

*STUDIES OF WHEEL-RUNNING REINFORCEMENT:
PARAMETERS OF HERRNSTEIN'S (1970) RESPONSE-STRENGTH
EQUATION VARY WITH SCHEDULE ORDER*

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Six male Wistar rats were exposed to different orders of reinforcement schedules to investigate if estimates from Herrnstein's (1970) single-operant matching law equation would vary systematically with schedule order. Reinforcement schedules were arranged in orders of increasing and decreasing reinforcement rate. Subsequently, all rats were exposed to a single reinforcement schedule within a session to determine within-session changes in responding. For each condition, the operant was lever pressing and the reinforcing consequence was the opportunity to run for 15 s. Estimates of k and R_O were higher when reinforcement schedules were arranged in order of increasing reinforcement rate. Within a session on a single reinforcement schedule, response rates increased between the beginning and the end of a session. A positive correlation between the difference in parameters between schedule orders and the difference in response rates within a session suggests that the within-session change in response rates may be related to the difference in the asymptotes. These results call into question the validity of parameter estimates from Herrnstein's (1970) equation when reinforcer efficacy changes within a session.

Key words: tandem fixed-ratio 1 variable-interval schedule, Herrnstein's single-operant matching law equation, within-session response patterns, wheel-running reinforcement, lever press, rats

Herrnstein's (1970) single-operant matching law describes the relation between response and reinforcement rates when there is only a single experimenter-arranged source of reinforcement and a single measured response. The response–reinforcer relation takes the form of a rectangular hyperbola described by the following equation:

$$B_1 = \frac{kR_1}{R_1 + R_O}, \quad (1)$$

where B_1 is the predicted response rate, R_1 is the obtained reinforcement rate, and k and R_O are fitted parameters. Because k is the response-rate asymptote, as reinforcement rate increases, response rate approaches, but does not exceed, k . It is expressed in the same units as the measured behavior (e.g., responses per minute) and has been interpreted as an index of a motoric component of a reinforced response (Heyman & Monaghan, 1987). R_O , on the other hand, is equivalent to the reinforcement rate that maintains one half the asymptotic rate of responding. This

parameter describes how quickly response rate rises toward the asymptote as reinforcement rate increases. R_O is expressed in the same units as the experimenter-arranged reinforcer (e.g., reinforcers per hour) and is typically interpreted as the rate of reinforcement from extraneous sources (Herrnstein, 1970), but has also been interpreted as an index of reinforcer efficacy (Heyman & Monaghan, 1987).

McSweeney, Weatherly, and Swindell (1995) suggested that within-session changes in responding may be problematic for this form of the matching law, particularly when several different reinforcement schedules are presented within a single session. McSweeney and colleagues (McSweeney, 1992; McSweeney & Hinson, 1992; McSweeney, Hinson, & Cannon, 1996; McSweeney & Roll, 1993; McSweeney, Roll, & Cannon, 1994; McSweeney, Roll, & Weatherly, 1994; McSweeney, Weatherly, & Swindell, 1995, 1996) have shown that, with reinforcement rate held relatively constant within a session, response rates typically increase, then decrease, or just increase or decrease, within a session. With constant reinforcement rates, McSweeney, Hinson, and Cannon (1996) attributed this change in response rates to a sensitization-habituation process. The changes are sufficient to warrant the possibility that

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the fitted parameters in Herrnstein's (1970) equation might be influenced by within-session changes in responding. Consider, for example, a condition in which the highest programmed rate of reinforcement from a series of reinforcement schedules presented within the same session occurs at the point in the session at which response rates from the within-session pattern are the lowest (e.g., at the beginning of the session). In this case, the response-rate asymptote from the fit of Equation 1 might be lower than if the highest programmed rate occurred at the point within the session at which response rates from the within-session pattern are highest.

To investigate this possibility, McSweeney et al. (1995) exposed rats and pigeons to different orders of the same variable-interval (VI) schedules across conditions. Reinforcement schedules presented within a session varied from VI 15 to VI 240 s. Each animal experienced the same schedules within a session, but in four different orders. Reinforcement schedules were presented in the following orders: decreasing reinforcement rate (i.e., VI 15 to VI 240 s), increasing reinforcement rate (i.e., VI 240 to VI 15 s), increasing then decreasing reinforcement rate (i.e., VI 240 to VI 15 to VI 120 s), and decreasing then increasing reinforcement rate (i.e., VI 15 to VI 240 to VI 30 s). Equation 1 was fitted to response and reinforcement rates generated by each schedule order in each session, and the fitted parameters were compared. Finally, within-session patterns of responding were determined by exposing the animals to a single VI 40-s schedule throughout the session. Fitted parameters did not vary systematically with schedule order or in a manner consistent with within-session patterns of responding.

