

*TRANSITIONAL AND STEADY-STATE CHOICE BEHAVIOR UNDER AN
ADJUSTING-DELAY SCHEDULE*

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Twelve rats made repeated choices on an adjusting-delay schedule between a smaller reinforcer (A) that was delivered immediately after a response and a larger reinforcer (B) that was delivered after a delay which increased or decreased by 20% depending on the subject's choices in successive blocks of trials. In two phases of the experiment (100 sessions and 40 sessions), reinforcer sizes were selected which enabled theoretical parameters expressing the rate of delay discounting and sensitivity to reinforcer size to be estimated from the ratio of the indifference delays obtained in the two phases. Indifference delays, calculated from adjusting delays in the last 10 sessions of each phase, were shorter when the sizes of A and B were 14 and 25 μl of a 0.6 M sucrose solution than when they were 25 and 100 μl of the same solution. The ratio of the indifference delays was significantly smaller than that predicted on the basis of an assumed linear relation between reinforcer size and instantaneous reinforcer value, consistent with a previous proposal that this relation may be hyperbolic in form. Estimates of the rate of delay discounting based on the ratio of the two indifference delays (mean, 0.08 s^{-1}) were similar to values obtained previously using different intertemporal choice protocols. Estimates of the size-sensitivity parameter (mean 113 μl) were similar to estimates recently derived from performance on progressive-ratio schedules. In both phases of the experiment, adjusting delays in successive blocks of trials were analyzed using the Fourier transform. The power spectrum obtained from individual rats had a dominant frequency that corresponded to a period of oscillation of the adjusting delay between 30 and 100 trial blocks (mean, 78). Power in the dominant frequency band was highest in the early sessions of the first phase and declined with extended training. It is suggested that this experimental protocol may have utility in neurobehavioral studies of intertemporal choice.

Key words: intertemporal choice, adjusting-delay schedule, delay discounting, reinforcer magnitude, Fourier transform, lever press, rat

In an intertemporal choice schedule, the subject chooses between reinforcers that differ with respect to their sizes and delays. For example, a subject may be confronted with two operanda, A and B; if it responds on A, a small reinforcer will be delivered after a short delay, whereas if it responds on B, a larger reinforcer will be delivered after a longer delay.

According to one model of intertemporal choice behavior (Mazur, 1987, 2001, 2006), the reinforcing value of each outcome is a declining hyperbolic function of the delay interposed between the response and the primary reinforcer.

$$V_A = q_A \cdot \frac{1}{1 + K \cdot d_A}; \quad V_B = q_B \cdot \frac{1}{1 + K \cdot d_B}, \quad (1a, 1b)$$

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where q_A and q_B are the sizes of the two primary reinforcers, d_A and d_B are the delays associated with each alternative, and K is a parameter expressing the rate of delay discounting. It is assumed that when faced with a choice between A and B, the subject selects the outcome that has the higher overall value at the moment of choice. It should be noted that V refers not to the value of the primary reinforcer, but to the overall value of the conditioned reinforcing stimuli that are present at the moment of choice. Thus Equations 1a and 1b do not imply that the primary reinforcer itself is devalued as a function of delay (Mazur, 1995).

Equations 1a and 1b imply direct proportionality between value and the size of a reinforcer. However, there is emerging evidence for a nonlinear relation between value and reinforcer size (Mazur & Biondi, 2009; Rickard, Body, Zhang, Bradshaw, & Szabadi, 2009), in keeping with the economic concept of diminishing marginal utility (Killeen, 2009; Pine, et al., 2009). Ho, Mobini, Chiang,

Bradshaw and Szabadi (1999) proposed a modification of Equations 1a and 1b to take into account the possibility of such a nonlinear relation. Ho *et al.* (1999) posited a hyperbolic relation, in which the effect of reinforcer magnitude on value is modulated by a single “size-sensitivity parameter”, Q :

$$V_A = \frac{1}{1 + Q/q_A} \cdot \frac{1}{1 + K \cdot d_A};$$

$$V_B = \frac{1}{1 + Q/q_B} \cdot \frac{1}{1 + K \cdot d_B}. \quad (2a, 2b)$$

By experimentally manipulating the delays and/or sizes of A and B, a point of indifference may be determined at which the subject shows no preference for either outcome. It is generally assumed that indifference implies that $V_A = V_B$. Equating the right-hand sides of Equations 2a and 2b and rearranging the terms yields the following linear relation between the *indifference delay* to the larger reinforcer, $d_{B(50)}$, and the delay to the smaller reinforcer, d_A (Ho *et al.*, 1999):

$$d_{B(50)} = \frac{1}{K} \cdot \left[\frac{Q/q_A - Q/q_B}{1 + Q/q_B} \right] + d_A \cdot \frac{1 + Q/q_A}{1 + Q/q_B}. \quad (3)$$

This relation can be used to examine the effects of neurobiological interventions on the hypothetical processes of delay discounting and sensitivity to reinforcer size. For example, if the sizes of Reinforcers A and B (q_A and q_B) are held constant and indifference delays are determined for a series of delays to Reinforcer A (d_A), a change in the slope of Equation 3 induced by a cerebral lesion implies a change in Q (i.e., a change in sensitivity to reinforcer size), whereas a change in the intercept without a concomitant change in slope implies a change in K (i.e., a change in the rate of delay discounting, Ho *et al.*, 1999; Mazur, 2006). Using this approach it has been found that excitotoxic and dopamine-depleting lesions of the orbital prefrontal cortex increase both Q and K (Kheramin, *et al.*, 2002, 2004), whereas destruction of the core of the nucleus accumbens or disconnection of the nucleus accumbens from the orbital prefrontal cortex produces a selective increase in K (Bezzina *et al.*, 2007, 2008). Equation 3 has also been applied successfully in experimental studies of inter-

temporal choice in humans (Hinvest & Anderson, 2010; Liang, Ho, Yang, & Tsai, 2010).

A significant practical difficulty with the application of Equation 3 is the length of time needed to collect sufficient data to fit the linear functions, because each value of $d_{B(50)}$ is derived from steady-state performance using a different value of d_A , which, in the case of animal subjects, may require 40–60 training sessions, and five or six $d_{B(50)}/d_A$ pairs are needed to obtain a reliable linear function (see, for example, Kheramin *et al.*, 2002). Since neurobehavioral experiments involving cerebral lesions typically entail two or more groups of 10 or more subjects, it is clear that this kind of experiment is very costly in terms of both time and money.

One purpose of this paper is to describe an abbreviated approach to estimating Q and K based on Equation 3, which requires the determination of only two values of $d_{B(50)}$. The logic of the method is as follows. If the smaller of the two reinforcers is delivered immediately (i.e. $d_A \approx 0$), Equation 3 becomes

$$d_{B(50)} = \frac{1}{K} \cdot \left[\frac{Q/q_A - Q/q_B}{1 + Q/q_B} \right]. \quad (3a)$$

Equation 3a is the limit of Equation 3 as $d_A \rightarrow 0$. If two indifference delays are determined using different pairs of reinforcer sizes (q_{A1} , q_{B1} , and q_{A2} , q_{B2}), then the ratio of the indifference delays is

$$\frac{d_{B(50)1}}{d_{B(50)2}} = \frac{1/q_{A1} - 1/q_{B1}}{1/q_{A2} - 1/q_{B2}} \cdot \frac{1 + Q/q_{B2}}{1 + Q/q_{B1}}. \quad (4)$$

If reinforcer sizes are selected such that $(1/q_{A1} - 1/q_{B1}) = (1/q_{A2} - 1/q_{B2})$, Equation 4 simplifies to

$$\frac{d_{B(50)1}}{d_{B(50)2}} = \frac{1 + Q/q_{B2}}{1 + Q/q_{B1}}, \quad \text{or}$$

$$Q = \frac{d_{B(50)1}/d_{B(50)2} - 1}{1/q_{B2} - (d_{B(50)1}/d_{B(50)2})/q_{B1}}. \quad (4a)$$

Q may thus be estimated empirically from the ratio of the indifference delays, and this estimate of Q may be substituted into Equation 3a in order to derive an estimate of K for each value of $d_{B(50)}$.

The derivation of Equations 3 and 4 is based on an assumed hyperbolic relationship be-

tween value and reinforcer size, as postulated in Equations 2a and 2b (Ho et al., 1999). However, a simpler version of Equation 4 may be derived from Equation 1, which assumes strict proportionality between value and reinforcer size. In this case, the ratio of two indifference delays is given by

$$\frac{d_{B(50)1}}{d_{B(50)2}} = \frac{q_{B1} - q_{A1}}{q_{A1}} \cdot \frac{q_{A2}}{q_{B2} - q_{A2}} \quad (5)$$

Equation 5 contains no free parameters, and therefore yields a specific numerical prediction for the ratio of the two indifference delays. A second aim of this experiment was to examine whether the empirically obtained ratios of the indifference delays would be compatible with this prediction.

