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Impulsive Choice in Lewis and Fischer 344 Rats: Effects of Extended Training[1, 2]

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Abstract

Delay discounting in Lewis and Fischer 344 was compared using a novel concurrent-chains procedure. In the initial-link, two levers were available and a random-interval schedule was in effect. One terminal link provided a smaller reinforcer (1 pellet) and the other terminal provided a larger reinforcer (4 pellets). Terminal-link entry was scheduled randomly, with the constraint that entries to each occurred equally often. The terminal link associated with the smaller reinforcer was always a fixed-interval (FI) 5-s (i.e., the delay to the smaller reinforce was always 5 s). Delay discount functions were obtained by varying the terminal-link FI associated with the larger reinforcer across blocks of cycles within each session. The order of the delays (5, 10, 20, 40, and 80 s) within each session was randomly determined to minimize carryover effects. Graded delay-discount functions were obtained which were well described by a hyperbolic-delay equation. Initially, the Lewis rats were more sensitive to the effects of delay to larger reinforcer than the Fischer 344 rats. With extended training, however, the Fischer 344 rats showed a greater change in sensitivity to the delayed larger reinforcer, achieving levels of impulsivity comparable to those reached by the Lewis rats. These data suggest that a) the concurrent-chains procedure arranged here provides an efficient method for producing within-sessions graded discount functions in individual subjects, and b) differences in delay discounting between Lewis and Fischer rats often reported (and attributed to neurobiological differences) are not apparent after extended training.

Key words: *Lewis rats, Fischer 344 rats, delay discounting, concurrent chain, impulsive choice, lever press, rat*.

Resumen

Se crearon programas concurrentes encadenados para comparar la ejecución de ratas Lewis y Fischer 344 en tareas de descuento temporal. Los eslabones iniciales ponían dos palancas operativas disponibles, cada una asociada a un programa de intervalo aleatorio. Un eslabón terminal entregaba una pella de comida (el reforzador pequeño- inmediato) y el otro cuatro pellas (el reforzador grande-demorado). El mismo número de entradas a los eslabones terminales se programó de manera aleatoria. Un programa de reforzamiento de Intervalo Fijo de 5 segundos (IF 5-s) entregó el reforzador pequeño (se demoró siempre 5 segundos). La demora a la entrega del reforzador grande (5, 10, 20, 40 y 80 s) se arregló en orden aleatorio para minimizar efectos de acarreo de una demora a otra. Las funciones de demora al reforzamiento se obtuvieron en bloques arreglados en ciclos dentro de una misma sesión. Una ecuación hiperbólica de descuento temporal describió adecuadamente las funciones de demora al reforzamiento.

[1] The reference to this article in Internet is: http://conductual.com/content/impulsive-choice-lewis-and-fischer-344-rats

[2] The authors like to thank Carla M. Huff for her technical assistance in data collection. We are grateful to an anonymous reviewer that made helpful comments to an early version of the manuscript. Portions of this paper were presented at the 36TH Annual Convention of the Association for Behavior Analysis International.

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Inicialmente, las ratas Lewis mostraron mayor sensibilidad al reforzamiento demorado. Sin embargo, después del entrenamiento extenso las ratas Fischer 344 fueron mas sensibles que las ratas Lewis al reforzamiento demorado, alcanzando niveles de impulsividad comparables a los que mostraron las Lewis al inicio del estudio. Estos hallazgos sugieren que a) los programas concurrentes encadenados aquí utilizados representan un método eficiente para obtener funciones de descuento temporal dentro de las sesiones en individuos, y b) las diferencias en tareas de descuento temporal entre las ratas Lewis y Fischer (frecuentemente reportadas y atribuidas a diferencias neurobiológicas entre estas dos cepas) no son evidentes después de un entrenamiento extenso.

Palabras clave: *Ratas Lewis, ratas Fischer 344, descuento temporal, concurrente encadenado, elección impulsiva, presión de palanca, ratas.*

Delay discounting refers to the process by which a delay between behavior and its consequences diminishes the effectiveness, or "value," of those consequences. Delay discounting appears to play an important role in a variety of behavior patterns often described as "impulsive" and, thus, this process has received considerable attention recently (see Madden & Bickel, 2010). Non-human animal models have been particularly useful in characterizing delay discounting, and in examining variables that affect impulsive choice. In the basic experimental arrangement with non-humans, a subject (e.g., rat) chooses between a smaller reinforcer (e.g., 1 food pellet) presented immediately (the smaller-sooner food, or SSF) and a larger (e.g., 4 food pellets) presented after a delay (the larger-later food, or LLF). As the delay to the LLF is increased, the likelihood of choosing it decreases.

Mazur's (1987) hyperbolic-decay model often is used to characterize data from experiments on delay discounting.

$$V = \frac{A}{1 + kD}$$

In this model, *V* denotes the current value of the reinforcer (i.e., its effectiveness at the time of the choice), D is the delay between the choice and the delivery of the reinforcer (e.g., food), A is the amount or size of the reinforcer, and *k* is a free parameter that quantifies how rapidly reinforcement value is discounted with increases in D. Although a number of other methods have been used to describe the data (e.g., Myerson & Green, 1995), Equation 1 has proven to be remarkably general and is relatively parsimonious. It accurately describes data from a variety of studies with both humans and non-humans under a variety of experimental conditions, and does so with a single free parameter (see Madden & Johnson, 2010).

A variety of procedures have been used to generate delay-discount functions in non-human subjects (see Madden & Johnson, 2010). In a commonly used procedure (i.e., Evenden & Ryan, 1996), rats choose between LLF and SSF in discrete trials, and the delay to the LLF is manipulated within sessions across blocks of trials. Typically, at the start of each session, the delays to the LLF and SSF are equal (usually 0 s), and the delay to the LLF is increased across blocks. The first few trials of each block are forced trials, in which only one option is available, so that the subject is exposed to the contingencies associated with the choices for the remaining trials of the block.

Because an entire delay-of-reinforcement function is obtained within each session, the method developed by Evenden and Ryan (1996) provides an efficient method for examining effects of variables such drugs and other neurobiological manipulations (see Madden & Johnson, 2010). Unfortunately, however, this procedure has some limitations. First, it involves a single response on discrete trials

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between two fixed amounts of food, which can produce exclusive preference for one or the other option under a given set of parameters. Thus, in some cases, discount functions emerge only when individual functions are averaged to form a group function. Second, it appears that choice on a given trial often is controlled by variables other than the amount/delay combination currently in effect. For example, the shape of the discount function obtained in human and non-human subjects is affected by the order in which the delays to the larger reinforcer are manipulated (Fox, Hand, & Reilly, 2008; Robles & Vargas, 2007, 2008; Robles, Vargas, & Bejarano, 2009; Slezak & Anderson, 2009). Furthermore, non-human subjects (e.g., rats) with a history of increasing delays within a session often will show a decreasing choice of the larger reinforcer across blocks of trials during probe sessions in which the delay to the larger reinforce remains at 0-s throughout the session (Evenden & Ryan, 1996; Pitts & McKinney, 2005; Slezak & Anderson, 2009).

For some of the reasons stated above, it has been suggested that titration procedures may provide the most effective general method to determine delay-discounting functions (e.g., Madden & Johnson, 2010; Mazur, 1987; Stein, Pinkston, Brewer, Francisco, & Madden, 2012). In one type of titration procedure (the adjusting-amount procedure), rats choose between an immediate, adjusting, reinforcer and a delayed, fixed reinforcer. The amount of the immediate reinforcer is adjusted based upon the subject's choices; choices of the immediate reinforcer reduce its amount, and choices of the delayed reinforcer increase its amount. The amount of the immediate reinforcer at which the subject chooses each option approximately equally is called the "indifference point." Discount functions are obtained by determining indifference points at each of several delays to the fixed reinforcer; as the delay to the fixed reinforcer increases, choices of the more immediate reinforcer increase, thus decreasing the indifference point. Although these procedures are effective in generating graded discount functions in individual subjects (Stein et al., 2012), they require manipulating parameters associated with the fixed alternative across sessions. Furthermore, some aspects of these procedures (e.g., the manner in which force-trials are arranged) are idiosyncratic across studies, and, thus their impact on indifference points is unknown.

One purpose of the present study was to introduce a novel procedure to assess delay discounting in rats. It was designed to incorporate some of the advantages, while eliminating or minimizing some of the disadvantages, of each of the types of procedures described above. This procedure retained the efficiency of Evenden and Ryan's (1996) method in that the delay to the larger reinforcer was manipulated within sessions. Instead of a single response in discrete-trial format, however, it utilized a concurrent-chains procedure (e.g., Autor, 1960; Herrnstein, 1964; see Pitts & Febbo, 2004 for the use of a concurrent-chains procedure to generate delay-discount functions in pigeons). The delay to the LLF varied across blocks of cycles within each session by arranging an FI 5, 10, 20, 40, or 80-s schedule in the associated terminal link. To help minimize carry-over effects, the delays to LLF were presented in random order within each session. In this procedure, graded choice at each delay can be obtained by examining the distribution of responses on the two levers during the initial links. Furthermore, the distribution of responses across the two levers in the initial link can be analyzed with Baum's (1974) generalized matching law (GML), formerly expressed as follows:

$$\log\left(\frac{B_1}{B_2}\right) = s\cdot\log\left(\frac{r_1}{r_2}\right) + \log b$$

Where B_1 and B_2 are behavior allocation measured in time or responses, to Alternatives 1 and 2, r_1 and r_2 may be food rates or food amounts obtained from Alternatives 1 and 2, *b* is a measure of bias toward one alternative or the other arising from factors other r_1 and r_2, and *s* is sensitivity of behavior ratio to the reinforcer ratio.

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A second purpose of the present study was to compare performances of Lewis (LEW) and Fischer 344 (F344) rats under the present procedure. Several studies have reported that LEW rats show steeper discount functions than F344 rats (e.g., Anderson & Diller, 2010; Anderson & Woolverton, 2005; Huskinson, Krebs, & Anderson, 2012; Madden, Smith, Brewer, Pinkston, & Johnson, 2008; Stein et al., 2012). It has been suggested that these findings may be the result of important neurochemical differences between these strains, most notably, differences in dopamine (DA) and serotonin (5-HT) systems (see Cadoni & Di Chiara, 2007). LEW rats have lower overall concentrations of DA, fewer DA transporters, fewer D_2 receptors in the striatum and nucleus accumbens core, fewer D_3 receptors in the nucleus accumbens shell and olfactory tubercule, and fewer 5-HT binding sites in the hippocampus and frontal cortex than F-344 rats (see Burnet, Mefford, Smith, Gold, & Sternberg, 1996; Flores, Wood, Barbeau, Quirion, & Srivastava, 1998; Selim, & Bradberry, 1996).

