - .52 to .29).

Figure 8 shows the licks emitted to the spout of the bottle before starting the initial link (i.e., the time between the blackout and the first press on the back lever) plotted against delay components. The upper graphs show licks emitted in condition B_1 and the lower graphs show licks emitted in condition B_2. The left graphs show means of licks computed for the group of SHR rats (circles) and the group of LEW rats (squares), and the middle and right graphs show licks emitted by the individual SHR and LEW rats (different symbols), respectively. In condition B_1, the licks emitted by the group of the SHRs increasing from 924 to 1064 (*Mdn* = 987) were greater (*W* = 21, *p* = .036) than the licks emitted by the group of the LEWs increasing from 16 to 230 (*Mdn* = 48). Linear regression generated lines of best fit to licks emitted by the SHR rats (R^2 = .787) and LEW rats (R^2 = .757), showing positive correlations between licks emitted before starting the initial link and delays to LLF (*r* = .911 and .897, respectively). The y-intercept of the line fitting licks emitted by the SHR rats (10.9) is greater than the y-intercept of the line fitting licks emitted by the LEW rats (6.2), showing more licks emitted by the SHR rats across delay components than licks emitted by the LEW rats. But the slope of the line fitting licks emitted by the LEW rats is steeper (.037x) than the slope of the line fitting licks emitted by the SHR rats (.002x), indicating that licks emitted by the LEW rats increased faster across delay components than licks emitted by the SHR rats.

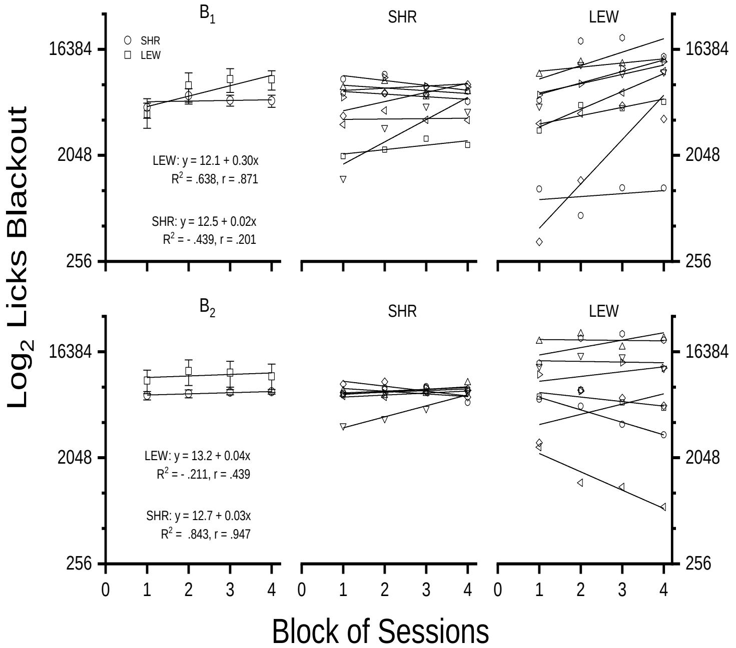


Figure 7. Licks to the spout of the bottle emitted by the SHR and LEW rats during blackout periods, plotted against blocks of sessions of conditions B_1 (top graphs) and B_2 (bottom graphs). The left graphs show means of licks computed for the group of SHR rats (circles) and the group of LEW rats (squares), and the middle and right graphs show licks emitted by the individual SHR and LEW rats (the different symbols), respectively. The least square method generated linear fits to means of licks produced by the groups of SHR and LEW rats, linear equations and parameters appear near to best fitting lines. Note logarithmic scale base-2 on the y-axis.

The upper-middle graph shows licks emitted by the individual SHR rats in condition B_1 (*Mdn* = 802, range from 2 to 3048) that are greater (*W* = 1176, *p* < .001) than those the upper-right graph shows for the individual LEW rats (*Mdn* = 22, range from 0 to 540). Pearson's *r* for correlations between licks emitted by the LEW rats and delay components (*Mdn* = .847, range from .361 to .950) were greater (W = 40, p = .022) than Pearson's *r* for correlations between licks emitted by the SHR rats and delay components (*Mdn* = .688, range from - .787 to .915). The y-intercepts of the lines fitting licks emitted by the SHR rats (*Mdn* = 10.8, range from 3.1 to 12.5) were greater (*W* = 45, *p* = .004) than the y-intercepts of the lines fitting licks emitted by the LEW rats (*Mdn* = 3.4, range from - 0.40 to 8.1), indicating that the SHR rats emitted more licks before starting the initial link than the LEW rats. Yet, the slopes of the lines fitting licks emitted by the LEW rats (*Mdn* = .064, range from .029 to .104) were greater (*W* = 45, *p* = .004) than the slopes of the lines fitting licks emitted by the SHR rats (*Mdn* = .002, range from - .002 to .042), indicating that licks emitted by the former increased faster across delay components than licks emitted by the latter strain of rats.