In the present experiment, indifference delays were determined using an adjusting-delay schedule (Mazur, 1987). In this schedule the delay to the larger of two reinforcers varies in accordance with the subject's choice. For example, if, in a block of trials, the subject shows a preference for the larger reinforcer (B), the delay to that reinforcer is increased in the following block; conversely, if it shows a preference for the smaller reinforcer (A), the delay to Reinforcer B is reduced in the following block. The principal dependent variable, the adjusting delay to the larger reinforcer (d_B), is seen to oscillate during an extended period of training, the amplitude of oscillation gradually declining as d_B approaches a quasi-stable value; this quasi-stable value of d_B is usually taken to represent the indifference delay, $d_{B(50)}$ (Mazur 1987, 1988). Adjusting-delay schedules have been used extensively in behavior analytic studies of intertemporal choice (e.g. Green, Myerson, Shah, Estle, & Holt, 2007; Mazur, 1987, 1988, 1994, 1995, 1996, 2000, 2005), but less often in neurobehavioral experiments (da Costa Araújo et al., 2009; Mobini et al., 2000). A potential advantage of adjusting-delay schedules in neurobehavioral investigations of intertemporal choice is that, in addition to generating quasi-stable indifference delays, the pattern of oscillation of the adjusting delay may also provide information about the effects of neurobiological interventions on the organism's adaptation to changing delays to reinforcement. An additional purpose of this paper is to describe a novel way of quantifying transitional behav-

ior in the adjusting-delay schedule based on analysis of the power spectrum of cyclical changes in the adjusting delay.

METHOD

Subjects

Twelve experimentally naive female Wistar rats (Charles River UK) approximately 4 months old and weighing 250–300 g at the start of the experiment were used. They were housed individually under a constant cycle of 12 hr light and 12 hr darkness (light on 0600–1800 hr), and were maintained at 80% of their initial free-feeding body weights throughout the experiment by providing a limited amount of standard rodent diet after each experimental session. Tap water was freely available in the home cages.

Apparatus

The rats were trained in standard operant conditioning chambers (CeNeS Ltd, Cambridge, UK) of internal dimensions 25 × 25 × 22 cm. One wall of the chamber contained a central recess covered by a hinged clear Perspex flap, into which a peristaltic pump could deliver a 0.6 M sucrose solution. Two apertures situated 5 cm above and 2.5 cm to either side of the recess allowed insertion of motorized retractable levers (CeNeS Ltd, Cambridge, UK) into the chamber. The levers could be depressed by a force of approximately 0.2 N. The chamber was enclosed in a sound-attenuating chest with additional masking noise generated by a rotary fan. No houselight was present during the sessions. An Acorn microcomputer programmed in Arachnid BASIC (CeNeS Ltd, Cambridge, UK) located in an adjoining room controlled the schedules and recorded the behavioral data.

Procedure

The experiment was carried out in accordance with UK regulations governing experiments on living animals.

At the start of the experiment the food deprivation regimen was introduced and the rats were gradually reduced to 80% of their free-feeding body weights. They were then trained to press two levers (A and B) for the sucrose reinforcer (50 μl, 0.6 M), and were exposed to a discrete-trials continuous rein-

forcement schedule in which the two levers were presented in random sequence for three sessions. Then they underwent daily 42-min training sessions under the discrete-trials adjusting-delay schedule for the remainder of the experiment. Each experimental session consisted of seven blocks of four trials. The trials were 90 s in duration. The first two trials of each block were forced-choice trials in which each lever was presented alone in random sequence. The other two trials were free-choice trials in which both levers were presented. The beginning of each trial was signaled by illumination of the central light above the reinforcer recess. After 2.5 s the lever or levers (depending on the type of trial) were inserted into the chamber. When a lever press occurred, the lever(s) were withdrawn, the central light was extinguished, and the light located above the lever that had been depressed was illuminated. This light remained illuminated until the delivery of the reinforcer, and was then extinguished. The chamber remained in darkness until the start of the following trial. If no lever press occurred within 5 s of the lever(s) being inserted, the lever(s) were retracted and the central light extinguished. (This seldom happened except during the first few training sessions.) A response on Lever A resulted in immediate delivery of the smaller reinforcer, of size q_A (i.e. $d_A \approx 0$). A response on Lever B initiated a delay d_B whose duration was increased or decreased systematically from one trial block to the next as a function of the choices in the prior block; at the end of this delay the larger reinforcer, of size q_B , was delivered. The positions of Levers A and B (left vs. right) were counterbalanced across subjects.

In each block of trials, the delay to the larger reinforcer, d_B , was determined by the rat's choices in the free-choice trials in the preceding block. If Lever A was chosen in both free-choice trials of block n , d_B was reduced by 20% in block $n+1$; if Lever B was chosen in both free-choice trials of block n , d_B was increased by 20% in block $n+1$; if Lever A and Lever B were each chosen in one free-choice trial in block n , d_B remained unchanged in block $n+1$. The value of d_B in the first block of each session was determined in the same way by the choices made in the final block of the previous session. Maximum and minimum values of d_B were set at 60 s and 0.75 s.

The experiment consisted of two Phases (I and II), the first lasting 100 sessions and the second 40 sessions. There were two experimental Conditions (1 and 2); for half the rats Condition 1 was in effect in Phase I and Condition 2 in Phase II; for the other rats the order of conditions was reversed. In Condition 1, the sizes of the two reinforcers (volume of 0.6 M sucrose solution) were $q_{A1} = 25 \mu\text{l}$ and $q_{B1} = 100 \mu\text{l}$; in Condition 2, the sizes of the reinforcers were $q_{A2} = 14 \mu\text{l}$ and $q_{B2} = 25 \mu\text{l}$. In the first block of the first session of each phase, d_B was set at 0.75 s.

Experimental sessions were carried out 7 days a week, at the same time each day, during the light phase of the daily cycle (between 0800 and 1400 hr).

Data Analysis

Indifference delays and parameter estimation. For each rat, the mean value of d_B in the last 10 sessions of each phase was taken as the indifference delay, $d_{B(50)}$. These data were analyzed by a two-factor analysis of variance [condition (1,2) \times order of condition (1-first vs. 2-first)] with repeated measures on the former factor. As this analysis showed no significant main effect of order and no significant order \times condition interaction, the order factor was ignored in all further treatment of the data. The ratio of the values of $d_{B(50)}$ obtained under the two conditions was calculated for each rat, and these values were used to calculate estimates of Q as described in the Introduction, using the formula

$$Q = \frac{d_{B(50)1}/d_{B(50)2} - 1}{1/25 - (d_{B(50)1}/d_{B(50)2})/100},$$

100 and 25 being the sizes of Reinforcer B (volumes of 0.6 M sucrose, in μl) in the two conditions of the experiment (q_{B1} and q_{B2} , respectively). This estimate of Q was used to derive an estimate of K for each rat by substitution into Equation 3a.

The obtained ratios of the indifference delays were also compared with the ratio predicted on the basis of an assumed linear relation between reinforcer size and instantaneous value. Based on Equation 1, the indifference delay is

$$d_{B(50)} = \frac{1}{K} \cdot \frac{q_B - q_A}{q_A}.$$

Substituting the actual reinforcer sizes used in this experiment into this equation, the ratio of the indifference delays should be

$$\frac{d_{B(50)1}}{d_{B(50)2}} = \frac{100-25}{25} \cdot \frac{14}{25-14} = 3.81.$$

(cf. Equation 5: Introduction). The obtained ratios were compared with this theoretical value using a *t*-test.

Transitional behavior. In order to characterize the pattern of oscillation of d_B during the course of training, a power spectrum analysis was carried out on the values of d_B obtained in each trial block during each phase of the experiment. The method is illustrated in Figure 1. Plots were obtained of $\log d_B$ versus blocks of trials (Phase I, 700 blocks; Phase II, 280 blocks: see upper panel of Figure 1). These data, expressed as deviations from the mean value of d_B , were subjected to a Fourier transform (Spike-2, version 4.23: Cambridge Electronic Design, Ltd) in order to derive power spectra (power vs. frequency: see lower panels of Figure 1). The reciprocal of the frequency is the cycle time (period) of oscillation of d_B , in blocks. The power of the dominant frequency of the spectrum within the frequency range of 0.01 (period = 100 blocks) and 0.04 (period = 25 blocks) and the length of the period corresponding to the dominant frequency were derived for each rat in each phase of the experiment (da Costa Araújo et al., 2009). Inspection of the data indicated that the amplitude of oscillation of d_B declined during the 100 sessions of Phase I. This impression was tested by comparing the power spectra derived from the first and final 280 blocks of trials of Phase I; comparisons were also made between the spectra derived from the final 280 blocks of Phase I and the 280 blocks that comprised Phase II.