Despite these neurobiological differences, LEW rats do not always show steeper discount functions than F344 rats. Under some conditions, researchers have failed to find differences in impulsive choice between these two strains (e.g., Stein et al., 2012; Wilhelm & Mitchell, 2009). Although the reasons for the disparities in data comparing LEW and F344 rats across studies is not completely clear, it appears that procedural issues are important (see Stein et al., 2012). Given these disparities, it is imperative to determine the conditions under which LEW and F344 rats will, and will not, show differences in delay discounting.

One procedural characteristic that appears to be relevant to the comparisons of LEW and F344 rats is length of exposure to each of the conditions. Studies reporting differences between LEW and F344 rats typically have employed steady-state procedures involving at least 10 baseline sessions to each delay/amount combination (e.g., Anderson & Diller, 2010; Anderson & Woolverton, 2005; Huskinson, Krebs, & Anderson, 2012; Madden et al., 2008; Stein et al., 2012); whereas, those studies that have failed to find differences between these strains used rapid-determination assessment of indifference points where a maximum of 5 sessions were arranged under adjusting procedures (Stein et al., 2012; Wilhelm & Mitchell, 2009). Additionally, it has been shown that LEW rats acquired lever pressing for food (Anderson & Elcoro, 2007) and drug-maintained responding (Kosten et al., 1997) faster than F344 rats, suggesting that the sensitivity to these consequences observed in the LEW rats may influence the presence or the absence of a strain difference. Perhaps several sessions (i.e., more than 5 sessions) of training are required to detect a strain difference mainly driven by the LEW rats, and with extended training (i.e., 10 or more sessions per condition), it gradually diminished as the F344 rats achieve steady-state performance.

More generally, differences in performance between LEW and F344 rats raise the possibility that measures of delay discounting can change systematically with extended training. If that is the case, data from comparisons across species might depend upon the degree of experience with a given procedure. For that reason, LEW and F344 rats were given extended exposure (225 sessions) to the present procedure, and performance was compared at different points throughout.

Method

Subjects

Eight LEW (Q1-Q8) and eight F344 (R1-R8) male rats (from Harlan Laboratories, Indiana) between 60-90 days old at the start of the study, served as subjects. During the experiment, rats were placed on a regimen of food restriction; post-session feedings of Purina® Lab Chow (approximately 10 g) were provided such that the weights for the LEW and F344 rats ranged from approximately 320 to 350 g, and 280 to 310 g, respectively. Between sessions, the rats were individually housed in plastic cages with

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water permanently available within a temperature-controlled colony room providing 12:12 hr light/dark cycle (lights on at 0700).

Apparatus

Eight modular operant conditioning chambers, six manufactured by Med Associates® (Model ENV-008, with interior dimensions of 30.5 cm x 24.1 cm x 21.0 cm) and two manufactured by Lehigh Valley Electronics® (Model E10-10SF, with interior dimensions of 29.0 cm x 25.0 cm x 29.0 cm), were contained within sound-attenuating enclosures. The front and back walls of each chamber were made of stainless steel and the sidewalls were made of Plexiglas. The front wall of each chamber contained two retractable levers (Med Associates® model #ENV112BM), two 28-V DC stimulus lights, and a 4.0 by 4.0 cm opening that provided access to a receptacle into which 45-mg grain pellets (BioServ®) were delivered. Each "front lever" was 4.5 cm wide and located 7.0 cm above the floor; the edge of each lever was 1.0 cm from its respective sidewall. When extended, each lever required a downward force of approximately 0.25 N to operate; lever extension/retraction required approximately 1.0 s. Each stimulus light was located 7.0 cm directly above its corresponding lever, and the dipper opening was centered 4.0 cm from the floor. The rear wall of the chamber contained a single fixed lever (the "rear lever"), which was 4.5 cm wide and centered 7.5 cm above the floor. A 28-V DC house light provided ambient illumination either centered on the back wall 3.0 cm below the ceiling (6 chambers) or mounted in the center of the ceiling (2 chambers).

Continuous white noise was present in the surrounding room to mask extraneous sounds, and each enclosure was equipped with a ventilation fan that provided air circulation within the experimental space. Experimental events were programmed and data were recorded in a separate room by a Windows®-controlled computer using Med Associates® (Georgia, VT) software and interfacing equipment operating at 0.01-s resolution.

Procedure

Initial training.

Four 45-mg grain pellets were placed into the food receptacle and training started after rats had eaten the pellets. They were trained to press the two front levers by inserting each lever into the chamber during separate sessions. Each press on the extended lever produced a food pellet (fixed-ratio (FR) 1); sessions ended after 60 pellets were delivered, or 30 min elapsed, whichever happened first. After each rat consistently pressed each of the front levers, the rear lever was mounted on the back wall of the chamber and the rats were trained to press it. During these sessions, the front levers were retracted and presses on the rear lever produced a food pellet under a FR 1 schedule. Once the rats consistently pressed the rear lever, a final session was arranged in which all three levers were available simultaneously in the chamber and presses on each lever produced a food pellet according to a FR 1 schedule.

Choice procedure.

After initial training was complete, the rats were exposed to the concurrent-chains procedure. Each session consisted of a series of choice cycles. Each cycle began with the illumination of the houselight. A single press on the rear lever extended the two front levers, illuminated the stimulus lights above them, and started the initial link (the choice phase of each cycle); for the remainder of the cycle, presses on the rear lever had no programmed consequences. The initial links used a single RI 10-s schedule that was generated by sampling a probability generator every second with the probability set at 0.1. Accordingly, during the initial links, terminal-link entry was set up with a constant probability of 0.1 each second. Once terminal-link access was set up by the RI 10-s schedule, one of the front levers was

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selected as "active" (the selection process is described below). A press on the active lever retracted the other lever, turned off the stimulus light above the other lever, and initiated the terminal-link schedule (the delay portion of each cycle) associated with the active lever. A 2-s changeover delay (COD) was in effect during the initial link such that a press on a given lever could not gain entry into its terminal link until 2 s had passed since a changeover to that lever.

For one lever (the SS-lever), the terminal-link was a FI 5-s schedule; the first press after 5 s retracted the lever, turned off the associated stimulus light, and produced a single food pellet. That is, this terminal link arranged a SSF after a fixed (5-s) delay. For the other lever (the LL lever), the terminal link was an FI schedule, the value of which changed for each block of cycles (FI 5, 10, 20, 40, or 80 s); the first press after the arranged interval elapsed retracted the lever, turned off the associated stimulus light, and produced 4 food pellets (delivered 0.5-s apart). Therefore, the terminal link arranged a LLF presented after a delay that varied across blocks of cycles. Each block was in effect for 10 cycles, and the order of the blocks (delays to the LLF) was determined randomly for each session. Upon delivery of the food associated with the terminal link, a black out (inter-cycle interval) was initiated. Black outs following LL-food deliveries were always 10 s. Black outs following SS-food deliveries were adjusted so that the overall cycle duration within a block was constant.

Terminal-link entry was arranged by randomly selecting one of the levers as active for each cycle, with the constraint that each lever was selected 5 times within each block of 10 cycles. Thus, within each block, both terminal links occurred 5 times. For half of the rats within each strain, the terminal-link that arranged the SSF was associated with the left lever and the terminal-link that arranged the LLF was associated with the right lever; for the other half of the rats within each strain, this was reversed (i.e., LLF with the left lever and SSF with the right lever). Sessions ended after 50 cycles (5 blocks) or 60 min, whichever occurred first. Sessions were conducted 7 days per week at about the same time each day.

Data Analysis

The data of all 225 sessions, organized into 15 blocks of 15 sessions each, were analyzed. For each subject, initial-link responses on the LLF and SSF levers were counted separately for each delay and aggregated across sessions of the same block. Computations obtained across sessions of the same block of individual rats of the same strain, were used to calculate the medians of responses on the LL lever and SS lever for the group; medians instead of means were used because data in delay discounting often are not normally distributed (Myerson & Green, 1995). Computations of responses for individual rats and medians of the groups were use to calculate the corresponding percentages of LL choice (LL / (LL + SS)). Nonlinear curve fitting to percentages of LL choice was performed with Equation 1, which was entered manually into Origin® (version 8.5) as a user-defined equation; Accordingly, A was free to vary (i.e., it was not assumed to be 100% LL choice at the y-intercept) and the resulting value of k was used to estimate the rate of delay discounting. The ratios of responses (LL-lever/SS-lever) and delays to food delivery (LL-F delay/SS-F delay) were also computed and transformed into logarithm base 2. These computations were analyzed according to the generalized matching law (Baum, 1974) by conducting a linear-regression analysis (i.e., the least squares method) with the log of response ratio (LL-lever/SS-lever) plotted against the log of delay ratio (LL-F delay/SS-F delay); the slope estimated sensitivity of choice to within session changes in the ratio of delay to food delivery (i.e., a measure of "impulsiveness"), and the y-intercept (divided by 2 to account for the difference in the amount of food) estimated bias for the LL-lever. Myerson's, Green, and Warusawitharana (2001) method was used to calculate the area under the empirical discounting curve (AUC), providing a theory-free estimate of delay discounting. This dependent variable was expressed as a proportion of the maximum AUC, where values close to 1.0 indicate little or no discounting, and values close to zero indicate maximum discounting. Differences between strains in

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values of *k,* slopes of the regression lines from the generalized matching law, and AUC were examined using nonparametric statistical Mann-Whitney U-tests. Linear curve fitting and nonparametric statistical tests, at the alpha level of .05, were implemented with Origin®.