The present study adopted a similar procedure using wheel-running rather than food reinforcement. Previous research with wheel-running reinforcement showed that both lever-pressing and wheel-running rates increase throughout the session. Belke (1997) showed that on tandem fixed-ratio (FR) 1 VI 30-s schedules, lever-pressing rate increased throughout the session when reinforcer duration was 30 and 60 s but not 120 s. Concurrent with these changes in lever-pressing rate, wheel-running rate within the reinforcer duration also increased throughout the session.

Further evidence suggesting that within-session patterns of responding may affect fitted parameters comes from between-group differences in response-rate asymptotes. Belke and Dunlop (1998) exposed different groups of rats to increasing and decreasing orders of tandem FR 1 VI schedules for wheel-running reinforcement. Rats exposed to the increasing reinforcement-rate order had higher response-rate asymptotes than rats exposed to the decreasing rate order. That is, response-rate asymptotes were lower in animals exposed to the highest reinforcement rate at the beginning of the session, when response rates would be lowest within the session, assuming a within-session pattern of responding similar to that observed by Belke (1997). Because the number of animals in each group was small, this between-group difference does not necessarily reflect a within-subject difference.

Together these observations suggest that the fitted parameters from Equation 1 may vary with schedule order and that within-session changes in responding and running observed when the programmed reinforcement rate is held constant may be related to this variance in the parameters. To test this possibility, animals in the present study were exposed to different schedule orders, and Equation 1 was fitted to the response and reinforcement rates generated by each order. In addition, within-session patterns of responding and running were assessed by placing the animal on a single reinforcement schedule for the entire session.

METHOD

Subjects

Six experimentally naive male Wistar rats obtained from Charles River Breeding Laboratories served as subjects. The animals were approximately 4 months old at the start of the experiment. When not in the experimental apparatus, the rats were individually housed in standard polycarbonate cages (48 cm by 27 cm by 22 cm) in a colony room maintained at 20 °C with a 12:12 hr light/dark cycle (lights on at 8:00 a.m.). Subjects were maintained at a target weight that was approximately 85% of a free-feeding body weight taken when the weights of the rats rose just

beyond 400 g (i.e., adult weight). As a result, target weights varied around $340 \text{ g} \pm 10 \text{ g}$. Animals were maintained on food restriction because previous research showed that tendency to run varies inversely with body weight. Distilled water was freely available in the home cages.

Apparatus

Subjects were tested in activity wheels (three Wahmann and three Lafayette Instruments Model 86041 A) without side cages. The diameters of the wheels were 35.5 cm. Each wheel was located in a soundproof shell equipped with a fan for ventilation and to mask extraneous noise. A retractable lever (Med Associates ENV-112) was mounted so that the surface from which the lever extended was flush against the opening that provided access to the wheel. The opening to the wheel was 7 cm wide by 9 cm long. The plane of the lever was 4.5 cm above the base of the opening and 7 cm above the floor of the wheel. The lever extended 1.8 cm through the opening. The force required to close the lever microswitches ranged between 0.18 and 0.27 N.

A solenoid-operated brake was attached to the base of each wheel. When the solenoid was operated, a rubber tip attached to a metal shaft contacted the outer rim of the wheel and stopped the wheel. A microswitch attached to the wheel frame recorded wheel revolutions. Lights (24 V DC) mounted on the sides of the wheel frame illuminated the inside of the wheel chamber. Experimental events and recording of data were controlled by IBM[®] personal computers interfaced to the wheels.

Procedure

The training phase began with selecting the rats as noted in the *Subjects* section above from a group of 23 rats. To do this, each rat was placed in a running wheel for 30-min sessions each day over a 10-day period. The number of wheel revolutions was recorded for each rat on each day. After 10 days, 17 rats, including those used in the present study, were selected based on the criterion of running rates in excess of 10 revolutions per minute.