RESULTS

Indifference Delays and Parameter Estimation

Figure 2 (left-hand panel) shows the values of $d_{B(50)}$ derived from the last 10 sessions of each phase. In all but 1 of the 12 rats, the value of $d_{B(50)1}$ (Condition 1: $q_{A1} = 25 \mu\text{l}$, $q_{B1} = 100 \mu\text{l}$) was higher than that of $d_{B(50)2}$ (Condition 2: $q_{A2} = 14 \mu\text{l}$, $q_{B2} = 25 \mu\text{l}$). Analysis of variance indicated that there was a significant effect of condition ($F_{1,10} = 28.3$, $p < .001$), but no

significant effect of the order of conditions ($F_{1,10} = 1.3$, $p > .1$) and no significant interaction ($F_{1,10} = 2.7$, $p > .1$). Accordingly, the data from all 12 rats were pooled in all subsequent analyses. Figure 2 (right-hand panel) shows the ratios of the two values of $d_{B(50)}$; the horizontal line indicates the ratio predicted on the basis of an assumed linear relation between reinforcer size and reinforcer value (3.81: see Data Analysis section in the Method). The observed ratio (mean \pm SEM: 2.34 ± 0.19) was significantly lower than the predicted ratio ($t_{11} = 7.6$, $p < .001$).

The ratios of the $d_{B(50)}$ s were used to compute estimates of the two parameters of Equation 2, Q and K . The results of this analysis are shown in Figure 3. There was one clear outlier in the case of both parameters, this being the rat that showed no difference between the $d_{B(50)}$ s in the two conditions (see above). The parameter that expresses sensitivity to reinforcer size (Q) was derived by substitution of the ratio of the indifference delays into Equation 4a. The group mean value of Q (\pm SEM) was $113.8 \pm 27.9 \mu\text{l}$. Estimates of the delay discounting parameter (K) were derived by substituting each rat's estimated value of Q into Equation 3a. The group mean value (\pm SEM) was $0.082 \pm 0.012 \text{ s}^{-1}$.

Transitional Behavior

In all 12 rats, the adjusting delay to the larger reinforcer, d_B , showed an oscillating pattern of change during the early stages of training, the amplitude of the oscillations tending to decline during extended training (see Figure 1 for an example; the data from all 12 rats are shown in the Appendix). Power spectra were derived for each rat's data from three segments of training: the first and last 280 trial blocks of Phase I and the 280 blocks of Phase II. The power in the dominant frequency band and the period corresponding to the dominant frequency from each segment are shown in Figure 4 (upper panels: rats exposed to Condition 1 [$q_{A1} = 25 \mu\text{l}$, $q_{B1} = 100 \mu\text{l}$] in Phase I and Condition 2 [$q_{A2} = 14 \mu\text{l}$, $q_{B2} = 25 \mu\text{l}$] in Phase II; lower panels: rats exposed to the two conditions in the reverse order).

In both groups of rats, power in the dominant frequency band (Figure 4, left panels) was greatest in the initial segment of Phase I. Analysis of variance showed a significant main effect of segment ($F_{2,20} = 29.7$, $p < .001$),

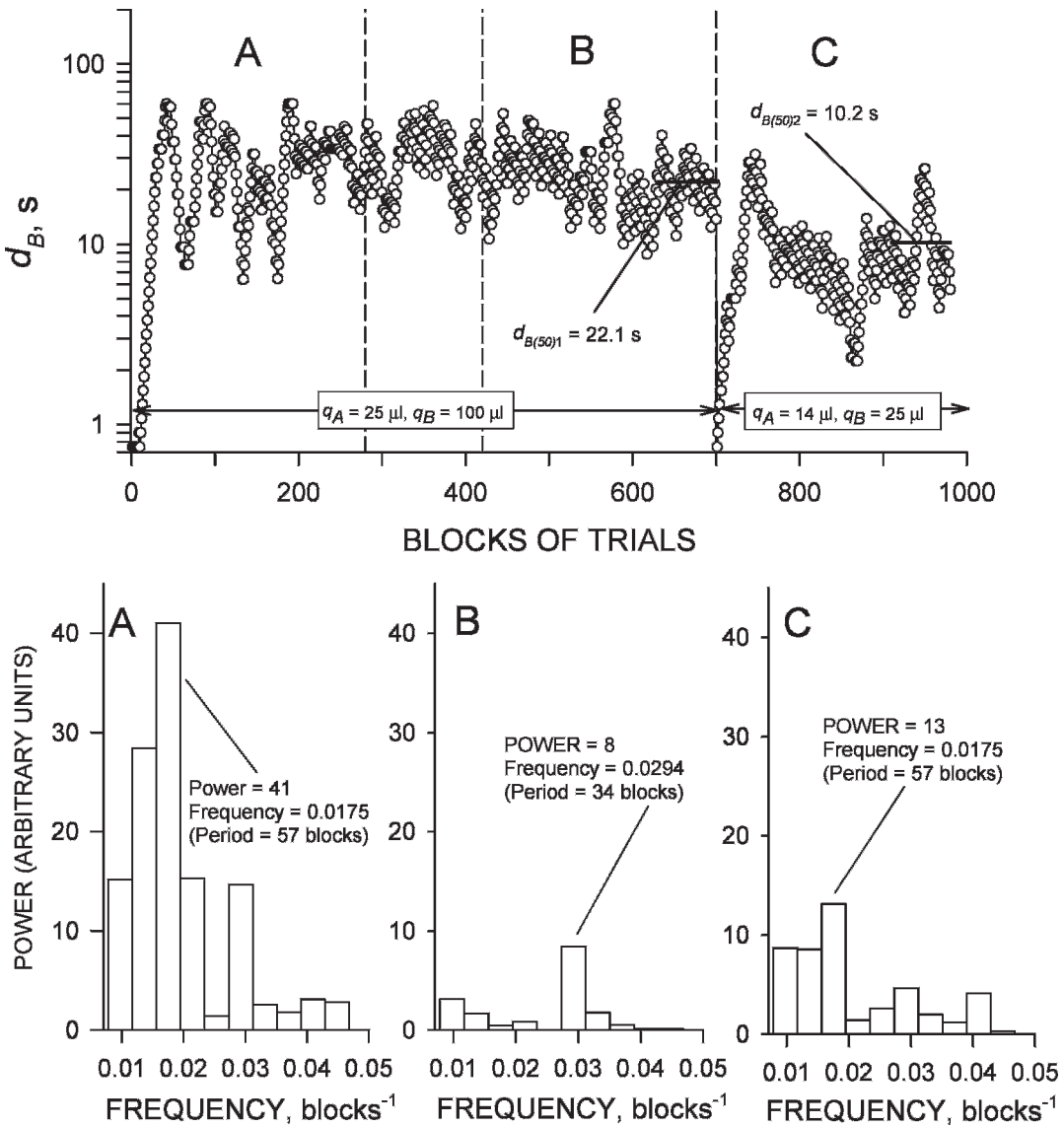


Fig. 1. Example of one rat's performance on the adjusting-delay schedule during the entire experiment, illustrating the methods of data analysis. *Upper graph*: Adjusting delay to the larger reinforcer (d_B , s) plotted against blocks of trials in the two phases of the experiment. In Phase I (trial blocks 1–700), the sizes of the reinforcers (q_A , q_B) were 25 and 100 μl of a 0.6 M sucrose solution; in Phase II they were 14 and 25 μl . The segments A, B, and C, demarcated by the broken lines, comprise the first (A) and final (B) 280 blocks of Phase I and the 280 blocks of Phase II (C) that were used in the Fourier transform analysis. The short horizontal lines indicate the mean values of d_B in the final 10 sessions (70 blocks) of the two phases ($d_{B(50)1}$ and $d_{B(50)2}$). *Lower panels*: Power spectra derived from Fourier transform analysis of the d_B data from segments A, B, and C (see above). Power is plotted against frequency (blocks $^{-1}$). The period of oscillation corresponding to the dominant frequency band, and the power within that band, are shown for each segment.

but no significant effect of group ($F_{1,10} = 2.9$, $p > .05$) and no significant interaction ($F_{2,20} = 4.1$, $p > .05$). In both groups, power was significantly lower in the last segment of Phase I and in Phase II compared to the initial

segment of Phase I. The period corresponding to the dominant frequency (Figure 4, right panels) showed no significant effects of segment or group, and no significant interaction (all $F_s < 1$).