Results

The first analysis focused on choice in the initial link. Figure 1 shows the percentage of responses the LLF option plotted as a function of delay in (s) to LLF delivery. The top, middle, and bottom rows show data from early (Blocks 4-5), intermediate (Blocks 9-10), and advanced (Blocks 14-15) stages of training, respectively. The left column of panels in Figure 1 shows group medians (LEW circles and F344 squares), and the central and right columns show data for individual LEW and F344 rats, respectively. In all cases, the percentage of choice for the LL lever decreased with increasing delay to LLF delivery. For the individual LEW and F344 rats, and group's medians, Table 1 shows the values of the intercept (*A*), *k,* and R^2 obtained for blocks of sessions 4-5, 9-10, and 14-15 using Equation 1. The hyperbolic-decay model provided a good fit of the data, accounting for a large proportion of the variability for both LEW and F344 rats (all but one of the R^2 values were above 0.95) that occurred as a function of within session changes in delay to LL-F delivery (see Table 1). Estimates of *k* show that, overall, discounting rates for both strains were relatively low under this procedure (range: 0.005 to 0.016). Differences in group's medians of rate of delay discounting between LEW and F344 rats (*k* values of 0.011 and 0.005, respectively) that occurred early in the training (Blocks 4-5), continued during the intermediate stage of training (k values of 0.016 and 0.008, respectively, during Blocks 9-10), indicating that, on average, LEW rats were choosing more impulsively than F344 rats. However, extended training notoriously reduced the difference in the rate of delay discounting between LEW and F344 rats (k values of 0.012 and 0.011, respectively, for Blocks 14-15).

Statistical comparisons (via Mann-Whitney U test) of the distributions of *k* values for the individual LEW and F344 rats across the selected blocks generally confirmed the above characterization of the data. The distribution of *k* values for the LEW rats was significantly higher than that for the F344 rats in Blocks 4-5 ($U = 54$, $p = .024$; but not in Blocks 9-10 ($U = 44$, $p = .227$) or Blocks 14-15 ($U = 34$, $p = .874$).

Figure 2 shows the results of the analysis based upon the generalized matching law. In this figure, log2 (LL/SS) response ratios are plotted against the log2 delay ratios. Overall, these data show a negative relation between response ratio and delay ratio for both strains, indicating sensitivity of choice to within session changes in the ratio of delay to food delivery. In Blocks 4-5, group median sensitivity to delay ratio was higher for the LEW (slope -.46) than the F344 rats (slope - .34). However, bias for the LL lever was stronger in the F344 rats than in the LEW rats (intercepts of 0.88 and 0.65, respectively). Lines of best fit accounted for most of the variability in the group functions (values of R^2 of .908 and .910, respectively). For both strains of rats, sensitivity to delay was higher in Blocks 9-10 (middle panel) than in Blocks 4-5, but the slope for the LEW is still steeper (- .54) than for the F344 rats (- .46); that is, sensitivity to delay was higher for the LEW than for the F344 rats during the intermediate stage of training. Again, bias for the LL lever was stronger in the F344 rats (0.93) than in the LEW (0.56) rats, and R^2 values are .901 and .946, respectively. By Blocks 14-15 (bottom panel), the difference in sensitivity to delay between the strains has completely disappeared (the slope of the function for the LEW, -.53, is actually slightly lower than for the F344, -.57). This was the result of an increase in sensitivity to delay for the F344 rats over the final five blocks of sessions. Both strains show the highest levels of bias for the LL lever (intercepts of 1.11 and 0.82, respectively) with lines of best-fit explaining most of variability in response ratios (R^2 of .975 and .897, for F344 and LEW, respectively) that occurred as a function of changes in the ratio of delay to food delivery. Accordingly, sensitivity of choice to delay ratio increased and bias for the

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LL lever was strengthened with extended training in the choice situation. These trends are supported with the data of individual LEW (central panels) and F344 rats (right panels). Table 2 shows the empirical values of the intercept (bias), slope, and R^2 obtained for blocks of sessions 4-5, 9-10, and 14-15 using Equation 2 (GML). There were no significant differences between strains in slopes values computed for individual rats in Blocks 4-5 (U = 15, p = 0.083), 9-10 (U = 28, p = 0.713) and 14-15 (U = 39, p = 0.494). Nor were there between-strains differences in values of bias in Blocks 4-5 (U = 20, p = 0.227), 9-10 (U = 20, p = 0.227), and 14-15 (U = 23, p = 0.372).

Figure 1. Percentage of LL choice (LL / (LL + SS)) as a function of delay in (s) to LLF delivery. Left column graphs show medians of the LEW (circles) and F344 (squares) groups; central and right column graphs show data from individual LEW and F344 rats represented with different symbols. L and F stand for the LEW and F344 groups of rats, respectively. R^2 values appear between parentheses next to values of k (Eq. 1). Bk stands for blocks of sessions.

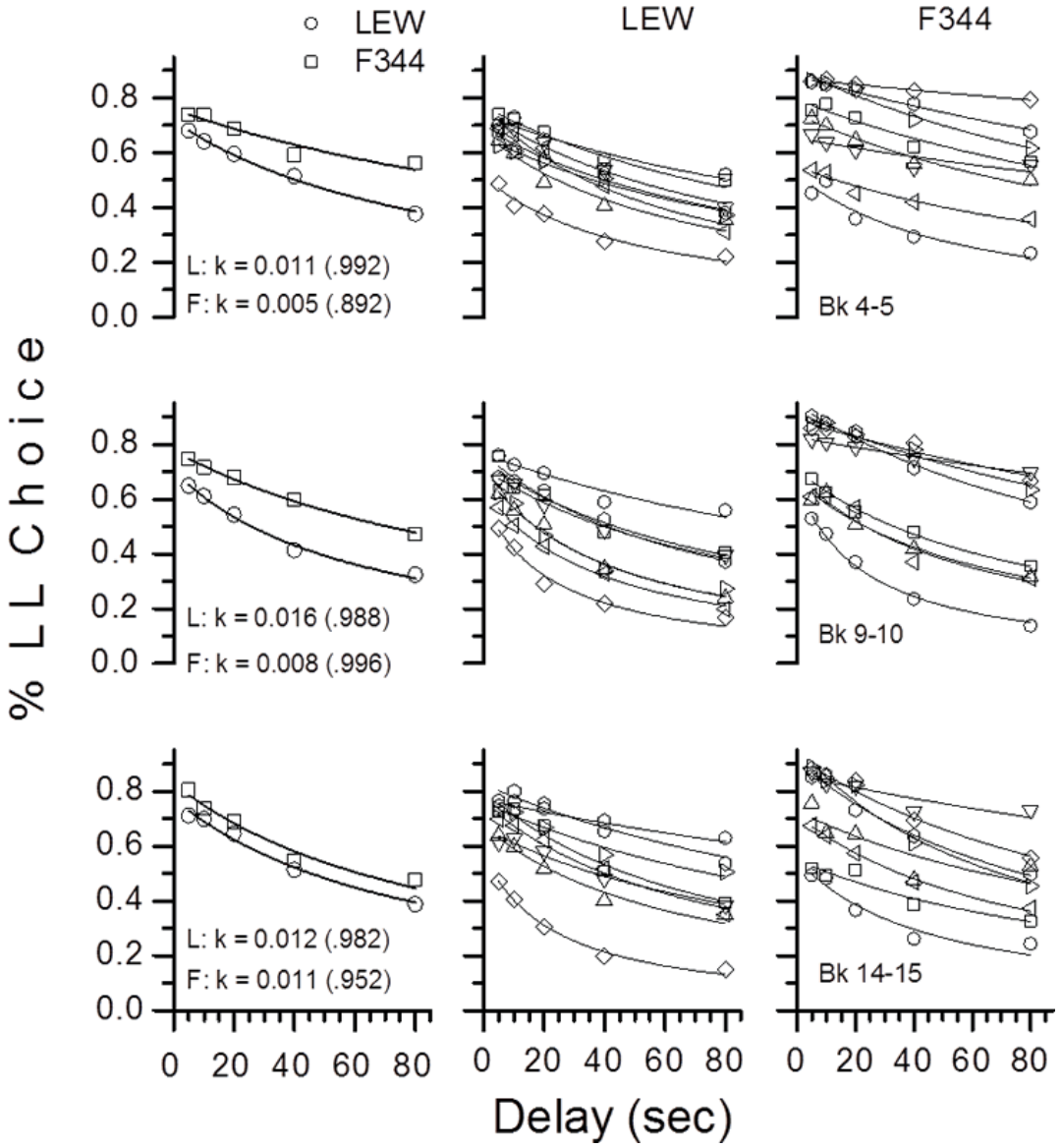

Table 1. Parameters, percentage of LL choice, hyperbolic discounting.