In condition B_2 (left-lower graph), the licks emitted by the group of SHR rats increasing from 1350 to 1763 (*Mdn* = 1505) were greater (*W* = 21, *p* = .036) than the licks emitted by the group of the LEW rats increasing from 40 to 246 (*Mdn* = 133). Linear fits to licks emitted by the group of SHR (R^2 = .874) and LEW rats (R^2 = .639) indicate positive correlations between licks emitted before starting the initial link and delay components (*r* = .948 and .843). The y-intercept of the line fitting licks emitted by the SHR rats (11.5) is greater than the y-intercept of the line fitting licks emitted by the LEW rats (7.2), showing that the SHR rats emitted more licks before starting the initial link than the LEW rats. However, the slope of the line fitting the LEWs' licks (.025x) is steeper than the slope of the line fitting the SHRs' licks (.004x) indicating that licks emitted by the LEW rats before starting the initial link increased faster across delay components than licks emitted by the SHRs. A comparison between licks emitted in condition B_1 (the left-upper graph) and licks emitted in condition B_2 (the left-lower graph), reveals that in condition B_2 both groups of rats emitted more licks before starting the initial link (W = 21, p = .036) than in condition B_1.

The lower-middle graph shows licks emitted by the individual SHR rats (*Mdn* = 1624, range from 0 to 3691) that are greater (W = 811.5, p < .001) than those the lower-right graph shows for the individual LEW rats (*Mdn* = 8, range from 0 to 1289). Positive correlations between licks emitted by the SHR rats and delay components (*Mdn* = .889, range from - .494 to .948), were comparable (W = 22, p = .312) to positive correlations between licks emitted by the LEW rats and delay components (*Mdn* = .797, range from .668 to .920). The y-intercepts of the lines fitting licks emitted by the SHR rats (*Mdn* = 11.6, range from - 0.23 to 12.7) were greater (W = 35, p = .010) than the y-intercepts of the lines fitting licks emitted by the LEW rats (*Mdn* = 2.7, range from - 0.31 to 9.8), indicating that the SHR rats emitted more licks before starting the initial link of condition B_2 than the LEW rats. Yet, the slopes of the lines fitting licks emitted by the LEW rats (*Mdn* = .058, range from .022 to .098) were steeper (W = 36, p = .007) than the slopes of the lines fitting licks emitted by the SHR rats (*Mdn* = .007, range from - .001 to .060), indicating that licks emitted by the LEW rats increased faster across delay components than licks emitted by the SHR rats.