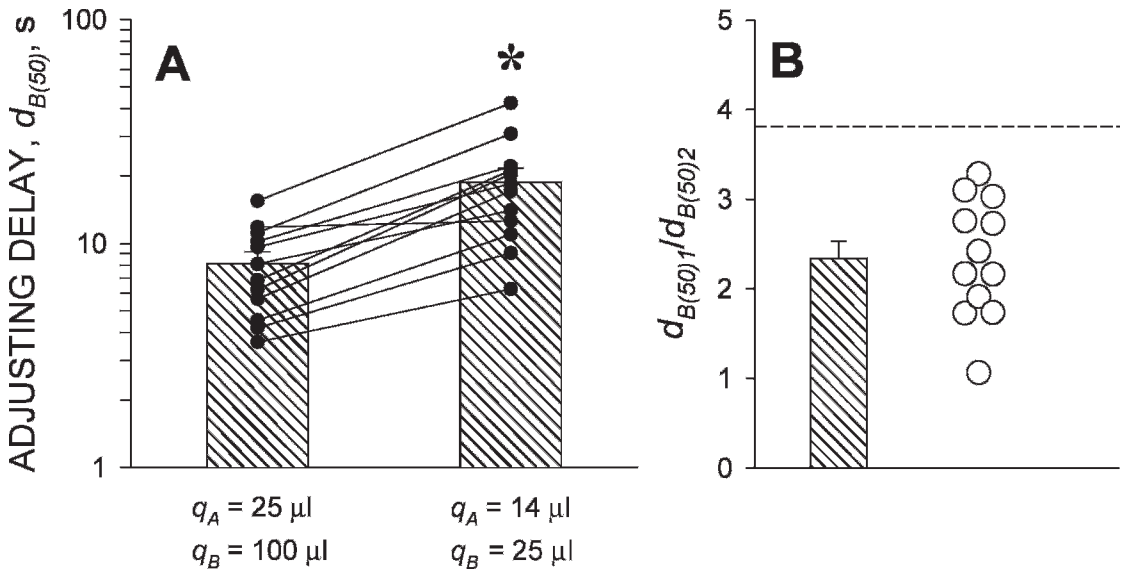


Fig. 2. A. Values of $d_{B(50)}$ (s) obtained under the two conditions. Columns are group mean data; connected points are data from individual rats. $d_{B(50)}$ was significantly longer under Condition 1 (reinforcer sizes: $q_A = 25 \mu\text{l}$, $q_B = 100 \mu\text{l}$) than under Condition 2 (reinforcer sizes: $q_A = 14 \mu\text{l}$, $q_B = 25 \mu\text{l}$). B. Ratio of the values of $d_{B(50)}$ obtained under the two conditions. Column shows the group mean ratio (+SEM); open circles show data from individual rats. Horizontal broken line shows the expected ratio based on the assumption that reinforcer value is linearly related to reinforcer size (see text).

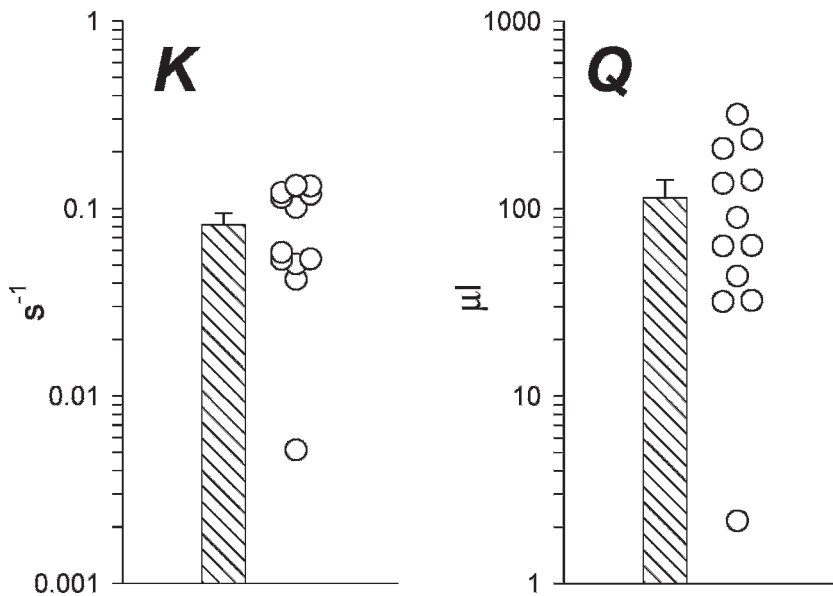


Fig. 3. Estimates of the parameters of Equation 2 expressing the rate of delay discounting, K (s^{-1}), and sensitivity to reinforcer size, Q (μl of the 0.6 M sucrose solution). Columns are group mean data (+SEM); open circles show estimates for individual rats. (In the case of both parameters, the outlier is the rat that produced the lowest ratio of the two values of $d_{B(50)}$; see Fig. 2.)

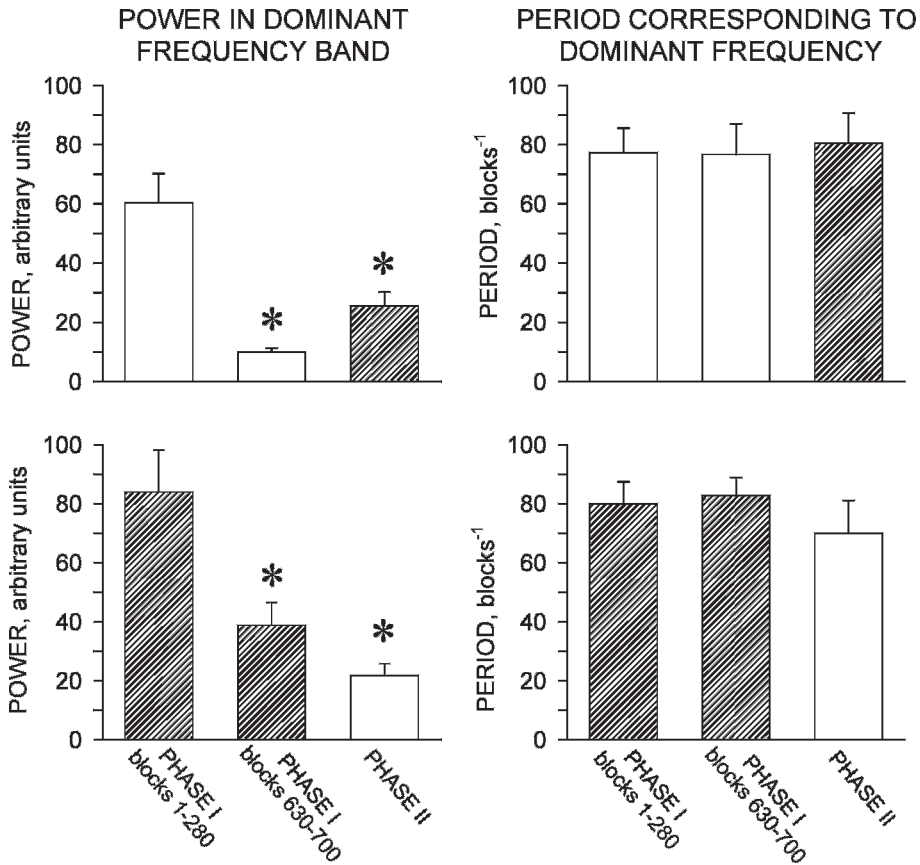


Fig. 4. Results of the power spectrum analysis in three segments of the experiment (see Fig. 1). *Left panels*: power in the dominant frequency band; *right panels*: period of oscillation corresponding to the dominant frequency. *Upper panels*: data from the rats that were exposed to Condition 1 (open columns) first and Condition 2 (shaded columns) second; *lower panels*: data from the rats that were exposed to the conditions in the reverse order. In Condition 1, the sizes of the reinforcers (q_A , q_B) were 25 and 100 μl of a 0.6 M sucrose solution; in Condition 2, they were 14 and 25 μl . Columns show group mean data (+ SEM). In both groups, power was significantly less in the final segment of Phase I and in Phase II than in the initial segment of Phase I (* $p < .05$). The period of oscillation did not vary significantly across the three segments.

Figure 5 shows the individual-subject data and the mean data from the rats in both groups in the terminal segment of Phase I and the segment comprising Phase II. Comparisons between the two conditions showed that power was significantly higher in Condition 2 than in Condition 1 ($t_{11} = 3.7$, $p < .01$), but there was no significant difference between period in the two conditions ($t < 1$).

DISCUSSION

Indifference Delays and Parameter Estimation

The quasi-stable adjusting delays seen during the last 10 days of training under each condition were taken as indifference delays,

$d_{B(50)}$. The value of $d_{B(50)}$ was higher in Condition 1, when the reinforcer sizes were 25 and 100 μl of the sucrose solution, than in Condition 2, when they were 14 and 25 μl . This was an expected result, because $d_{B(50)}$ is assumed to depend on the relative instantaneous value of Reinforcer B, which was higher under Condition 1 than under Condition 2 (cf. Equation 3).