			Intercept	SE	k	SE	R^2
Bk 4-5	**LEW**	Q-1	**0.768**	0.027	**0.008**	0.002	**0.919**
		Q-2	**0.736**	0.021	**0.006**	0.001	**0.912**
		Q-3	**0.672**	0.036	**0.014**	0.003	**0.919**
		Q-4	**0.746**	0.018	**0.010**	0.001	**0.974**
		Q-5	**0.513**	0.026	**0.019**	0.004	**0.953**
		Q-6	**0.769**	0.030	**0.016**	0.003	**0.967**
		Q-7	**0.661**	0.013	**0.009**	0.001	**0.979**
		Q-8	**0.693**	0.018	**0.010**	0.001	**0.968**
		Median	**0.715**	0.023	**0.010**	0.001	**0.960**
	F344	R-1	**0.793**	0.022	**0.005**	0.001	**0.912**
		R-2	**0.519**	0.043	**0.017**	0.006	**0.870**
		R-3	**0.741**	0.015	**0.007**	0.001	**0.964**
		R-4	**0.653**	0.023	**0.003**	0.001	**0.649**
		R-5	**0.869**	0.004	**0.001**	0.000	**0.961**
		R-6	**0.549**	0.017	**0.007**	0.001	**0.929**
		R-7	**0.901**	0.016	**0.006**	0.001	**0.968**
		R-8	**0.882**	0.006	**0.004**	0.000	**0.988**
		Median	**0.767**	0.016	**0.006**	0.001	**0.945**
Bk 9-10	**LEW**	Q-1	**0.766**	0.038	**0.013**	0.003	**0.924**
		Q-2	**0.765**	0.023	**0.005**	0.001	**0.892**
		Q-3	**0.697**	0.024	**0.023**	0.003	**0.984**
		Q-4	**0.711**	0.011	**0.011**	0.001	**0.989**
		Q-5	**0.589**	0.043	**0.042**	0.009	**0.966**
		Q-6	**0.637**	0.014	**0.025**	0.002	**0.995**
		Q-7	**0.699**	0.029	**0.023**	0.003	**0.975**
		Q-8	**0.736**	0.021	**0.011**	0.002	**0.967**
		Median	**0.705**	0.024	**0.018**	0.002	**0.971**
	F344	R-1	**0.706**	0.010	**0.012**	0.001	**0.993**
		R-2	**0.653**	0.027	**0.042**	0.005	**0.991**
		R-3	**0.666**	0.029	**0.014**	0.003	**0.949**
		R-4	**0.825**	0.003	**0.002**	0.000	**0.992**
		R-5	**0.889**	0.018	**0.004**	0.001	**0.917**
		R-6	**0.688**	0.047	**0.016**	0.004	**0.904**
		R-7	**0.914**	0.016	**0.005**	0.001	**0.960**
		R-8	**0.945**	0.015	**0.008**	0.001	**0.983**
		Median	**0.766**	0.017	**0.010**	0.001	**0.971**
Bk 14-15	**LEW**	Q-1	**0.803**	0.031	**0.013**	0.002	**0.954**
		Q-2	**0.769**	0.017	**0.003**	0.001	**0.853**
		Q-3	**0.673**	0.027	**0.014**	0.002	**0.954**
		Q-4	**0.665**	0.018	**0.009**	0.001	**0.961**
		Q-5	**0.571**	0.024	**0.042**	0.005	**0.989**
		Q-6	**0.761**	0.020	**0.013**	0.002	**0.979**
		Q-7	**0.759**	0.017	**0.007**	0.001	**0.959**
		Q-8	**0.826**	0.027	**0.006**	0.001	**0.900**
		Median	**0.760**	0.022	**0.011**	0.001	**0.957**
	F344	R-1	**0.550**	0.026	**0.009**	0.002	**0.885**
		R-2	**0.552**	0.044	**0.022**	0.006	**0.901**
		R-3	**0.726**	0.061	**0.007**	0.004	**0.561**
		R-4	**0.857**	0.026	**0.003**	0.001	**0.700**
		R-5	**0.930**	0.021	**0.008**	0.001	**0.968**
		R-6	**0.712**	0.009	**0.012**	0.001	**0.995**
		R-7	**0.965**	0.039	**0.013**	0.002	**0.955**
		R-8	**0.915**	0.023	**0.011**	0.001	**0.975**
		Median	**0.792**	0.026	**0.010**	0.002	**0.928**

Figure 2. Log 2 of response ratio (LL/SS) as a function of log 2 of delay to food delivery (LLF delay-s/SSF delay-s) ratio. Equations near to regression lines show results of the GML for the LEW (Y_L) and F344 (Y_F) rats. Other details as in Figure 1.

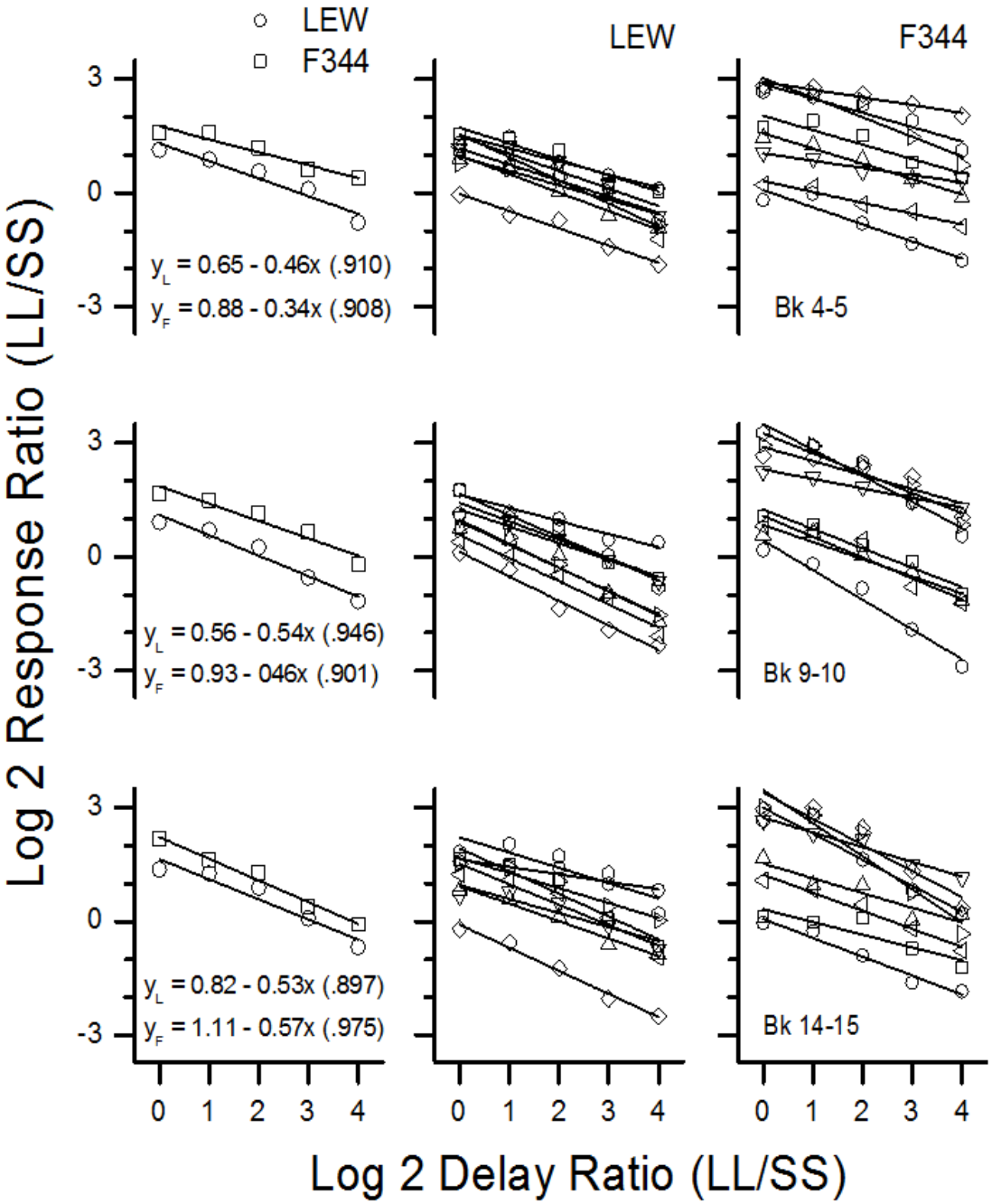

Table 2. Parameters, response ratio vs delay ratio, GML (Baum's 1974)

			Intercept	SE	Slope	SE	R^2
Bk 4-5	**LEW**	Q-1	**1.718**	0.169	**-0.420**	0.069	**0.900**
		Q-2	**1.515**	0.161	**-0.344**	0.066	**0.868**
		Q-3	**0.978**	0.089	**-0.486**	0.036	**0.978**
		Q-4	**1.489**	0.244	**-0.459**	0.100	**0.834**
		Q-5	**-0.029**	0.108	**-0.452**	0.044	**0.963**
		Q-6	**1.547**	0.282	**-0.609**	0.115	**0.871**
		Q-7	**0.959**	0.204	**-0.380**	0.083	**0.832**
		Q-8	**1.167**	0.161	**-0.422**	0.066	**0.910**
		Median	**1.328**	0.165	**-0.437**	0.067	**0.885**
	F344	R-1	**2.029**	0.208	**-0.379**	0.085	**0.825**
		R-2	**0.072**	0.201	**-0.450**	0.082	**0.879**
		R-3	**1.569**	0.095	**-0.402**	0.039	**0.963**
		R-4	**1.037**	0.075	**-0.189**	0.030	**0.904**
		R-5	**2.919**	0.077	**-0.202**	0.031	**0.911**
		R-6	**0.310**	0.086	**-0.286**	0.035	**0.942**
		R-7	**3.018**	0.261	**-0.514**	0.107	**0.848**
		R-8	**2.864**	0.183	**-0.377**	0.075	**0.860**
		Median	**1.799**	0.139	**-0.378**	0.057	**0.891**
Bk 9-10	**LEW**	Q-1	**1.662**	0.139	**-0.569**	0.057	**0.961**
		Q-2	**1.636**	0.114	**-0.346**	0.046	**0.932**
		Q-3	**0.977**	0.202	**-0.631**	0.082	**0.935**
		Q-4	**1.242**	0.133	**-0.443**	0.054	**0.943**
		Q-5	**0.127**	0.141	**-0.644**	0.058	**0.969**
		Q-6	**0.573**	0.170	**-0.608**	0.069	**0.950**
		Q-7	**0.926**	0.126	**-0.609**	0.052	**0.972**
		Q-8	**1.420**	0.250	**-0.486**	0.102	**0.844**
		Median	**1.110**	0.140	**-0.589**	0.057	**0.946**
	F344	R-1	**1.247**	0.149	**-0.511**	0.061	**0.946**
		R-2	**0.433**	0.212	**-0.782**	0.087	**0.953**
		R-3	**0.844**	0.199	**-0.453**	0.081	**0.883**
		R-4	**2.302**	0.044	**-0.251**	0.018	**0.980**
		R-5	**2.892**	0.257	**-0.370**	0.105	**0.740**
		R-6	**1.079**	0.271	**-0.549**	0.111	**0.856**
		R-7	**3.255**	0.257	**-0.526**	0.105	**0.858**
		R-8	**3.505**	0.217	**-0.687**	0.089	**0.937**
		Median	**1.775**	0.214	**-0.518**	0.088	**0.910**
Bk 14-15	**LEW**	Q-1	**1.922**	0.239	**-0.598**	0.098	**0.902**
		Q-2	**1.630**	0.087	**-0.196**	0.035	**0.881**
		Q-3	**0.923**	0.108	**-0.459**	0.044	**0.964**
		Q-4	**0.957**	0.215	**-0.369**	0.088	**0.806**
		Q-5	**-0.089**	0.099	**-0.608**	0.041	**0.982**
		Q-6	**1.513**	0.248	**-0.538**	0.101	**0.872**
		Q-7	**1.665**	0.135	**-0.395**	0.055	**0.926**
		Q-8	**2.211**	0.329	**-0.402**	0.134	**0.665**
		Median	**1.572**	0.175	**-0.430**	0.072	**0.891**
	F344	R-1	**0.316**	0.234	**-0.334**	0.095	**0.738**
		R-2	**0.060**	0.129	**-0.496**	0.053	**0.957**
		R-3	**1.522**	0.219	**-0.388**	0.089	**0.817**
		R-4	**2.725**	0.106	**-0.386**	0.043	**0.952**
		R-5	**3.390**	0.336	**-0.689**	0.137	**0.859**
		R-6	**1.230**	0.116	**-0.476**	0.047	**0.962**
		R-7	**3.460**	0.381	**-0.874**	0.156	**0.884**
		R-8	**2.996**	0.268	**-0.687**	0.109	**0.906**
		Median	**2.124**	0.226	**-0.486**	0.092	**0.895**