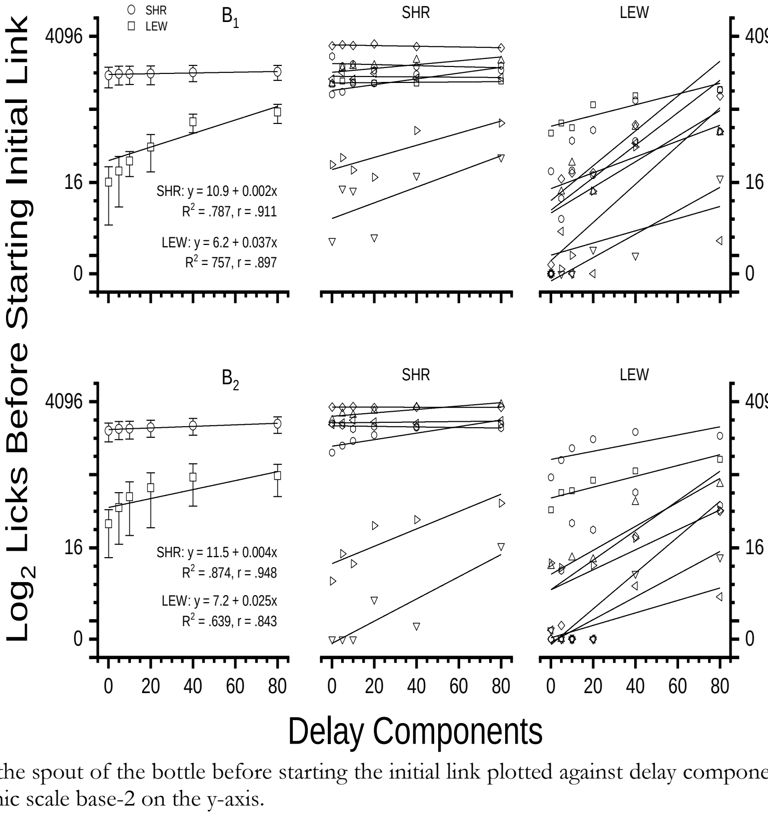


Figure 8. Licks emitted to the spout of the bottle before starting the initial link plotted against delay components (other details as in Figure 7). Note logarithmic scale base-2 on the y-axis.

Figure 9 shows licks emitted in the initial link after pressing on the SS lever (left graphs) and LL lever (right graphs) plotted as a function of the delay to the LLF. The upper graphs show licks emitted in condition B_1, and the lower graphs show licks emitted in condition B_2. Unfilled symbols stand for licks emitted by individuals and filled symbols for means of licks computed for the group of SHR (circles) and LEW (squares) rats. Each pair of graphs shows licks emitted by the SHR rats (left panel) and LEW (right panel) rats. Two results stand out: (1) Licks in the initial link increased with the increasing delay to the LLF arranged by the terminal link; And (2) the SHR rats emitted more licks in the initial link after pressing on the SS and LL levers than the LEW rats. In condition B_1 the licks emitted by the SHR rats after pressing on the SS lever (*Mdn* = 351, range from 2 to 1958) were greater ($W = 771$, $p = .030$) than the licks emitted by the LEW rats (*Mdn* = 34, range from 0 to 3260). A linear regression fitting licks emitted by the group of SHR rats ($R^2 = .950$) did better than fitting licks emitted by the group of LEW rats ($R^2 = .499$), with regression lines showing positive correlations between licks emitted after pressing on the SS lever and delays to LLF (r = .980 and .774, respectively). The y-intercept of the line fitting licks emitted by the SHR rats (9.3) is greater than the slope of the line fitting licks emitted by the LEW rats (6.4), showing the SHR rats emitted more licks after pressing on the SS lever than the LEW rats. But the slope of the line fitting licks emitted by the LEW rats (.07x) is steeper than the slope of the line fitting the licks emitted by the SHR rats (.01x), indicating that the LEWs' licks increased faster with delays to LLF than the SHR's licks.

The licks emitted by the individual SHR rats after pressing on the LL lever (*Mdn* = 378, range from 0 to 2431) were greater ($W = 976$, $p < .001$) than the licks emitted by the individual LEW rats (*Mdn* = 36, range from 0 to 1597). A linear regression fitting means of licks computed for the group of SHR rats ($R^2 = .921$) and the group of LEW rats ($R^2 = .601$), indicated positive correlations (upper-right graphs) between licks emitted after pressing on the LL lever and delays to LLF (r = .968 and .825, respectively). The y-intercept of the line fitting licks emitted by the SHR rats (9.2) is greater than the y-intercept of the line fitting licks emitted by the LEW rats (7.2), showing more licks emitted by the SHR rats across delays to LLF than licks emitted by the LEW rats. But the slope of the line fitting licks emitted by the LEW rats (.04x) is steeper than the slope of the line fitting licks emitted by the group of SHR rats (.02x), indicating that the LEWs' licks increased faster across delays to LLF arranged by the terminal link than the SHRs' licks.