Training the animals to press a lever for the opportunity to run began by shaping lever

pressing using sucrose reinforcement in standard operant conditioning chambers. Each lever press produced 0.1 ml of a 15% sucrose solution. When subjects reliably pressed the lever, the schedule of reinforcement was shifted from an FR 1 schedule to a variable-ratio (VR) 3 schedule. This VR schedule remained in effect for approximately four sessions, with each session terminating when 50 sucrose reinforcers had been obtained.

After four sessions on the VR 3 schedule, sessions in the operant conditioning chamber were discontinued. At this point, the retractable lever in each wheel chamber was extended during the wheel-running sessions, and the opportunity to run for 60 s was made dependent upon a single lever press. When a press occurred, the lever retracted and the brake released, leaving the wheel free to turn for 60 s. Once 60 s had elapsed, the reinforcement period was terminated by the application of the brake, and the lever was extended. Each session consisted of 30 opportunities to run. The schedule of reinforcement was changed in the following sequence: FR 1, VR 3, VR 5, VR 9, and VR 15. Subjects remained on each schedule for four sessions before advancing to the next schedule.

Following the 4th day on the VR 15 schedule, the reinforcement requirement was changed to a sequence of four tandem FR 1 VI schedules of reinforcement presented within the same session. The schedules for the VI components were VI 80, VI 40, VI 15, and VI 5 s. Each VI schedule was composed of 10 intervals. Intervals for each schedule were generated from a list of 10 intervals that approximated an exponential distribution (Fleshler & Hoffman, 1962) and had a mean value of 5 s. To generate the different schedules, each value in the set of 10 intervals was multiplied by either 1, 3, 8, or 16. At this point in training, the duration of the reinforcer was decreased to 15 s.

Each component of this series of tandem FR 1 VI schedules consisted of 13 reinforcers. The first three reinforcers of each component were warm-up reinforcers, arranged to diminish interactions between the schedules. The interval values for these warm-up reinforcers were determined by multiplying the values of 4, 5, and 6 by the same multiplier that was used to produce the intervals for the remaining 10 reinforcers that comprised the

VI schedules. After the completion of each component, there was a 2-min blackout period during which lights were extinguished and the brake was applied.

Rats LD2, LD6, and LD18 first were exposed to an increasing reinforcement-rate order (i.e., VI 80, VI 40, VI 15, and VI 5), and Rats LD9, LD14, and LD17 were exposed to a decreasing reinforcement-rate order (i.e., VI 5, VI 15, VI 40, and VI 80). After 50 sessions, rats exposed to the increasing order were shifted to the decreasing order, and rats exposed to the decreasing order were shifted to the increasing order. Again these conditions remained in effect for 50 sessions. Following this condition, the rats were returned to their home cages for 5 days. After 5 days, each rat was exposed to the same series of tandem FR 1 VI schedules with the VI schedule in all four components set at 15 s. This condition was in effect for 30 sessions.

Dependent measures recorded in each session were total lever presses, total lever-pressing time (exclusive of postreinforcement-pause [PRP] duration and reinforcer duration), total cumulative PRP duration, and total wheel revolutions. Equivalent measures were also recorded for each reinforcement to assess within-session effects. That is, for each reinforcer, the number of lever presses, the lever-pressing time, the PRP following the termination of the previous reinforcer (or latency to lever press in the case of the first reinforcer of each component), and number of revolutions were recorded.

Wilkinson's (1961) method was used to estimate the parameters of the hyperbolic functions that were fitted to the response and reinforcement rates generated in the two schedule order conditions. Response rates were lever-pressing rates calculated as presses divided by lever-pressing time and expressed as presses per minute. Reinforcement rates were calculated as the number of reinforcers divided by the time spent lever pressing (i.e., exclusive of PRP and reinforcer duration) and expressed as reinforcers per hour.

Response and reinforcement rates from

the five sessions that met the following stability criterion were analyzed. After 25 sessions, the range of response rates in each component was determined, and for data to be considered stable the response rates in each component had to fall within the range of high and low values for the previous five consecutive sessions. If a new high or low value occurred within any component, data were not considered stable. The number of sessions required to meet this criterion varied between 30 and 45 for the increasing reinforcement-rate condition and 31 and 44 for the decreasing rate condition. Response rates, reinforcement rates, and mean PRPs from the five sessions that met the stability criterion are given in Appendix A.

Because schedule orders were changed after a fixed number of sessions rather than when responding was stable, response and reinforcement rates from the last 10 sessions in each condition were also analyzed. Estimates from this additional analysis were in general agreement with those obtained from sessions that met the stability criterion (see Appendix B). Finally, for the assessment of within-session patterns of lever pressing and wheel running with a single schedule of reinforcement, data from the last 10 sessions were used.