The above analyses revealed two important results: 1) delay discounting in LEW and F344 rats was well described by Equation 1 (Figure 1), and 2) an adapted version of the generalized matching law (Equation 2) also did a good job in explaining the choices of both strains (Figure 2). The above analyses were based upon the combination of responses on the two levers during the initial links (Figure 1: percentage of LL responses; Figure 2: log ratio of LL/SS responses). These can change as a function of changes in the responses on the LL option, changes in responses on the SS option, or both. To explore these possibilities, the sums of initial-link responses on the LL and SS levers, computed Blocks 4-5, 9-10,

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and 14-15, were analyzed separately. For the individual LEW and F344 rats and the medians of the groups these computations were plotted in Figures 3 and 4, respectively, as a function of delay to LLF delivery. Panels in the left column show the medians of the groups (LEW circles and F344 squares), and panels in the central and right columns the data of the individual LEW and F344 rats identified with different symbols. Best fitting lines to the data points of responses on the LL lever were generated with Equation 1, and lines corresponding to data points of responses on the SS lever were fitted with linear regression.

Responses on the LL lever (Figure 3) decreased with increasing delay to the LLF delivery; Equation 1 adequately described this relation, explaining most of the variability in LL responses that occurred as a function of within session changes in the delay to LLF delivery. For LL responses of individual LEW and F344 rats, and the group's medians, Table 3 shows the values of the intercept (*A*), *k,* and R^2 obtained for blocks of sessions 4-5, 9-10, and 14-15 using Equation 1. Estimates of k revealed that responses on the LL lever decreased at similar rates in both strains. No significant differences in values of k were observed in blocks of sessions 4-5 (U = 44, p = .227), 9-10 (U = 48, p = .103), and 14-15 (U = 26, p = .564).

Figure 4 shows that total responses on the SS lever increased linearly with increasing delay to food delivery for responses on the LL lever. Slopes ranging from 0.004 to 0.013 show a positive relation between responses on the SS lever and delay to LLF. Linear regression provided an adequate fit of this relation for both strains (average R^2 of 0.880 and 0.788 for LEW and F344 rats, respectively). Positive relations for individual rats are displayed in the central and right columns of Figure 4. Table 4 shows the values of the intercept, slope, and R^2 obtained for blocks of sessions 4-5, 9-10, and 14-15 using standard linear regression. No significant differences in values of slopes were found in blocks of sessions 4-5 (U = 43, p = 0.270), 9-10 (U = 26, p = 0.564), and 14-15 (U = 18, p = 0.156).

To further illustrate the changes in delay discounting in both strains of rats across the course of the study, the values of k (Equation1), AUC, and values of slopes obtained with the GML were plotted in Figure 5 against the block of sessions. The top and middle panels of this figure show changes in *k* and AUC, respectively, of the discount functions. The bottom panel shows the changes in the slope of the GML functions. All curves show the groups' medians of LEW (continuous line) and F344 (broken line) rats. For Blocks 1-10, Figure 5 shows (panels from top to bottom) that the choices of the LEW rats were more impulsive than those of the F344 rats. That is, LEW rats had higher k and lower AUC values. In the last five blocks (11-15), the group medians for all three of these dependent variables were similar for both strains. To further examine strain differences in *k*, AUC, and absolute values of slopes, separate Mann-Whitney U tests were conducted using the data of the individual LEW and F344 rats (not showing in Figure 5). For Blocks 1-5, the values of *k* for the LEW rats were significantly higher (U = 54, p = 0.024) than those for the F344 rats, values of AUC for the LEW rats were significantly lower (U = 11, p = 0.031) than those for the F344 rats, and absolute values of slopes for the LEW were significantly higher (U = 55, p = 0.018) than those for the F344 rats. In Blocks 6-10 values of *k* for individual LEW rats were not significantly different from those for the F344 rats (U = 49, p = 0.083), values of AUC for the LEW rats were significantly lower (U = 10, p = 0.024) than those for the F344 rats, and absolute values of slopes for the LEW were not significantly different from (U = 46, p = 0.156) those for the F344 rats. In the last five blocks of sessions (11-15), there were no significant differences between strains in the values of *k* (U = 35, p = 0.973), AUC (U = 33, p = 0.958), or absolute slopes (U = 25, p = 0.495) obtained for individual LEW and F344 rats. Thus, initial differences between strains in values of *k*, AUC, and absolute slopes were not apparent after extended training in the choice situation.

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Figure 3. Total responses on the LL lever as a function of delay in (s) to LLF delivery. Curves represent best fitting functions using Equation 1. Other details as in Figure 1.

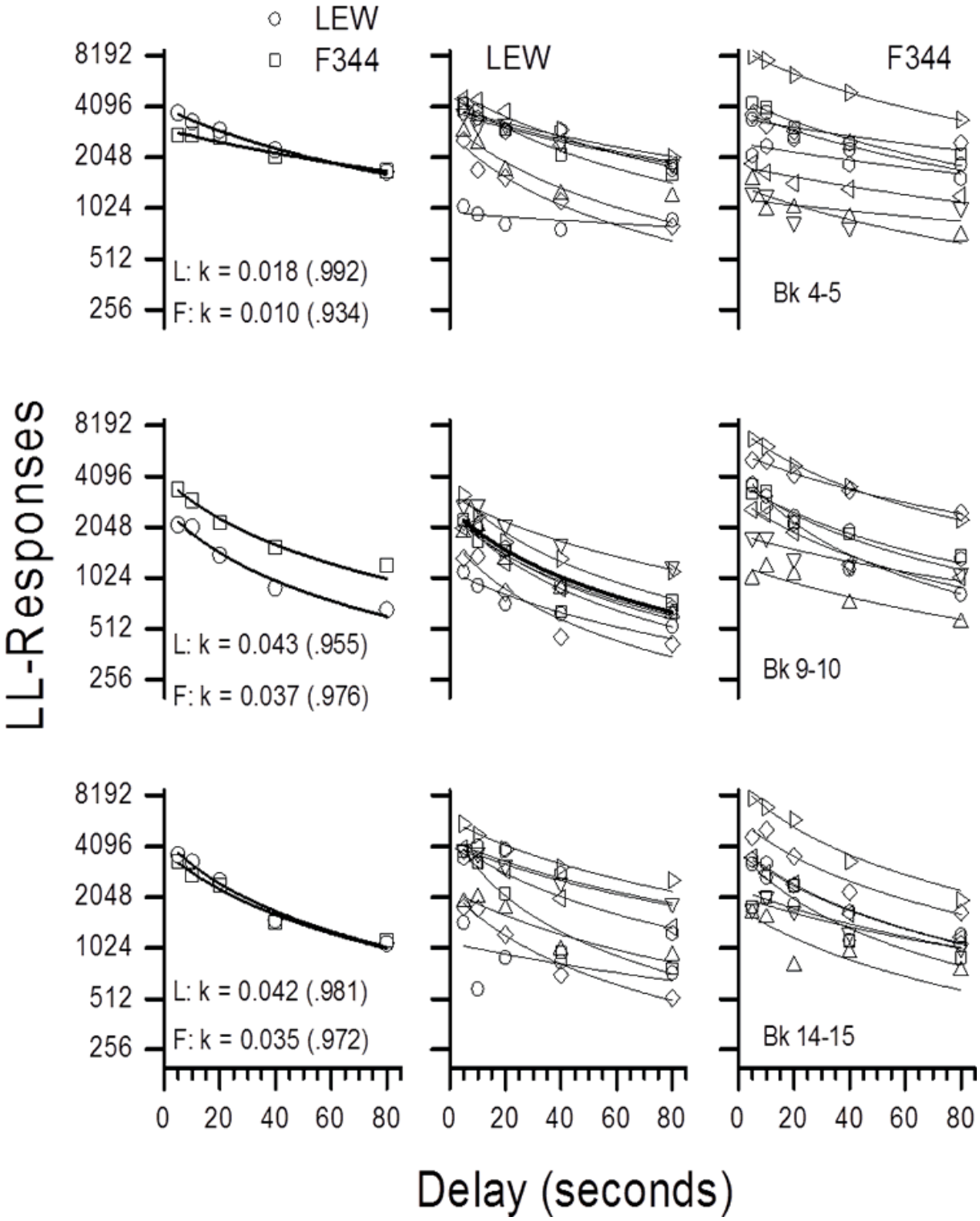

Table 3. Parameters, LL-responses, hyperbolic discounting.