The ratio of the indifference delays, $d_{B(50)1}/d_{B(50)2}$, was compared with a predicted value of 3.81, which was calculated from the physical sizes of the reinforcers, based on the assumption that instantaneous reinforcer value is linearly related to reinforcer size (cf. Equation 1). The observed ratios were consistently

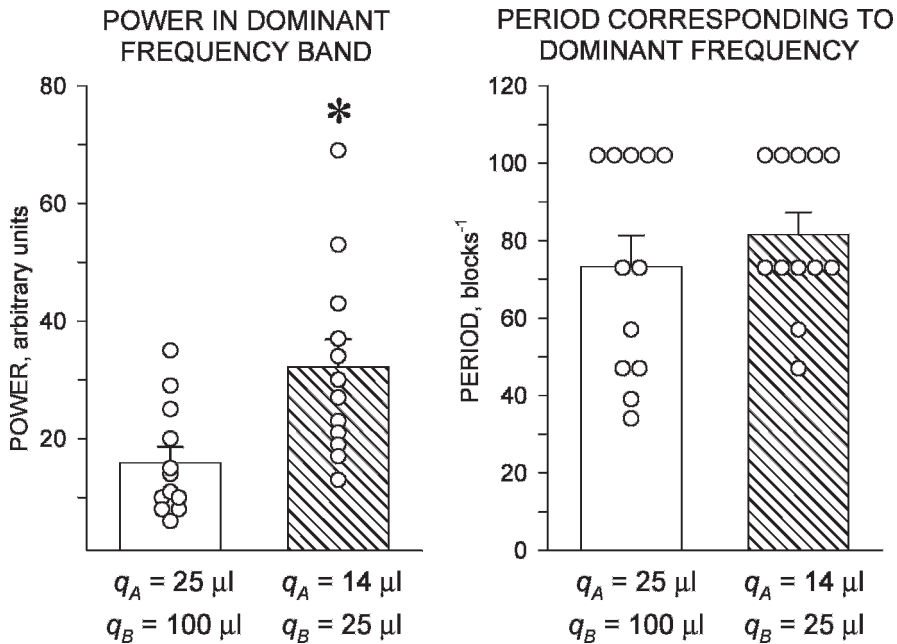


Fig. 5. Results of the power spectrum analysis. Comparison of power in the dominant frequency band and period of oscillation corresponding to the dominant frequency seen under Conditions 1 (open columns; reinforcer sizes: $q_A = 25 \mu\text{l}$, $q_B = 100 \mu\text{l}$) and 2 (shaded columns; reinforcer sizes: $q_A = 14 \mu\text{l}$, $q_B = 25 \mu\text{l}$). Columns show group mean data; open circles show data from individual rats. Power was significantly higher under Condition 2 than under Condition 1 (* $p < .05$); there was no difference between the period of oscillation under the two conditions.

smaller than 3.81, suggesting a nonlinear relation between size and value. A nonlinear relation is assumed by the model of intertemporal choice proposed by Ho et al. (1999), which formed the basis of the method adopted here to derive numerical estimates of discounting parameters. According to this model, instantaneous reinforcer value is hyperbolically related to reinforcer size, the relation being defined by a single free parameter, Q , which specifies the reinforcer size corresponding to the half-maximal value. Note that other nonlinear size/value functions have recently been proposed, for example, by Killeen (2009) and Pine et al. (2009).

The present experiment employed two pairs of reinforcer sizes that allowed Q to be determined from the ratio of the two indifference delays (Equation 4a). It is of interest to compare the value of Q obtained using this tactic (mean = 113.8 μl) with a value of Q derived using a different approach. Rickard et al. (2009) trained rats under a progressive-ratio schedule using a wide range of reinforcer sizes (different volumes of a 0.6 M sucrose

solution). Response rates in successive ratios were analyzed using an equation derived from Killeen's (1994) "mathematical principles of reinforcement". The "specific activation" parameter of Killeen's model (a), which is presumed to reflect the incentive value of the reinforcer, was a monotonically increasing function of reinforcer volume. A hyperbolic function was fitted to the relation between a and reinforcer volume, from which it was determined that the value of Q was 158.9 μl . The fact that these radically different methods yielded numerical estimates of Q that were in same order of magnitude inspires some confidence in the general utility of this parameter as a descriptor of sensitivity to reinforcer size.

By substituting the estimates of Q into Equation 3, it was possible to derive estimates of the delay-discounting parameter, K . The mean value of K (0.082 s^{-1}) was similar to values of this parameter obtained in previous experiments with rats (approximately 0.1 s^{-1} : Green, Myerson, Holt, Slevin, & Estle, 2004; Mazur, 2007; Mazur & Biondi, 2009).

Methodological Considerations

The derivation of Equation 4 entails the simplifying assumption that when no delay is scheduled for Reinforcer A, $d_A = 0$. In fact, a brief delay necessarily occurs between the initiation of the reinforcer delivery and the subject's consumption of the reinforcer. Informal observation of rats trained under the present procedure suggests that this delay is in the order of half a second, and we therefore think it unlikely that the approximation $d_A = 0$ significantly compromises the validity of Equation 4. Moreover, there is no measurable delay between the response on Lever A and the presentation of exteroceptive stimuli associated with reinforcer delivery, which presumably acquire some conditioned reinforcing properties.

It must be pointed out that the algebraic substrate of the present method imposes some restrictions on the range of reinforcer sizes that may be employed. For example, in the present experiment we set $q_{B2} = q_{A1}$ (25 μ l) and $q_{B1} = 4 \cdot q_{A1}$ (100 μ l); the value of q_{A2} required in order to preserve the equality $(1/q_{A1} - 1/q_{B1}) = (1/q_{A2} - 1/q_{B2})$ was approximately 14 μ l. Other reinforcer sizes might have been used, but the choice is not limitless. For example, instead of determining the required value of q_{A2} for given values of q_{B1} , q_{A1} and q_{B2} , the value of q_{A2} might have been preselected, and the required value of q_{B2} calculated accordingly. In this case, when $q_{B2} = q_{A1}$, the chosen value of q_{A2} would have had to be less than $q_{B2}/2$, otherwise an appropriate value of q_{B1} could not have been found (e.g., if $q_{A2} = 25$, and $q_{B2} = q_{A1} = 50$, $q_{B1} = \infty$). Choosing convenient values of q_{A1} , q_{B1} and q_{B2} and calculating the required value of q_{A2} circumvents this limitation. Figure 6A shows the required values of q_{A2} for a range of values of q_{B2} , when q_{B1} is set at 100 and q_{A1} is set at 12.5, 25 or 50; the points indicate the values corresponding to the particular condition used in the present experiment, in which $q_{A1} = q_{B2}$. The figure shows that despite the limitation outlined above, the method can in principle accommodate a broad range of reinforcer sizes.

The equations also impose constraints on the range of $d_{B(50)}$ ratios that can generate meaningful values of the parameter Q . Inspection of Equation 4a shows that the range of allowable ratios has a lower boundary of 1.0

and an upper boundary defined by q_{B1} and q_{B2} . If $(d_{B(50)1}/d_{B(50)2})/q_{B1} = 1/q_{B2}$, the recovered value of Q is ∞ ; higher $d_{B(50)}$ ratios yield negative values of Q , which are, of course, meaningless. The relation between Q and $d_{B(50)1}/d_{B(50)2}$ is illustrated in Figure 6B. Setting q_{B1} at 100 and $q_{B2} = 25$ (the values used in the present experiment), meaningful values of Q require $d_{B(50)}$ ratios < 4 (for $q_{B2} = 50$ the upper limit is < 2 ; for $q_{B2} = 12.5$, it is < 8). Within a substantial proportion of the range of allowable ratios (approximately 1.5–3.5 in the present instance), the relation between $\log Q$ and the $d_{B(50)}$ ratio is approximately linear. As shown in Figure 6B, the data from 11 of the 12 rats in this experiment fell within this band. The nature of the relation between the $d_{B(50)}$ ratio and Q dictates that small changes in the size of the ratio will tend to produce larger changes in Q at higher ratio sizes than at lower ratio sizes. This suggests that it may be appropriate for statistical tests on values of Q derived using the present method (for example in experiments examining the effect of neurobiological interventions on this parameter) to be carried out on logarithmically transformed parameter values.

It must be emphasized that the constraint on the range of allowable $d_{B(50)}$ ratios is theoretical rather than methodological. In other words, it is not peculiar to the present application of Equation 4; rather, it arises from the assumptions underlying Equations 2a and 2b, which form the basis of Hø *et al.*'s (1999) multiplicative hyperbolic model. A more stringent constraint is imposed by Equation 1, which does not incorporate a size-sensitivity parameter. When applied to the present protocol, Equation 1 specifies a $d_{B(50)}$ ratio of exactly 3.81. As discussed above, the present data do not comply with this specification. They are, however, compatible with the limits imposed by Equation 4, and are therefore compatible with the multiplicative hyperbolic model. It is possible, of course, that future applications of the present method may reveal empirical $d_{B(50)}$ ratios that are incompatible with Equation 4; such an occurrence would constitute a refutation of the underlying model.