In condition B_2 (left-lower graph), the licks emitted by the individual SHR rats after pressing on the SS lever (*Mdn* = 553, range from 0 to 3247) were greater (W = 614, p < .001) than the licks emitted by the individual LEW rats (*Mdn* = 36, range from 0 to 1447). Also, the licks emitted by the individual SHR rats after pressing on the LL lever (*Mdn* = 582, range from 0.3 to 3020) were greater (W = 779, p < .001) than the licks emitted by the individual LEW rats (*Mdn* = 27, range from 0 to 1227). A linear regression did a better job fitting the means of licks emitted by the group of the SHR rats after pressing on the SS and LL levers ($R^2 = .926$ and .947, respectively) than fitting the means of licks emitted by the group of the LEW rats ($R^2 = .783$ and .602, respectively). Positive correlations between licks emitted in the initial link after pressing the SS and LL levers and delays to LLF computed for the group of the SHR rats (r = .970 and .979, respectively), were greater than those computed for the group of the LEW rats (r = .909 and .826). The y-intercepts of the lines fitting means of licks emitted by the group of the SHR rats (9.5 and 9.6) are greater than the y-intercepts of the lines fitting means of licks emitted by the group of the LEWs (7.8 and 7.6), indicating that in condition B_2 the SHR rats emitted more licks in the initial link after pressing on the SS and LL levers than the LEW rats. But the slopes of the lines fitting licks emitted by the group of LEW rats (.03x and .04x) are steeper than the slopes of the lines fitting licks emitted by the group of SHR rats

(.02x and .02x), indicating that the LEWs' licks increased faster across delays to LLF arranged by the terminal link than the SHRs' licks.

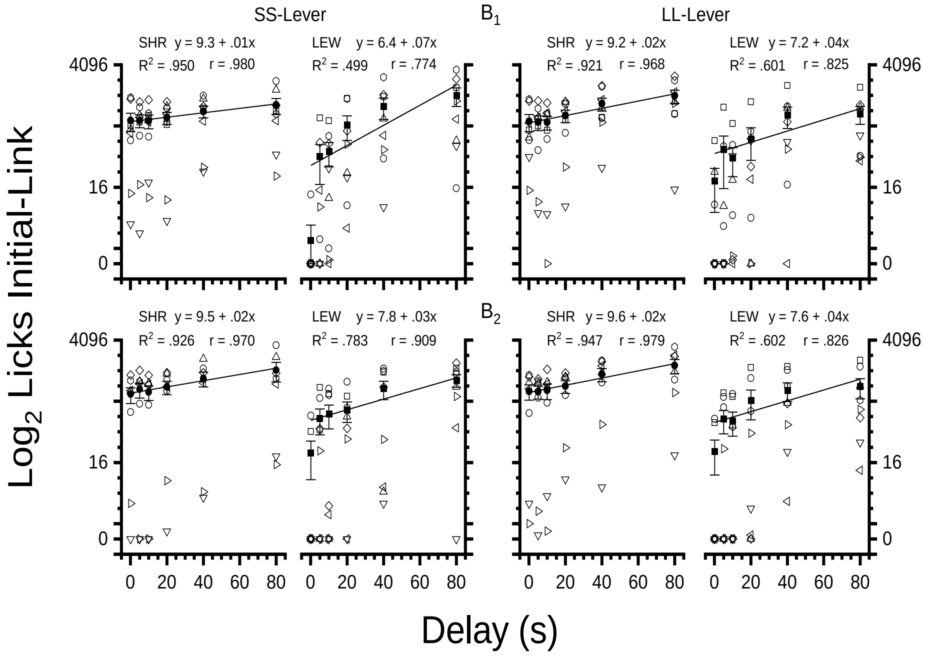


Figure 9. Licks emitted in the initial link after pressing the SS lever (left graphs) and LL lever (right graphs) plotted as a function of the delay to the LLF. The upper graphs show licks emitted in condition B_1, and the lower graphs show licks emitted in condition B_2. Unfilled symbols stand for licks emitted by individuals, and filled symbols are means of licks computed for the group of SHR (circles) and LEW (squares) rats. Each pair of graphs shows licks emitted by the SHR rats (left panel) and LEW (right panel) rats. The least square method generated linear fits to means of licks produced by the groups of SHR and LEW rats, linear equations and parameters appear near to best fitting lines. Note logarithmic scale base-2 on the y-axis.