			Intercept	SE	k	SE	R^2
Bk 4-5	**LEW**	Q-1	**4919.79**	203448	**0.030**	0.004	**0.983**
		Q-2	**958.12**	79321	**0.003**	0.003	**0.022**
		Q-3	**3339.09**	387376	**0.037**	0.013	**0.893**
		Q-4	**3850.68**	164746	**0.013**	0.002	**0.945**
		Q-5	**2907.24**	391881	**0.043**	0.016	**0.889**
		Q-6	**5310.78**	318524	**0.024**	0.005	**0.956**
		Q-7	**4063.25**	245269	**0.012**	0.003	**0.880**
		Q-8	**3988.18**	276952	**0.013**	0.004	**0.873**
		Median	**3919.43**	261110	**0.019**	0.004	**0.891**
	F344	R-1	**4616.06**	298201	**0.019**	0.005	**0.920**
		R-2	**3893.17**	321379	**0.016**	0.005	**0.850**
		R-3	**1397.27**	183644	**0.015**	0.008	**0.633**
		R-4	**1160.23**	174424	**0.004**	0.005	**-0.069**
		R-5	**3512.52**	238226	**0.007**	0.003	**0.678**
		R-6	**1825.15**	108216	**0.008**	0.003	**0.785**
		R-7	**9058.00**	176659	**0.021**	0.001	**0.994**
		R-8	**2485.36**	268029	**0.006**	0.004	**0.440**
		Median	**2998.94**	210935	**0.011**	0.005	**0.732**
Bk 9-10	**LEW**	Q-1	**2771.09**	437791	**0.054**	0.022	**0.893**
		Q-2	**1132.24**	99556	**0.019**	0.006	**0.856**
		Q-3	**2458.40**	344358	**0.038**	0.015	**0.881**
		Q-4	**3167.01**	168089	**0.022**	0.004	**0.959**
		Q-5	**1808.18**	294410	**0.053**	0.022	**0.896**
		Q-6	**2646.74**	401262	**0.044**	0.019	**0.884**
		Q-7	**3691.75**	498683	**0.047**	0.017	**0.895**
		Q-8	**2701.59**	159049	**0.040**	0.007	**0.979**
		Median	**2674.16**	319384	**0.042**	0.016	**0.894**
	F344	R-1	**3747.31**	352142	**0.025**	0.008	**0.894**
		R-2	**4797.87**	444719	**0.060**	0.014	**0.972**
		R-3	**1219.00**	124229	**0.014**	0.006	**0.769**
		R-4	**1843.58**	138329	**0.011**	0.004	**0.787**
		R-5	**5628.11**	169066	**0.016**	0.002	**0.980**
		R-6	**3016.87**	180230	**0.029**	0.006	**0.964**
		R-7	**7852.57**	157492	**0.031**	0.002	**0.996**
		R-8	**3906.17**	447311	**0.030**	0.011	**0.871**
		Median	**3826.74**	174648	**0.027**	0.006	**0.929**
Bk 14-15	**LEW**	Q-1	**5601.56**	734275	**0.085**	0.025	**0.966**
		Q-2	**1100.13**	297713	**0.008**	0.012	**-0.069**
		Q-3	**2272.87**	239962	**0.021**	0.008	**0.847**
		Q-4	**4267.06**	84050	**0.017**	0.001	**0.991**
		Q-5	**2311.22**	230200	**0.045**	0.012	**0.951**
		Q-6	**4523.52**	169729	**0.030**	0.004	**0.987**
		Q-7	**5861.40**	345101	**0.021**	0.004	**0.940**
		Q-8	**4456.69**	694761	**0.017**	0.010	**0.689**
		Median	**4361.87**	268837	**0.021**	0.009	**0.945**
	F344	R-1	**2288.18**	476107	**0.015**	0.013	**0.463**
		R-2	**3941.20**	525451	**0.049**	0.017	**0.905**
		R-3	**1790.78**	332294	**0.026**	0.016	**0.634**
		R-4	**2072.05**	191491	**0.013**	0.005	**0.780**
		R-5	**5934.56**	752449	**0.033**	0.013	**0.884**
		R-6	**3997.05**	187029	**0.034**	0.005	**0.982**
		R-7	**9756.84**	732714	**0.042**	0.009	**0.970**
		R-8	**4148.94**	194309	**0.035**	0.005	**0.984**
		Median	**3969.13**	404201	**0.033**	0.011	**0.895**

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Figure 4. Total responses on the SS lever as a function of delay in (s) to LLF delivery. Best fitting lines were generated with the least squares method. Other details as in Figure 1.

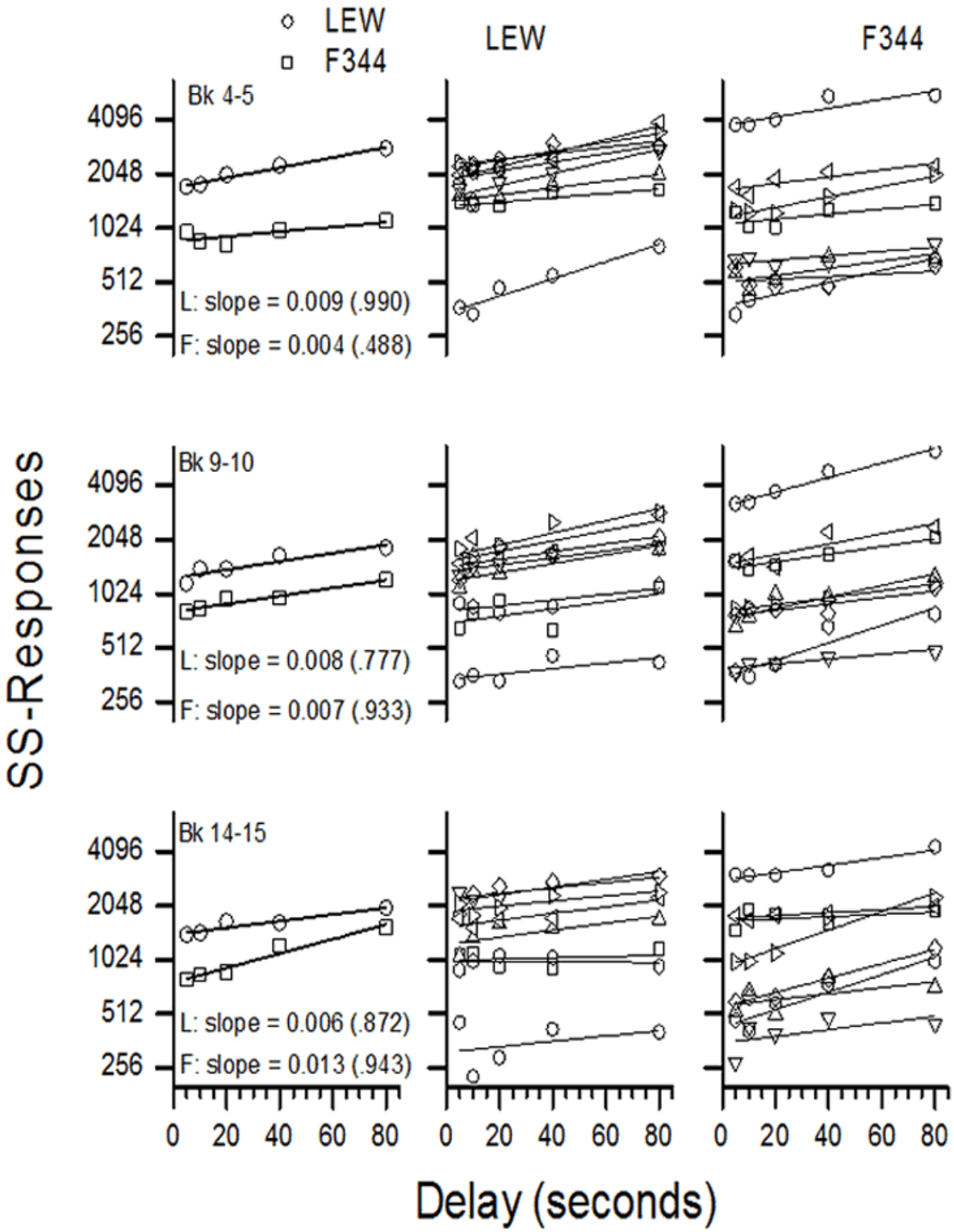

Table 4. Parameters, SS-responses, linear regresssion.

			Intercept	SE	Slope	SE	R^2
Bk 4-5	**LEW**	Q-1	**10.397**	0.053	**0.004**	0.001	**0.690**
		Q-2	**8.421**	0.094	**0.016**	0.002	**0.923**
		Q-3	**10487**	0.047	**0.006**	0.001	**0.881**
		Q-4	**10.561**	0.085	**0.011**	0.002	**0.877**
		Q-5	**11162**	0.080	**0.006**	0.002	**0.645**
		Q-6	**10.881**	0.059	**0.013**	0.001	**0.951**
		Q-7	**11087**	0.045	**0.008**	0.001	**0.936**
		Q-8	**10.896**	0.062	**0.008**	0.002	**0.873**
		Median	**10.721**	0.061	**0.008**	0.001	**0.879**
	F344	R-1	**10.074**	0.111	**0.005**	0.003	**0.319**
		R-2	**11890**	0.098	**0.008**	0.002	**0.730**
		R-3	**8.981**	0.137	**0.007**	0.003	**0.442**
		R-4	**9.326**	0.082	**0.004**	0.002	**0.436**
		R-5	**8.996**	0.147	**0.003**	0.004	**-0.139**
		R-6	**10695**	0.082	**0.006**	0.002	**0.691**
		R-7	**10.188**	0.053	**0.010**	0.001	**0.934**
		R-8	**8.543**	0.135	**0.011**	0.003	**0.728**
		Median	**9.700**	0.104	**0.007**	0.003	**0.566**
Bk 9-10	**LEW**	Q-1	**9.448**	0.210	**0.007**	0.005	**0.161**
		Q-2	**8.406**	0.115	**0.005**	0.003	**0.375**
		Q-3	**10223**	0.100	**0.008**	0.002	**0.730**
		Q-4	**10.404**	0.050	**0.006**	0.001	**0.873**
		Q-5	**10491**	0.156	**0.007**	0.004	**0.388**
		Q-6	**10595**	0.172	**0.009**	0.004	**0.509**
		Q-7	**10671**	0.118	**0.011**	0.003	**0.785**
		Q-8	**9.672**	0.086	**0.005**	0.002	**0.567**
		Median	**10.313**	0.116	**0.007**	0.003	**0.538**
	F344	R-1	**10.445**	0.060	**0.007**	0.001	**0.850**
		R-2	**11612**	0.054	**0.013**	0.001	**0.964**
		R-3	**9509**	0.127	**0.011**	0.003	**0.738**
		R-4	**8.612**	0.042	**0.004**	0.001	**0.819**
		R-5	**9.572**	0.082	**0.006**	0.002	**0.664**
		R-6	**10.537**	0.131	**0.010**	0.003	**0.666**
		R-7	**9.671**	0.012	**0.006**	0.000	**0.992**
		R-8	**8.445**	0.143	**0.016**	0.003	**0.839**
		Median	**9.622**	0.071	**0.008**	0.002	**0.829**
Bk 14-15	**LEW**	Q-1	**9.991**	0.121	**0.001**	0.003	**-0.270**
		Q-2	**8.296**	0.308	**0.005**	0.007	**-0.165**
		Q-3	**10291**	0.143	**0.006**	0.003	**0.386**
		Q-4	**11135**	0.058	**0.005**	0.001	**0.737**
		Q-5	**11066**	0.130	**0.007**	0.003	**0.502**
		Q-6	**10.611**	0.069	**0.006**	0.002	**0.760**
		Q-7	**10.905**	0.075	**0.005**	0.002	**0.580**
		Q-8	**9.970**	0.086	**0.000**	0.002	**-0.327**
		Median	**10.451**	0.104	**0.005**	0.003	**0.444**
	F344	R-1	**10718**	0.119	**0.002**	0.003	**-0.145**
		R-2	**11470**	0.055	**0.007**	0.001	**0.869**
		R-3	**9.153**	0.189	**0.005**	0.005	**0.100**
		R-4	**8.459**	0.208	**0.006**	0.005	**0.116**
		R-5	**9.127**	0.041	**0.013**	0.001	**0.979**
		R-6	**10.758**	0.026	**0.003**	0.001	**0.832**
		R-7	**9.865**	0.109	**0.017**	0.003	**0.912**
		R-8	**8.756**	0.124	**0.016**	0.003	**0.875**
		Median	**9.509**	0.114	**0.007**	0.003	**0.850**