Transitional Behavior on the Adjusting-Delay Schedule

In agreement with previous reports (e.g. da Costa Araújo *et al.*, 2009; Mazur, 1987), the

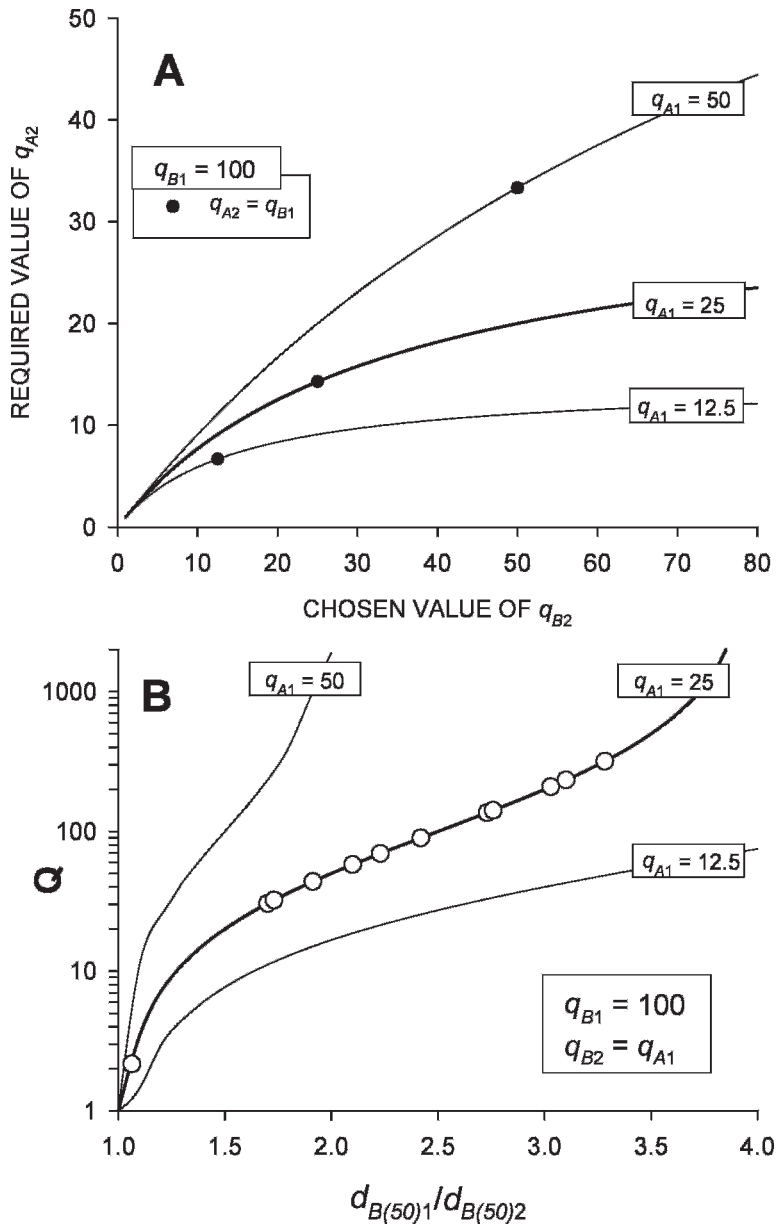


Fig. 6. A. Relation between the required size of the smaller reinforcer in Condition 2 of the present method (q_{A2}) for a range of sizes of the larger reinforcer (q_{B2}). The three curves show the relation between q_{A2} and q_{B2} for three chosen sizes of the smaller reinforcer in Condition 1 ($q_{A1} = 12.5, 25$ and 50), the size of the larger reinforcer (q_{B1}) being set at 100 in each case. The thick curve corresponds to the value of q_{A1} used in this experiment ($25 \mu\text{l}$ of a 0.6 M sucrose solution). The points indicate the required values of q_{A2} for the particular case of $q_{A1} = q_{B2}$, adopted in the present experiment; when $q_{A1} = q_{B2} = 25$, $q_{A2} \approx 14$. B. Relation between the recovered value of the size-sensitivity parameter Q and the ratio of the two indifference delays ($d_{B(50)1}/d_{B(50)2}$) in the present method. The curve shows the relation between $\log Q$ and $d_{B(50)1}/d_{B(50)2}$ in the case of the particular reinforcer sizes used in the present experiment ($q_{B1} = 100$ and $q_{B2} = q_{A1} = 25$). Meaningful values of Q are generated by ratios between 1 and 4 . It can be seen that the relation is approximately linear between 1.5 and 3.5 . Points show the data from the 12 subjects of the present experiment; data from all but one of the rats fall within that range. See text for further explanation.

adjusting delay to Reinforcer B (d_B) showed cyclical changes which gradually declined in amplitude as training progressed. We attempted to characterize the fluctuation of d_B by using the Fourier transform to derive a power spectrum of the frequency of oscillation. This analysis showed that the dominant frequency of the spectrum corresponded to a period of oscillation of approximately 80 trial blocks. A similar value for the period of oscillation was obtained in a recent experiment investigating the effect of lesions of the core of the nucleus accumbens on behavior on the adjusting-delay schedule (da Costa Araújo *et al.*, 2009). Since da Costa Araújo *et al.*'s experiment used qualitatively different reinforcers (food pellets) and different ratios of reinforcer sizes from those used in the present experiment, it seems that the period of oscillation of d_B may be relatively insensitive to reinforcer variables.

There was a consistent trend for the power of oscillation to be highest in the initial segment of the first phase of the experiment. The decline in power during Phase I presumably reflects some adaptation to the schedule contingencies during extended training (see below for further discussion). Interestingly, although there was a consistent trend for power in the dominant frequency band to be higher under Condition 2 ($q_A = 14 \mu\text{l}$, $q_B = 25 \mu\text{l}$) than under Condition 1 ($q_A = 25 \mu\text{l}$, $q_B = 100 \mu\text{l}$), there was no overall difference between the power of oscillation seen in the second phase and that seen in the final segment of the first phase. This suggests that the gradual adaptation to the adjusting-delay contingencies was not disrupted by the change in reinforcer sizes at the start of the second phase.

As in our previous experiments with adjusting-delay schedules (da Costa Araújo *et al.*, 2009; Ho, Wogar, Bradshaw, & Szabadi, 1997; Mobini *et al.*, 2000; Wogar, Bradshaw, & Szabadi, 1992, 1993), we used proportional rather than fixed adjustment of d_B . The decision to use proportional adjustment was based on the assumption that sensitivity to changes in delay of reinforcement would conform to Weber's law, as is the case with temporal discrimination in many types of timing schedule (Gibbon, 1977; Killeen & Fetterman, 1988). Weber's Law implies that proportional changes should be similarly discriminable across a broad range of delays,

whereas a fixed increment of, say, 1 s would be less discriminable if the preceding value of d_B were 30 s than if it were 2 s. However, fixed changes in d_B are commonly used (e.g. Green *et al.*, 2007; Mazur, 1994, 1995, 1996; Pietras, Cherek, Lane, Tcheremissine, & Steinberg, 2003), and it remains to be seen whether the use of different adjustment rules influences the pattern of oscillation of d_B revealed by the power spectrum.

Simulating Behavior on the Adjusting-Delay Schedule

Adjusting-delay schedules entail complex contingencies, and the processes underlying the oscillating pattern of changes in d_B remain conjectural at this time. We offer the following speculative model as a preliminary account of some of the processes that may be involved in the schedule used in this experiment.

We start by assuming that the value of each outcome is determined by Equations 2a and 2b. As there is no delay to Reinforcer A, ($d_A = 0$), the value of A (V_A) depends only upon its size, q_A , and the size-sensitivity parameter, Q . The value of B (V_B), however, varies from trial block to trial block, due to the influence of d_B , modulated by the delay-discounting parameter, K . Next, we postulate that the subject discriminates between V_A and V_B , and selects the outcome that has the higher value at the moment of choice. Thus, in any trial block in which $V_B > V_A$, the subject selects B, resulting in an increment in d_B in the following block; B will be selected repeatedly until $V_A > V_B$, at which point the process will be reversed. Figure 7A shows how d_B would oscillate in the present protocol if behavior were following this simple principle.