Figure 10 shows licks emitted in the terminal link plotted against delays to LLF greater than 0.1 seconds. The upper graphs show licks emitted in condition B_1, and the lower graphs show licks emitted in condition B_2. The left graphs show means of licks computed for the group of SHR (circles) and LEW (squares) rats, and the middle and right graphs show licks emitted by the individual SHR and LEW rats, respectively. In condition B_1 the licks emitted by the SHR rats (*Mdn* = 58, range from 2.6 to 367.4) were greater ($W = 15$, $p = .029$) than the licks emitted by the LEW rats (*Mdn* = 1.3, range from 0 to 169.7). A linear regression fitted licks emitted by the SHR rats ($R^2 = .637$) and LEW rats ($R^2 = .803$), with the lines of best fit showing positive correlations between licks emitted in the terminal link and delays to LLF ($r =$ .869 and .949, respectively). The y-intercept of the line fitting licks emitted by the SHR rats (4.5) is greater than that of the line fitting licks emitted by the LEW rats (- .08), showing that the SHR rats emitted more licks across delays to LLF than the LEW rats. The slope of the line fitting licks emitted by the LEW rats (.12x) is steeper than the slope of the line fitting licks emitted by the SHR rats (.07x), indicating that licks emitted by the LEW rats increased faster with increasing delays to LLF than licks emitted by the SHR rats. The upper middle and right graphs show that the licks emitted by the individual SHR rats (*Mdn* = 34, range from 0 to 881) were greater ($W = 566$, $p < .001$) than the licks emitted by the individual LEW rats (*Mdn* = 0, range from 0 to 933), respectively. The lines of best fit show positive correlations between licks emitted by the SHR rats and delays to LLF (*Mdn* = .862, range from .811 to .973) that are comparable (W = 20, p = .812) to positive correlations between licks emitted by the LEW rats and delays to LLF (*Mdn* = .898, range from - .011 to .954). The y-intercepts of the lines fitting licks emitted by the SHR rats (Mdn = 2.4, range from - 0.5 to 5.4) are greater (*W* = 42, *p* = .024) than the y-intercepts of the lines fitting licks emitted by the LEW rats (*Mdn* = - 0.8, range from - 1.8 to 1.2), showing that the SHR rats emitted more licks across delays to LLF than the LEW rats. Yet, the slopes of the lines fitting licks emitted by the SHR rats (*Mdn* = .090, range from .067 to .126) are like (*W* = 27, *p* = .636) the slopes of the lines fitting licks emitted by the LEW rats (*Mdn* = .107, range from - .001 to .166) showing that their licks increased similarly across delays to LLF.

In condition B_2 (left-lower graph) the licks emitted by the group of the SHR rats (*Mdn* = 71, range from 4 to 647) were greater (*W* = 15, *p* = .029) than the licks emitted by the group of the LEW rats (*Mdn* = 9, range from 0 to 100). A linear regression fitted licks emitted by the SHR rats (R^2 = .744) and LEW rats (R^2 = .883) well, showing positive correlations between licks and delays to LLF (r = .899 and .955, respectively). Consistent with results showed in condition B_1, the y-intercept of the line fitting licks emitted by the SHR rats (5.5) is greater than the y-intercept of the line fitting licks emitted by the LEW rats (- 0.5), showing that the SHR rats emitted more licks across delays to the LLF than the LEW rats. Yet, the slope of the line fitting licks emitted by the LEW rats (.11x) is steeper than the slope of the line fitting licks emitted by the SHR rats (.06x), indicating that licks emitted by the LEW rats increased faster across delays to LLF than licks emitted by the SHR rats. The lower middle and right graphs show the licks emitted by the individual SHR rats (*Mdn* = 32, range from 0 to 1505) that are greater (*W* = 416, *p* < .001) than the licks emitted by the individual LEW rats (*Mdn* = 0, range from 0 to 644), respectively. The regression lines show positive correlations between licks emitted by the SHR rats and delays to LLF (*Mdn* = .893, range from .765 to .921) comparable (W = 9, p = .233) to positive correlations between licks emitted by the LEW rats and delays to LLF (*Mdn* = .953, range from .807 to .985). Similarly, the slopes of lines fitting licks emitted by the SHR rats (*Mdn* = .101, range from .064 to .136) are comparable (*W* = 29, *p* = .141) to the slopes of the lines fitting licks emitted by the LEW rats (*Mdn* = .064, range from .031 to .110), indicating that their licks increased similarly across delays to LLF. But the y-intercepts of the lines fitting licks emitted by the SHR rats (Mdn = 1.9, range from 0.3 to 5.8) are greater (*W* = 36, *p* = .014) than the y-intercepts of the lines fitting licks emitted by the LEW rats (*Mdn* = - 0.5, range from - 0.9 to 3), indicating that the SHR rats emitted more licks across delays to the LLF than the LEW rats.