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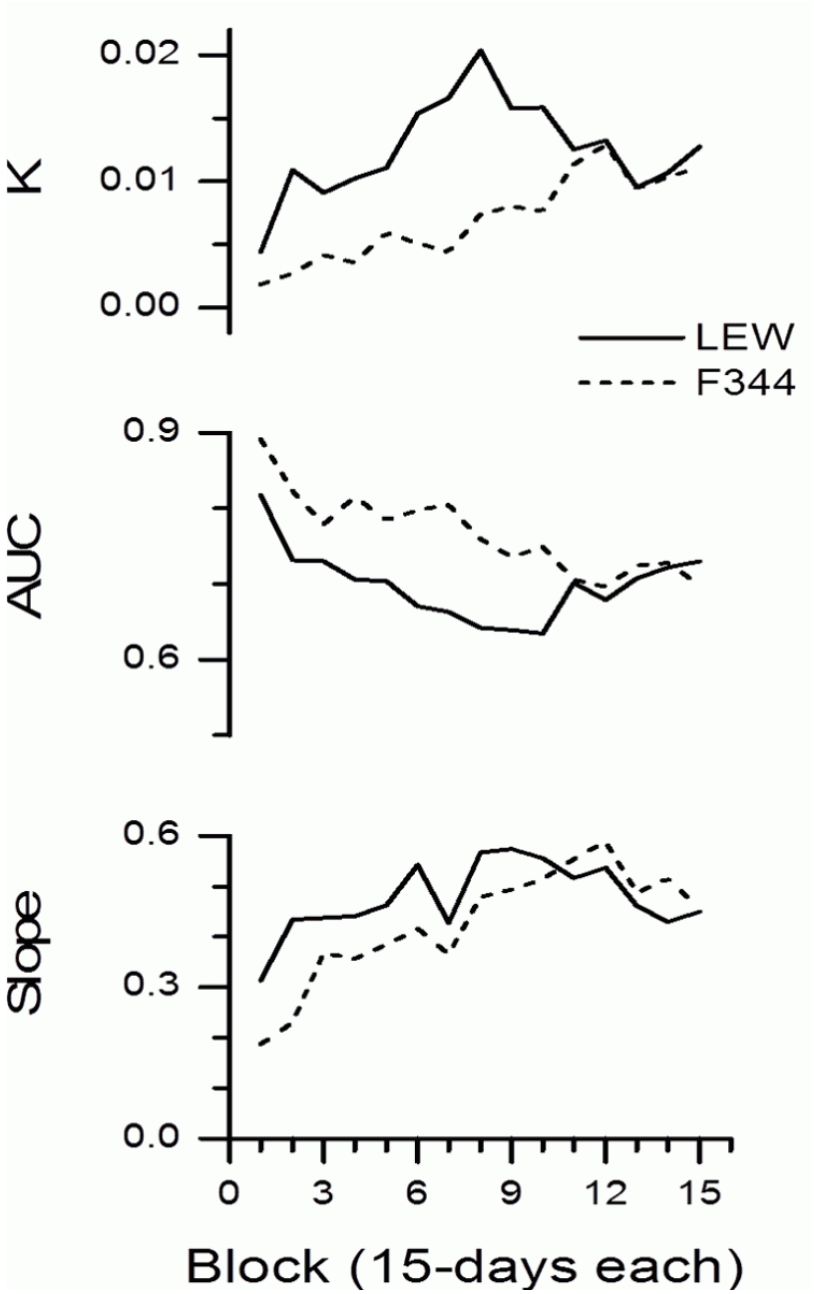
Figure 5. Values of *k* (top panel), AUC (middle panel), and absolute slopes (bottom panel) as a function of blocks of sessions. For each block, panels show groups' medians (LEW continuous line and F344 broken line) obtained across sessions of the same block of individual rats of the same strain.



The fact that in this study both Equation 1 and the GML explained the impulsive choices of LEW and F344 rats well, suggests some consistencies between these two models of choice. To further explore this possibility, the values of *k* computed for the LEW and F344 rats were plotted against the absolute values of the slopes. The two upper panels of Figure 6 show correlations obtained with the medians of the groups (LEW circles and F344 squares) and the multiple panels below them, correlations obtained with values of individual LEW and F344 rats. In all cases, Figure 6 shows a positive relation between the values of k and the values of the slopes. Values of Pearson's *r* for the LEW (ranging from 0.827 to 0.961) were not significantly different (U = 26, p = 0.564) from those of the F344 rats (ranging from 0.580 to 0.964).

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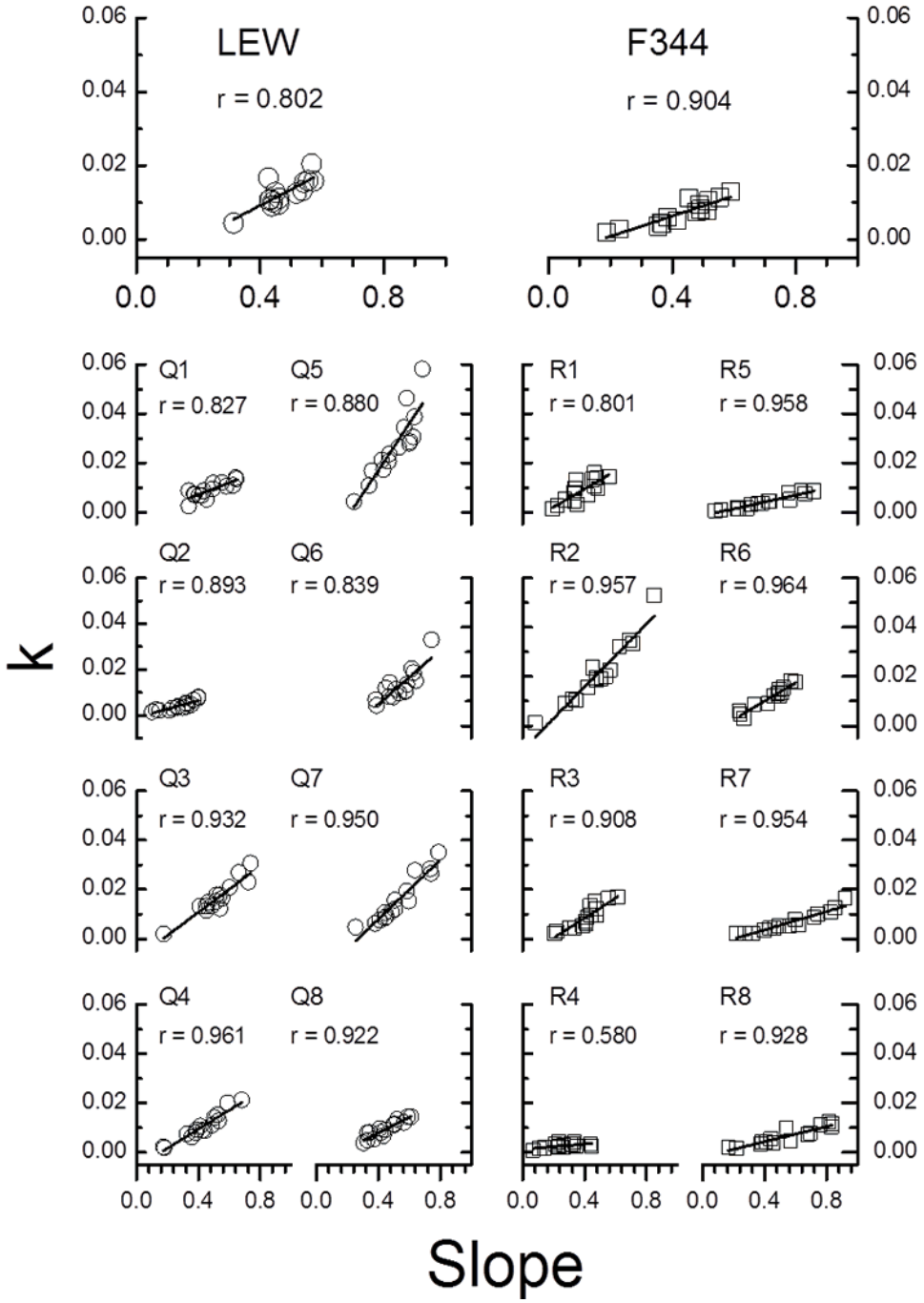
Figure 6. Values of *k* against absolute values of slopes. The upper panels show correlations, Pearson's *r*, computed with the medians of the groups (LEW circles and F344 squares) and the multiple panels correlations obtained with values of individual LEW (Q1-Q8) and F344 (R1-R8) rats.



Discussion

This study introduced a novel concurrent-chains procedure to compare delay discounting in LEW and F344 rats. Delay to the larger reinforcer was manipulated within sessions, retaining the efficiency of Evenden and Ryan's (1996) method for generating an entire delay-of-reinforcement function within each session. Response allocation in the initial-link was interpreted as a measure of preference for the LLF versus SSF terminal links (e.g., Grace, 1999). Terminal-link entry was arranged randomly such that both levers were active the same number of times during the session, thus controlling the potential confound

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between rate of food delivery and delay to food delivery. The FI value for the terminal-link associated with the LLF delivery was presented in random order within sessions, reducing the possibility of carry over effects of previous delay on current choice.