To make the model more realistic, we assume that rats' ability to discriminate reinforcer value is not perfect, and that standard psychophysical principles apply. In keeping with evidence from other delay-of-reinforcement paradigms (Gibbon & Fairhurst, 1994), we assume that rats' discrimination of value depends on the ratio of two values, rather than the absolute difference between them. A simple logistic function centered on $V_B/V_A = 1$ may be used to define the probability that B will be chosen: $p(B) = 1/(1+[V_B/V_A]^s)$, where s defines the slope of the function. [The probability that A will be chosen is $p(A) = 1-p(B)$.] Figure 7B shows the effect of intro-

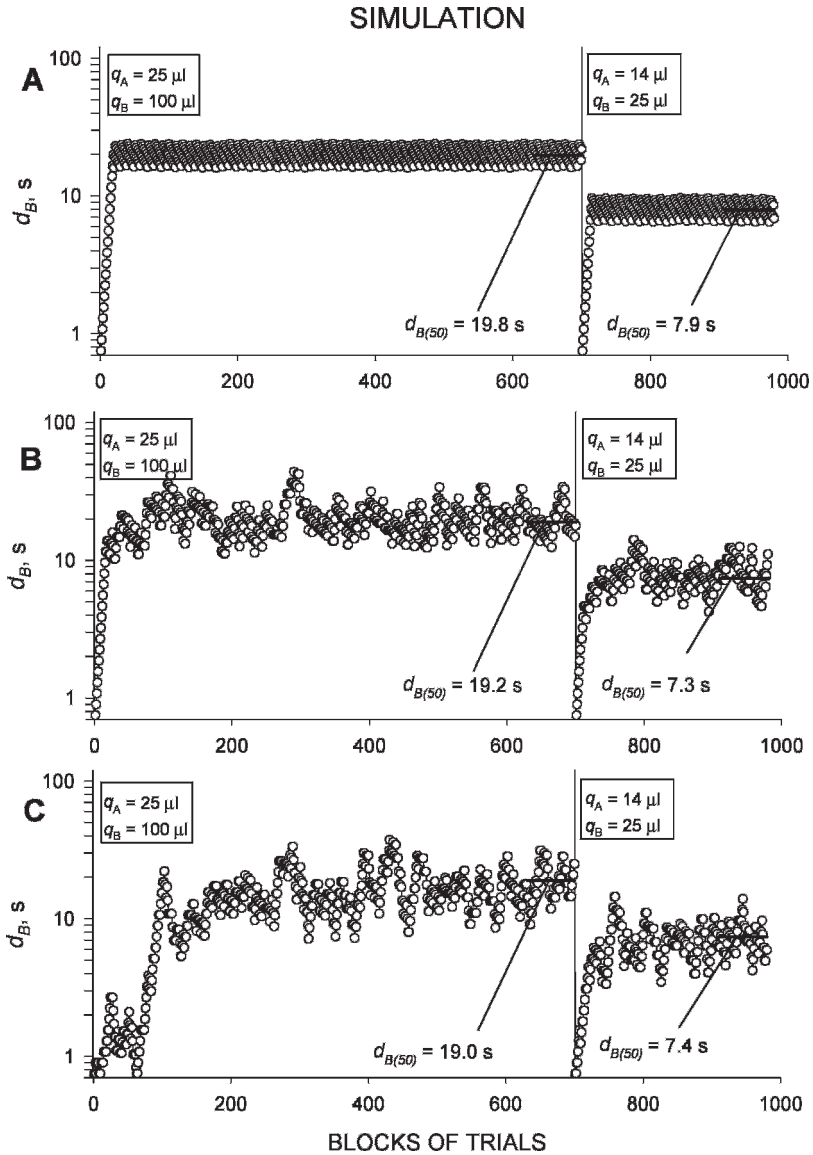


Fig. 7. Simulation of behavior under the adjusting-delay schedule, based on the model described in the text. *Ordinates*: adjusting delay to the larger reinforcer, d_B (s); *abscissae*: blocks of trials in the two phases of the experiment (cf. Fig. 1). The group mean estimated values of Q and K (see Fig. 5: $Q = 113.8 \mu\text{l}$, $K = 0.082 \text{ s}^{-1}$) were used in the simulations. The reinforcer volumes shown in the insets correspond to those used in Conditions 1 and 2 of the experiment. The recovered values of $d_{B(50)}$ are the means of the last 70 data points of each phase. *A*. Simulation based on the assumption of perfect discrimination between the values of the two outcomes, the subject invariably selecting B when $V_B/V_A > 1$, and A when $V_B/V_A < 1$. *B*. Simulation incorporating variability of discrimination generated by a logistic psychometric function in which the probability of selection of the larger reinforcer is $p(B) = 1/(1+[V_B/V_A]^s)$; the slope of the function, s , was set at 2 in this simulation. *C*. Simulation incorporating the additional assumption that s increases during training, starting at 0 and approaching its asymptote s_{max} (2, in this simulation) according to the function $s = s_{max} \cdot (1 - e^{-n/c})$, where n is the number of trial blocks and c is a learning parameter, which was set at 300 blocks in this simulation.

ducing this element of variability into choice between the two outcomes.

Finally, we suppose that rats' ability to discriminate reinforcer value improves with practice, and that the improvement takes the form of a progressive steepening of the psychophysical function that approaches an asymptote after extended training. Our simulation uses an exponential learning function: $s = s_{max}(1 - e^{-n/c})$, where s_{max} is the asymptote, n is the ordinal position of the trial block, and c defines the rate at which s approaches its asymptotic value. This function is incorporated into the simulation shown in Figure 7C.

The model captures some features of behavior on the schedule used in this experiment, although there is clearly room for improvement. Like the real rats, the model generates oscillation of d_B which declines in amplitude during the course of training. Entering the empirical values of Q and K into the model, it was found that d_B stabilized at values very close to the those seen in the two conditions of this experiment. Although transitional performance varied quite widely between simulations, the steady-state values of $d_{B(50)}$ were quite consistent: Using the parameters listed in the legend of Figure 7, 100 iterations of the simulation yielded mean values of $d_{B(50)}$ of 20.0 s (Condition 1: $q_A=25 \mu\text{l}$; $q_B=100 \mu\text{l}$) and 8.0 s (Condition 2: $q_A=14 \mu\text{l}$; $q_B=25 \mu\text{l}$), the coefficients of variation being 0.10 and 0.12, respectively. These values are reassuringly close to the group mean values shown in Figure 4 (18.8 s and 8.1 s).

The model was less successful in capturing the amplitude of oscillation of d_B in the early stages of training. In other words, the simulation tended to underestimate the power in the dominant frequency band during the initial part of Phase I. The reason for this is uncertain. Two possible explanations for the high-amplitude oscillations seen in this experiment are the following. (1) The rats may have had a tendency to perseverate; that is, under conditions of uncertainty, they may have tended to repeat the previous response, rather than selecting A or B randomly, as is assumed by the model. This would have had the effect of driving d_B towards the extremes of the range before the alternative response was selected. (2) Alternatively or additionally, choices may have been based on outcomes obtained in an

extended sequence of trial blocks, rather than being determined solely by the ratio of reinforcer values in the immediately preceding block, as is assumed in the present form of the model. Either or both of these hypothetical processes could be incorporated into the model. However, we believe that it may be premature to introduce additional parameters on an ad hoc basis, pending experimental exploration of the more basic aspects of the model.

Implications for Behavioral Neuroscience

The neural mechanisms underlying intertemporal choice have attracted considerable attention in recent years. A major incentive to research in this area has been the prospect of uncovering the biological bases of pathological "impulsiveness" (Carroll, Anker, Mach, Newman, & Perry, 2010; Sagvolden, Johansen, Aase, & Russell, 2005; Williams, 2010; Yi, Mitchell, & Bickell, 2010). It is widely believed that a tendency to make impulsive choices arises from an abnormally high rate of delay discounting, and therefore discovery of the neural underpinnings of this process may lead to a greater understanding of the causes of pathological impulsiveness and, perhaps, to the development of more effective treatments for this disabling condition. A common tactic in this area of research is to examine the effect of a neurobiological intervention on preference for the larger of two reinforcers while progressively increasing the delay to that reinforcer. A leftward displacement of the resulting preference function (i.e., a reduction of the indifference delay) is often taken as an index of impulsiveness, which is not infrequently equated with an increase in the rate of delay discounting. Unfortunately, the logic of this approach is undermined if the indifference delay is determined by two parameters (for example, K and Q), either or both of which may be influenced by biological interventions. Leftward displacement of a single preference function provides no clue as to whether the intervention in question has altered the rate of delay discounting or the sensitivity to reinforcer size (or both).

One way of overcoming this difficulty is to obtain several indifference delays corresponding to a range of delays to the smaller reinforcer (d_A), and thereby construct the linear indifference function defined by Equa-

tion 3. The slope and intercept of this function may then be used to infer changes in K and Q (Ho et al., 1999; Mazur, 2006). Although this method has been used successfully in studies examining the effects of brain lesions on intertemporal choice (see Introduction), the method is very time consuming. The approach adopted in the present experiment, based as it is on only two indifference delays, considerably reduces the time needed to obtain estimates of K and Q . It may be noted that the present method based on Equation 4 is one of several ways in which K and Q might be estimated from two indifference delays. For example, in the case of choice between two reinforcers of sizes q_A and q_B , indifference delays $d_{B(50)1}$ and $d_{B(50)2}$ might be obtained for two values of d_A (d_{A1} and d_{A2}). According to the linear indifference function defined by Equation 3, K may be determined from the formula (slope-1)/intercept. With d_{A1} set at 0, the slope is defined by $(d_{B(50)2} - d_{B(50)1})/d_{A2}$, allowing K to be calculated from the formula $[(d_{B(50)2} - d_{B(50)1})/d_{A2} - 1]/d_{B(50)1}$, and Q from the formula $(1 - \text{slope})/(\text{slope}/q_B - 1/q_A)$.