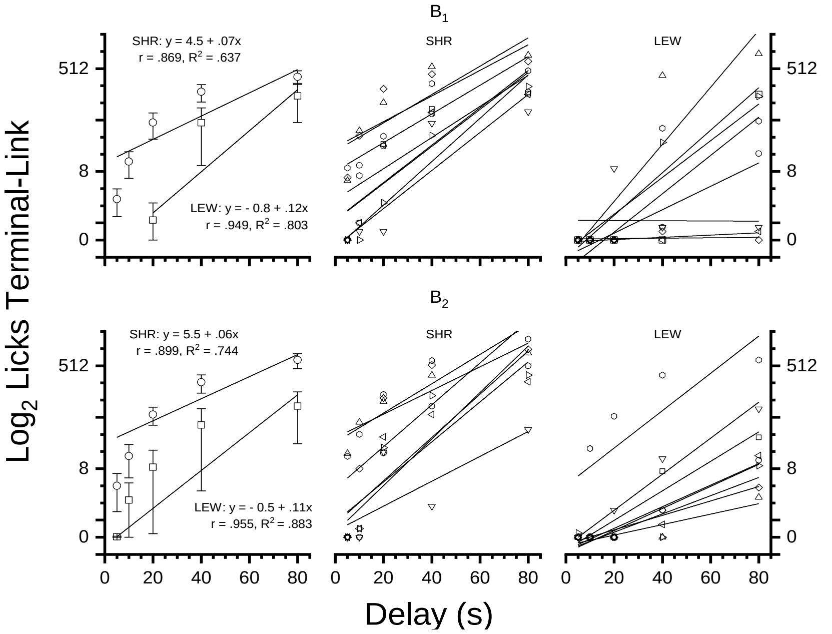


Figure 10. Licks emitted in the terminal link plotted against delays to LLF greater than 0.1 seconds (other details as in Figure 7). Note logarithmic scale base-2 on the y-axis.

Discussion

This study compared the performance of the SHR rat on a delay discounting task with the performance of the LEW rat looking for evidence supporting the notion that both strains of rats are potential models of ADHD. The delay discounting task used a concurrent-chains procedure (Aparicio et al., 2015; 2019) to assess choice with presses on two levers simultaneously available in the initial link (Grace, 1999). The levers associated with two non-independent random interval schedules averaging 11 s each (conc RI 11 s RI 11 s) arranged an equal number of terminal link entries keeping constant the relative rate of reinforcement (i.e., Stubbs and Pliskoff, 1969). When presses on a lever produced an entry to one terminal link, the other lever was retracted from the chamber and one press on the active lever produced food. One terminal link delivered the SSF after a 0.1-s delay, and the other terminal link delayed the LLF 0.1, 5, 10, 20, 40, or 80 seconds. Delays to the LLF were randomly presented during the session capitalizing on Evenden's and Ryan (1996) method to obtain an entire delay-of-reinforcement function in each session. Each food delivery (SSF or LLF) retracted the active lever from the chamber, forcing the rat to travel from the front wall to the rear wall of the chamber to press on the back lever to extend the front levers re-starting the initial link (Fig. 1). This locomotion to travel increased the rats' sensitivity to changes in the delay to reinforcement, because locomotion implies effort (Ren et al., 2022; Salamone and Correa, 2009), and sensitivity of choice to changes in the amount, frequency, or delay to reinforcement increases with effort (e.g., Aparicio, 2001; Aparicio and Cabrera, 2001).

Condition A_1 was a baseline condition assessing the effect of extended training-sessions on impulsive choice. The SHR and LEW rats pressed on two levers producing proportions of LL choice decreasing with the increasing delay to the LLF, preference for the LLF switched to the SSF generating discounting functions with hyperbolic shape (Fig. 2). Eq. 1 fitted the proportions of LL choice produced by the SHR and LEW rats extending the generality of findings indicating that Mazur's (1987) hyperbolic-decay model suitable describes the degree to which the efficacy of the LLF decays as a function of the increasing delay to obtain it (Aparicio, 2015; Aparicio et al., 2013; 2015; 2019; Farrar et al., 2003; Green et al., 2007; Mazur, 2012; Stein et al., 2012). The impulsive choices made by the SHR and LEW rats produced discounting functions showing discounting rates (k in Eq. 1) increasing with increasing block of sessions of condition A_1 (Fig. 3), supporting the conclusion that impulsive choice in SHR and LEW rats increases with their experience on the delay discounting task (Aparicio et al., 2022) regardless of their neurochemical and genetic differences and actual physiological conditions at the beginning of training (Aparicio et al., 2015; 2019). Also, both strains of rats produced discounting functions showing estimates of sensitivity of choice to the magnitude of the LLF (A in Eq.1) increasing with increasing block of sessions, indicating that when the parameter A is free to vary (it is not set to 1.0 LL choice at the y-intercept), A increases with the organism's experience on the choice situation (Aparicio et al., 2019). Summarizing, the results of condition A_1 showing discounting rates produced by the SHR rats greater than discounting rates produced by the LEW rats were consistent with findings indicating that SHR rats make more impulsive choices than LEW rats (Aparicio et al., 2022).