RESULTS

Figure 1 depicts hyperbolic curves fitted to the obtained response and reinforcement rates for each schedule order for each rat. Estimates from Equation 1 are presented in Table 1. Figure 1 shows that response-rate asymptotes were higher for each rat when reinforcement rates increased across the session. Mean values of k for the increasing and decreasing rate orders were 53.7 and 28.8 presses per minute, respectively, $t(5) = 3.45$, $p \leq .05$. Differences between asymptotes for the two schedule orders ranged from 8 to 58 presses per minute. Estimates of R_0 were also higher when reinforcement rates occurred in an increasing order. Mean R_0 values for the increasing and decreasing rate orders were

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 Fig. 1. Hyperbolic functions describing response rates as a function of reinforcement rates for rats exposed to the same series of reinforcement schedules arranged in order of increasing (filled circles) and decreasing (open triangles) reinforcement rates.

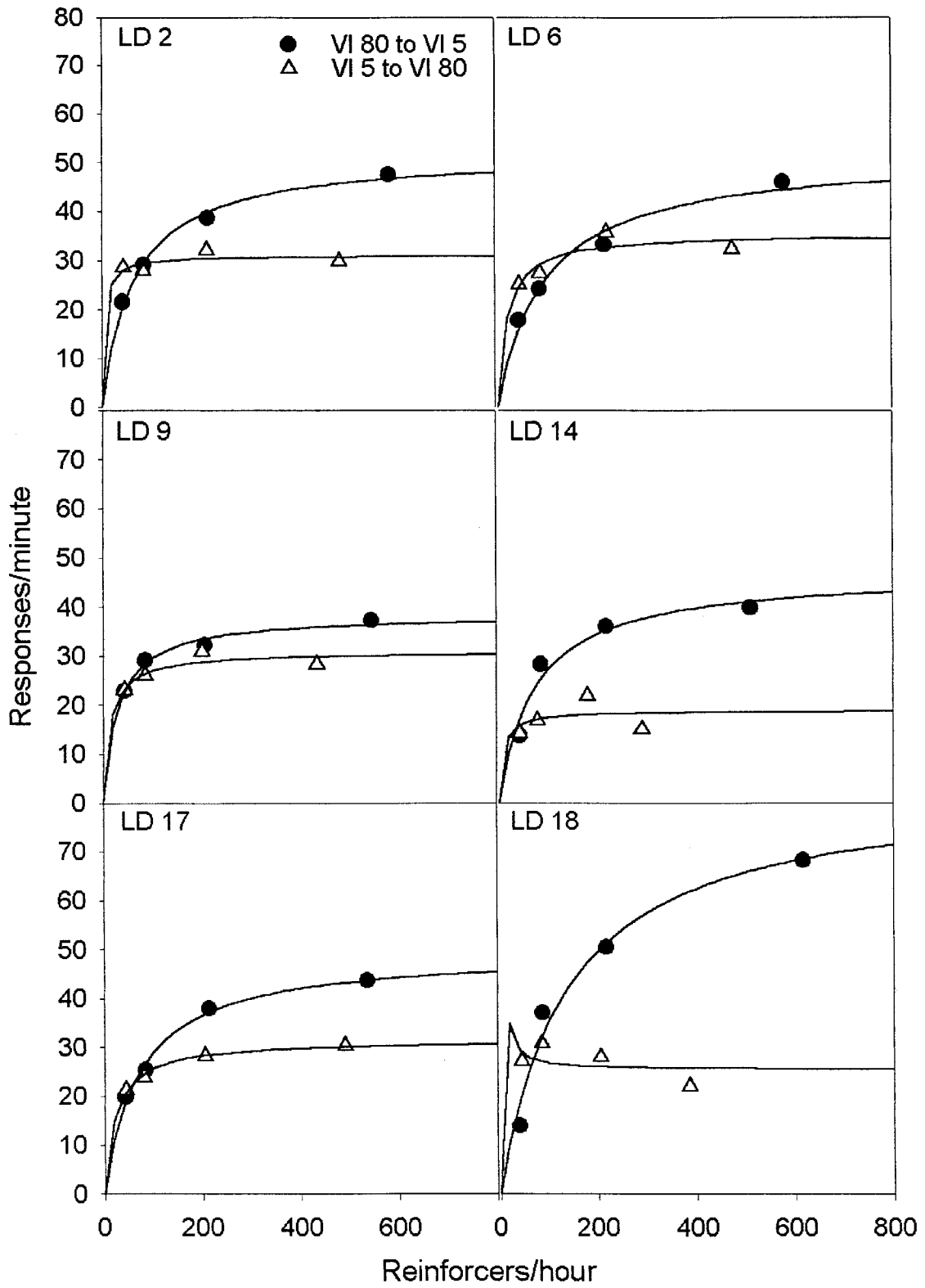


Table 1

Estimates of k , R_O , standard errors (SE), and variance accounted for (%VAC) for the increasing reinforcement rate and for the decreasing reinforcement rate.

Rat	k	R_O	$SE k$	$SE R_O$	%VAC
Increasing reinforcement rate order (VI 80 s to VI 5 s)					
LD2	52	65	1.7	7.2	99
LD6	52	98	4.0	22.3	97
LD7	38	30	1.3	4.8	97
LD14	47	73	4.4	20.1	93
LD17	49	70	1.9	8.8	99
LD18	84	137	8.4	33.4	96
M	54	79			97
Decreasing reinforcement rate order (VI 5 s to VI 80 s)					
LD2	31	5	1.5	4.3	39
LD6	36	19	2.7	9.5	77
LD9	31	14	1.9	6.6	78
LD14	19	8	4.3	27.2	0
LD17	31	23	0.6	2.6	98
LD18	25	-5	3.3	9.0	5
M	29	11			49

78.9 and 10.5 reinforcers per hour, respectively, $t(5) = 3.97$, $p \leq .05$.

Two general observations are noteworthy. First, response rates associated with the highest reinforcement rate were lower when that rate occurred at the beginning of the session. Second, less differentiation of response rates with changes in reinforcement rate was evident when reinforcement rates occurred in a decreasing order.

Figure 2 shows within-session changes in response rates with the reinforcement schedule held constant throughout the session for each rat. Response rates increased within the session for every rat. Mean response rates across consecutive components were 26.22, 29.13, 32.61, and 34.81 presses per minute. Differences between response rates in the last and the first components varied between 1.64 presses per minute and 15.96 presses per minute, with a mean difference of 8.59 presses per minute. A repeated measures analysis of variance (ANOVA) revealed a significant effect of session component, $F(3, 15) = 15.79$, $p \leq .0001$, and a significant linear trend, $F(1, 5) = 20.58$, $p \leq .01$, in lever-pressing rates.