A detailed assessment of the reliability of the estimates of Q and K obtained using the present method remains a task for future research. It is likely that the estimates based on two data points will show greater variability than estimates derived by fitting linear indifference functions to a family of data points covering a broad range of indifference delays. However, in neurobehavioral investigations of intertemporal choice, specifying the exact numerical values of the parameters is generally less important than determining whether a particular intervention affects one or other, or both, of the parameters in question (e.g., Bezzina et al., 2007; Kheramin et al., 2002). It may be noted that neurobiological interventions could provide a means of assessing the reliability and validity of the present approach. For example, experiments based on the linear indifference function defined by Equation 3 have indicated that destruction of the orbital prefrontal cortex results in increases in both K and Q , whereas destruction of the core of the nucleus accumbens has a selective effect on K . Confidence in the utility of Equation 4 would be greatly strengthened if the same effects of the lesions on the two parameters could be demonstrated using the present experimental protocol.

The present experiment used adjusting-delay schedules to obtain indifference delays. This is not an essential requirement. For example, progressive delay schedules (Evenden & Ryan, 1996), which have been used extensively in neurobehavioral experiments (see Cardinal, Robbins, & Everitt, 2003; Winstanley, 2010), are equally suitable. The adjusting-amount schedule (Richards, Mitchell, de Wit, & Seiden, 1997) may be particularly advantageous, as it has been reported to generate stable choice behavior within one or two sessions, as opposed to the many sessions needed to reach stability under adjusting-delay schedules (Green et al., 2007; Richards et al., 1997).

The utility of analyzing the power spectrum of oscillations of d_B remains to be explored. The method was used in a recent experiment examining the effect of destruction of the nucleus accumbens core on performance on an adjusting-delay schedule (da Costa Araújo et al., 2009). However, this study found no significant effect of the lesion on the power spectrum. Judgement on the method may have to await the results of further studies examining its sensitivity, or insensitivity, to a broader range of neurobiological interventions. One limitation of the approach is that a rather large data set is needed in order to derive a spectrum of reasonable frequency resolution. In the present experiment, 280 values were used in each Fourier analysis, which yielded spectra with a bandwidth of $0.0039 \text{ blocks}^{-1}$, allowing decomposition of the empirical spectra into 6–10 frequency bands. It remains to be seen whether this degree of resolution is adequate to detect changes in the period of oscillation of d_B induced by neurobiological interventions.

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APPENDIX

Raw data from the twelve rats.

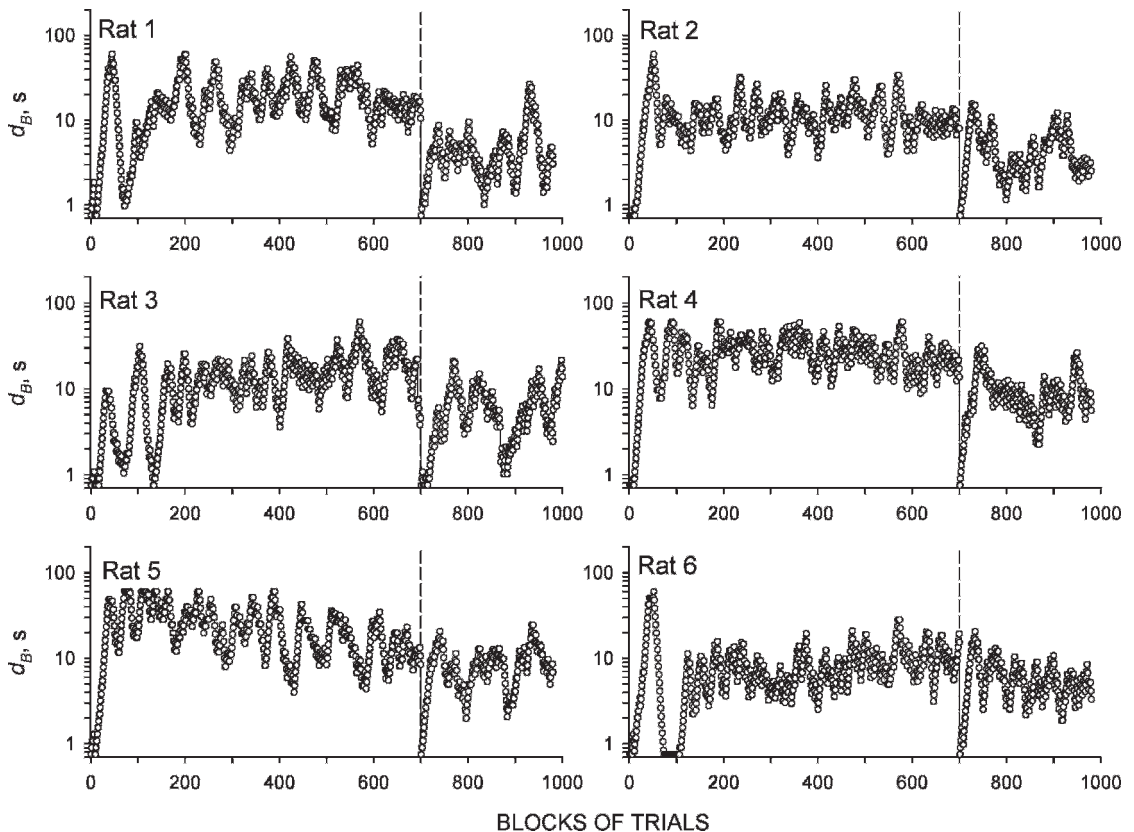


Fig. A1. Data from the 6 rats that were exposed to Condition 1 in Phase I and Condition 2 in Phase II (see Fig. 1 for explanation).

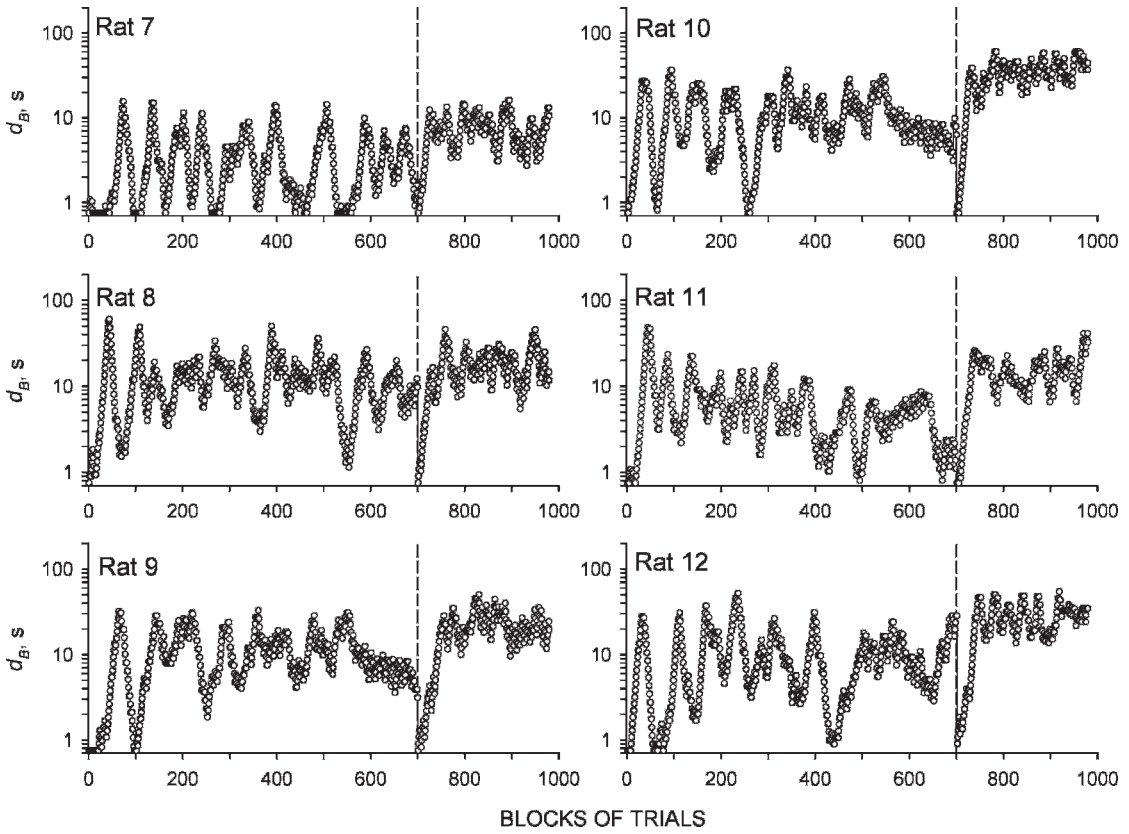


Fig. A2. Data from the 6 rats that were exposed to Condition 2 in Phase I and Condition 1 in Phase II (see Fig. 1 for explanation).