Postbaseline conditions (B_1, A_2, B_2, and A_3) lasted sixty days each and differed from one another in whether a bottle containing 100 ml of plain water was available in the chamber for the rats to drink during the session (B_1 and B_2), or it was not available (A_2 and A_3). In all conditions the SHR and LEW rats made impulsive choices producing discounting functions with hyperbolic shape (Mazur, 1987). But the SHRs made more impulsive choices producing steeper discounting functions indicating greater discounting rates than the LEW rats (Fig. 4). In conditions B_1 and B_2 the SHR rats showed a slight tendency to choose between the SSF and LLF less impulsively than in conditions A_2 and A_3. But this result was not replicated by the LEW rats choosing between the SSF and LLF more impulsively in conditions B_1 and B_2 than in condition A_2. It was not until the LEW rats responded to condition A_3 that their impulsive choices produced discounting functions steeper than those produced in conditions B_1 and B_2, suggesting that their impulsive choices did not reach asymptotic level in the previous no water conditions A_1 and A_2. These results showing no differences in discounting rates between the water and no water conditions are consistent with those showing no effect of scheduled induced-behavior on discounting rate (Ramos et al., 2019), questioning the idea that the organism will choose between the SSF and LLF less impulsively when it has an activity available to engage (drinking water) during the delay to the LLF (Grosch and Neuringer, 1981). Moreover, the present study analyzed the impulsive choices made by the SHR and LEW rats in postbaseline conditions (B_1, A_2, B_2 and A_3) with impulsive choices made in the last four blocks of sessions of condition A_1, looking for: (1) Discounting rates produced by the SHR and LEW rats in no water conditions (A_1, A_2, and A_3) greater than discounting rates in water conditions (B_1 and B_2) supporting Grosch's and Neuringer idea (1981); (2) The positive relation between polydipsia and impulsive choice suggested by Íbias and Pellón (2011). And (3) additional evidence supporting the claim that SHR rats make more impulsive choices producing discounting rates greater than LEW rats (i.e., Aparicio et al., 2022).

Figure 5 showed discounting rates produced by the SHR rats in conditions A_1, B_1, A_2, and B_2 greater than those produced by the LEW rats. In condition A_3, however, the discounting rates produced by the group of the SHR rats were comparable to the discounting rates produced by the group of the LEW rats suggesting that between strain differences in impulsive choice decreased with extended training on the delay discounting task (Aparicio et al., 2015; 2019). Comparisons of the discounting rates produced by the SHR and LEW rats in conditions A_1, A_2, and A_3 with the discounting rates produced in conditions B_1 and B_2 revealed mixed results. The discounting rates produced by the SHR rats in condition A_1 were like those produced in conditions B_1 and B_2. But the discounting rates produced by the SHRs in conditions A_2 and A_3 were greater than the discounting rates produced in condition B_1, and there were no differences between conditions B_2 and A_3 in the discounting rates produced by the SHR rats. The discounting rates produced by the LEW rats in condition A_1 were greater than those produced in condition B_1. But the LEW rats produced discounting rates in condition A_2 comparable to the discounting rates they produced in conditions B_1 and B_2, and there were no differences between conditions A_1 and B_2 in discounting rates produced by the LEW rats. Nonetheless, the LEW rats produced the greatest discounting rates in condition A_3. These inconsistencies in discounting rates between the no water (A_1, A_2, and A_3) and water conditions (B_1 and B_2) do not provide conclusive evidence supporting the idea that the organism will choose between the SSF and LLF less impulsively when it has an activity available to engage during the delay to the LLF (Grosch and Neuringer, 1981). Furthermore, the results showing discounting rates produced by the SHR and LEW rats in the no water conditions greater than those produced in the water conditions support the notion that discounting rate is not affected by polydipsia (Ramos et al., 2019), questioning a positive correlation between scheduled induced-behavior and impulsive choice (Íbias and Pellón, 2011). Even though the SHR and LEW rats developed polydipsia in the water conditions, they did not choose between the SSF and LLF more impulsively in conditions B_1 and B_2 than in the no water conditions A_1, A_2, and A_3.