The analysis of choice revealed that delay discounting in LEW and F344 rats was well described by Equation 1, a result that was first documented by Stein's et al. (2012) using a steady-state adjusting-amount procedure (i.e., Mazur, 2000) and a rapid version of it adapted from the method described by Richards, Mitchell, de Wit, and Seiden (1997). The present study extended the generality of this finding to a novel concurrent-chains procedure in which the responses on two levers occurring in the initial-link were not constrained by the discrete-trial format in the cycles of food delivery. Yet, the procedure was efficient in generating graded discount functions for individual rats within each session. During the early and intermediate stages of exposure to the procedure, the discount functions of the LEW were steeper than those of the F344 rats, that is, the former strain was choosing more impulsively than the latter strain of rats. This difference, however, disappeared completely with the extended experience under the concurrent-chains procedure, which is the main finding of this study further discussed below.

Values of *k* from the hyperbolic discount functions, ranging from 0.005 to 0.016, indicate that LEW and F334 rats discounted LLF deliveries at relatively low rates. This finding is consistent with values of *k* (i.e., 0.01) obtained in Wistar-Kyoto rats choosing between small/immediate and large/delayed reinforcers under procedures using discrete trials (see Fox et al., 2008 Table 1). In contrast, studies in LEW and F344 rats using a steady-state adjusting-amount procedure reported high values of *k* ranging from 0.43 to 1.76 (Stein' et al., 2012). However, when they used a rapid version of the adjusting-amount procedure utilized by Richards et al. (1997), values of *k* were more moderate, ranging from 0.25 to 0.82, showing no differences in delay discounting between LEW and F344 rats. Similarly, values of *k* ranging from 0.25 to about 0.60 across different strains of inbred rats were found using an adapted version of the adjusting-amount procedure (Wilhelm & Mitchell, 2009). Nonetheless, when the latter procedure was used to assess the effects of the reinforcer's magnitude (sucrose solution) on the impulsive choices of Sprague-Dawley rats, a wider range of *k* values (from 0.07 to 0.93) was observed, suggesting that the different concentrations of sucrose (3, 10, and 30%) were discounted at different rates (see Farrar, Kieres, Hausknecht, de Wit, & Richards, 2003 Table 1). Thus, a wide range of *k* values, varying from very low (i.e., 0.01 in Fox et al., 2008) to considerably high (i.e., 1.76 in Stein et al., 2012), describes the current field of delay discounting in non-human subjects. The low rates of delay discounting obtained in the present study may have resulted from employing a concurrent-chains procedure that required an equal number of terminal-link entries, or from the fact that the delays to LLF were presented in random order; more likely, low values of *k* were conjunctively determined by these two factors.

Bias for either the LL-lever or the SS-lever, and sensitivity of behavior ratio to delay to food delivery ratio were assessed with the generalized matching law (Baum, 1974) revealing three important results: (1) All LEW and F344 rats developed a clear bias for the LL lever regardless of whether the LLF was delivered for responding on the left or on the right lever (recall that it was balanced within each strain); (2) the behavior ratio decreased with increasing delay to food delivery ratio, indicating sensitivity of choice to within session changes in delay to food delivery ratio (i.e., a measure of "impulsiveness"); and (3) Sensitivity to delay of food delivery ratio increased, and bias for the LL lever was strengthened with extended training in the choice situation. Together, these findings confirm that the matching law (Herrnstein, 1970) also describes relations between preference and delay to food delivery (Ainslie, 1992).

Total responses on the LL lever decreased as a function of delay to LLF delivery according to a hyperbolic-decay function (e.g., Mazur, 1984, 1987, 1997, 2007, 2012). Generally, changes in total LL responses occurring as a function of delay to LLF delivery were well described by Equation 1 (median R^2

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of 0.945 and 0.845 for LEW and F344 rats, respectively, in Blocks 14-15). As far as we know, this is the first study showing that the hyperbolic-decay model (i.e., Mazur, 1987) does a good job describing changes in the responses occurring in the alternative associated with increasing delay to food delivery. Estimates of *k* indicated that responses on the LL lever decreased at similar low rates in both strains. Although in Blocks 4-5 and 9-10, the LEW rats generated steeper slopes than the F334 rats, in the last blocks (14-15) the values of *k* were slightly higher for the F344 rats (median of 0.033) than for the LEW rats (median of 0.021).

The result showing that responses on the LL lever decreased with increasing delay to LLF delivery, appears to be consistent with accounts of delay discounting claiming that the value of a reinforcer decreases with increasing delay between a choice response and its reinforcement (e.g., Mazur, 1987; Sopher & Sheth, 2006). But this interpretation alone is difficult to sustain here, because choosing the LL lever required rats to emit more than one response in the initial-link that arranged entries to the terminal-link. Moreover, the present study used FI schedules in the terminal-link to vary delay to LL-F delivery, allowing more that one response to occur during the delay. Research using a similar concurrent-chains procedure (Neuringer, 1969) has shown that animals are indifferent to FI and fixed-time (FT) terminal-links. Thus, isolated relations between a choice response and reinforcement hardly occurred in the present concurrent-chains procedure. LEW and F344 rats made several responses in the initial-link before entering the terminal-link to produce a reinforcer, and after producing it, rats travelled from the front to the back wall of the chamber to press the back-lever that re-started the cycle of the concurrent-chains procedure. In each cycle these activities implied effort to reach the choice point, and effort plays an important role in controlling choice (Salamone & Correa, 2009) and sensitivity to reinforcement (Aparicio, 2001; Aparicio & Baum, 1997; Aparicio & Cabrera, 2001; Aparicio & Otero, 2004). The current study might be another example of a choice situation where extended variables (i.e., effort/food ratio) and local variables (i.e., delay to LL-F delivery) conjointly controlled choice (e.g., Grace 1994; Killen, 1982; Madden, Bickel, & Jacobs, 2000; Squires & Fantino, 1971; Mazur, 2012).

Responses on the SS lever increased linearly as a function of increasing delay to LLF delivery, indicating that choice was controlled by the relative reciprocal of delay to food delivery on each lever (e.g., Chung & Herrnstein, 1967; Herbert 1970, Experiment I), and contrasting with exponential functions obtained in studies where immediate and delayed reinforcement was concurrently available in equal variable interval schedules (e.g., Chung, 1965).

Delay discounting was estimated with values of *k* (Equation 1) and AUC, a theoretically neutral measure of discounting (see Green & Myerson, 2010). In Blocks 1-10, values of *k* of the individual LEW rats were higher than those of the F344 rats, and values of AUC for the former strain were lower than those for the latter strain. But, in the last blocks of sessions (11-15) these dependent variables revealed comparable levels of delay discounting, estimates of *k* and AUC shown no significant differences between LEW and F344 rats. Further comparisons between *k* and AUC are beyond the scope of the present study aimed to investigate the contribution of extended training in controlling impulsive choice. Nonetheless, systematic comparisons between *k* and AUC (i.e., Green, Myerson, Shan, Estle, & Holt, 2007) are warranted in future research given the increasing trend in the number of studies that are using these metrics to describe delay discounting (e.g., Stein et al., 2012).

A remarkable finding in this study is that with extended training in the choice situation there were no differences between LEW and F344 rats in the following dependent variables: (1) percentage of LL choice, (2) rate of discounting, *k* in Eq. 1, (3) AUC, (4) log 2 of response ratio, (5) bias, (6) absolute values of slopes (GML), and (7) responses in the LL-lever and related values of *k*. One possible interpretation of these results is that with extended training in the current procedure the F344 rats developed patterns of

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choice similar to those the LEW rats showed in blocks of sessions 1 to 5, for the F344 rats measures of choice indicated enhanced sensitivity to delay of LLF delivery in the last blocks (14-15) of sessions. Thus, in the F344 rats the pattern of impulsive choice slowly emerged across blocks of sessions, whereas in the LEW rats it started earlier in training. At the end of this study, however, both strains displayed comparable performances; that is, the F344 rats matched the pattern of impulsive choice that the LEW rats exhibited early in training. Thus, the data from the present study combined with the findings of Wilhelm & Mitchell (2009) and those of Stein et al (2012) showing no differences in delay discounting between LEW and F344 rats using an adjusting-amount procedure, suggests that the type procedure and training (i.e., extended) can profoundly impact whether or not differences in delay discounting between LEW and F344 rats can be observed in studies of choice.

In conclusion, we introduced a novel procedure to prevent the development of exclusive preference for the lever delivering the LLF, and reduce the possibility of carry over effects of previous delays on current choice. One aim of the study was to investigate the potential contribution of extended training in controlling impulsive choices of LEW and F344 rats. These strains were used as subjects in this study because their genetic and neurochemical differences have implications for analyses of impulsive choice (Anderson & Diller, 2010), suggesting that the LEW make more impulsive choices than the F344 rats (e.g., Anderson & Diller, 2010; Anderson & Woolverton, 2005; Madden et al., 2008; Stein et al., 2012). The fact is that differences in impulsive choice between LEW and F344 rats have been taken for granted in studies using discrete-trial procedures in which usually a reduced number of sessions (about 5-sessions for each delay series) is instigated (e.g., Anderson & Diller, 2010; Anderson, & Woolverton, 2005; Wilhelm & Mitchell, 2009), or delay to the LL reinforces is manipulated between conditions lasting for a minimum of 10 sessions in which stable choices are assessed (e.g., Madden et al., 2008). Also, in studies where differences in delay discounting between LEW and F344 rats were found using a steady-state version of Mazur's (2000) adjusting-amount procedure, each delay condition lasted a minimum of 10 sessions (Stein et. al., 2012). In contrast, with extended experience (i.e., about 115 consecutive days) in the current choice situation there were no significant differences between LEW and F344 rats in several dependent variables; both strains exhibited parallel performances and levels of impulsivity. Therefore, differences in delay discounting between LEW and F344 rats, usually found early in training, might be transitory and should be taken with caution in making conclusions about underlying neurobiology of impulsive choices. Nevertheless, there are studies showing that independent of life experience aged F344 rats prefer larger delayed over small immediate reinforcers (i.e., show attenuated delay discounting) to a greater extend than young adult rats (Simon et al., 2010).

It is concluded that the current study may be another example of a choice situation where extended variables (i.e., effort/food ratio) and local variables (i.e., delays between LL-responses and food delivery) jointly determined preference (e.g., Grace 1994; Killen, 1982; Madden et al., 2000; Squires & Fantino, 1971; Mazur, 2012).

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