In sessions of condition B_1 the SHR rats consumed more water emitting a greater number of licks to the spout of the bottle than the LEW rats. The milliliters of water consumed by the SHR rats, and licks emitted to the spout of the bottle increased hyperbolically across sessions of condition B_1. In contrast, the milliliters of water consumed by the LEW rats, and licks emitted to the spout of the bottle increased linearly (Fig. 6). These results suggesting more impulsive action in the SHR rats (Winstanley et al., 2006) than in the LEW rats, were not observed in condition B_2. The SHR rats consumed less milliliters of water in condition B_2 and emitted fewer licks to the spout of the bottle than in condition B_1. But the LEW rats drank more water in condition B_2 and emitted more licks the spout of the bottle than in condition B_1. Thus, whereas the SHRs' impulsive action decreased in condition B_2, the LEWs' impulsive action increased in condition B_2. More evidence supporting this finding comes from the results showing the LEW rats emitting more licks during the blackouts of conditions B_1 and B_2 than the SHR rats (Fig. 7). Both strains of rats showed positive correlations between licks emitted in blackouts and blocks of sessions of conditions B_1 and B_2, but licks emitted by the LEW rats increased faster across block of sessions of condition B_2 than licks emitted by the SHR rats. Moreover, the SHR rats showed less between subjects variability in licks emitted during blackouts of condition B_2 indicating less impulsive action than the LEW rats. Licks emitted by the SHR rats before starting the initial link (Fig. 8), licks in the initial link after pressing the SS and LL levers (Fig. 9), and licks in the terminal link during the delay to the LLF (Fig. 10) were greater than licks emitted by the LEW rats possibly due to poor sustained attention (Diana, 2002) and learning deficiencies (Meneses and Hong, 1998) in the SHR rats.

Conclusions

This study compared the performance of the SHR rat on a delay discounting task varying the delay to the LLF within the session with the performance of LEW rat. Choosing between the SSF and LLF both strains of rats developed impulsivity producing discounting rates increasing with increasing training in the choice situation, and it occurred regardless of their neurochemical and genetic differences and actual physiological conditions at the start of the study (Aparicio et al., 2015; 2019). The SHR rats developed a stronger preference for the SSF in conditions A_1, B_1, A_2, and B_2 discounting the LLF steeper than LEW rats. But the discounting rates produced by the LEW rats in the last condition A_3 were comparable to the discounting rates produced by the SHR rats, replicating findings showing that between strain differences in impulsive choice decrease with extended training on the delay discounting task (Aparicio et al., 2015; 2019). With the water available to drink during the session the SHR and LEW rats developed polydipsia. But drinking water did not cause their impulsive choice to increase (Ramos et al., 2019), the discounting rates produced by the SHR and LEW rats in the water conditions were equivalent to the discounting rates produced in the no water conditions, discarding a positive relation between polydipsia and impulsive choice (Íbias and Pellón, 2011). There were no consistent differences in discounting rates between no water (A_1, A_2, and A_3) and water conditions (B_1 and B_2), questioning the claim that the organism will choose between the SSF and LLF less impulsively when it has an activity available to engage during the delay to the LLF (Grosch and Neuringer, 1981). The present study supports the claim that the SHR is a rodent-model of ADHD displaying behaviors characterizing ADHD in humans such as impulsivity (Fox et al., 2008), hyperactivity (Knardahl and Sagvolden, 1979), poor sustained attention (Diana, 2002), learning insufficiencies (Meneses and Hong, 1998), and hypersensitivity to delayed consequences (Johansen et al., 2005). It is concluded that the LEW rat is an alternative model of ADHD, the LEW rat develops impulsivity and possess a phenotype highly susceptible to drug addiction (Garcia-Lecumberri et al., 2011), representing a genetic model of human drug abuse (Kosten and Ambrosio, 2002). This is important because an appropriate model of ADHD warrants the examination of clinical diagnostic criteria, executive functions, and treatments with drugs to reduce symptoms of ADHD such as inattention, hyperactivity, and impulsivity (Kantak, 2022).

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