Table 2 shows the differences in lever-pressing rates between the last and the first components when the programmed reinforcement rate was held constant, the differences between the estimates of k in the increasing and decreasing conditions, and the corresponding differences in estimates of R_O . To assess the relation between these variables, the correlations between the within-session changes in lever-pressing rates and the differences in the estimated parameters were calculated. Pearson product-moment correlations between differences in k values and within-session response-rate increases and between differences in R_O values and within-session response-rate increases were 0.91 and 0.89, respectively. These correlation coefficients suggest that differences in the form of the hyperbolic curves may be related to the magnitude of changes in the within-session responding or that both are related to a common variable.

Figure 3 shows wheel-running rates across successive components within a session. In general, revolutions per reinforcer also increased within a session, both when the reinforcement schedule was held constant and when it decreased. The three conditions were analyzed separately.

With the reinforcement schedule constant, mean revolutions per reinforcer across successive components were 10.08, 11.99, 11.95, and 11.43. For most rats, wheel-running rate was lower in the first component than in successive components, but rates among the remaining components did not differ systematically. A repeated measures ANOVA revealed a significant effect of component, $F(3, 15) = 12.16$, $p \leq .001$. Dunnett t -test comparisons (two tailed) revealed that revolutions per opportunity to run in the first component were significantly lower than those in the remaining components, $t^d(15) = 5.28, 5.17, \text{ and } 3.73$, all $ps \leq .01$.

For the decreasing reinforcement-rate condition, mean revolutions per reinforcer across successive components were 8.68, 11.56, 12.31, and 12.71. Figure 3 shows that

Fig. 2. Mean lever-pressing rates (presses per minute) for each animal across successive components when the schedule of reinforcement in each component was a tandem FR 1 VI 15-s schedule. Vertical lines indicate standard deviations.

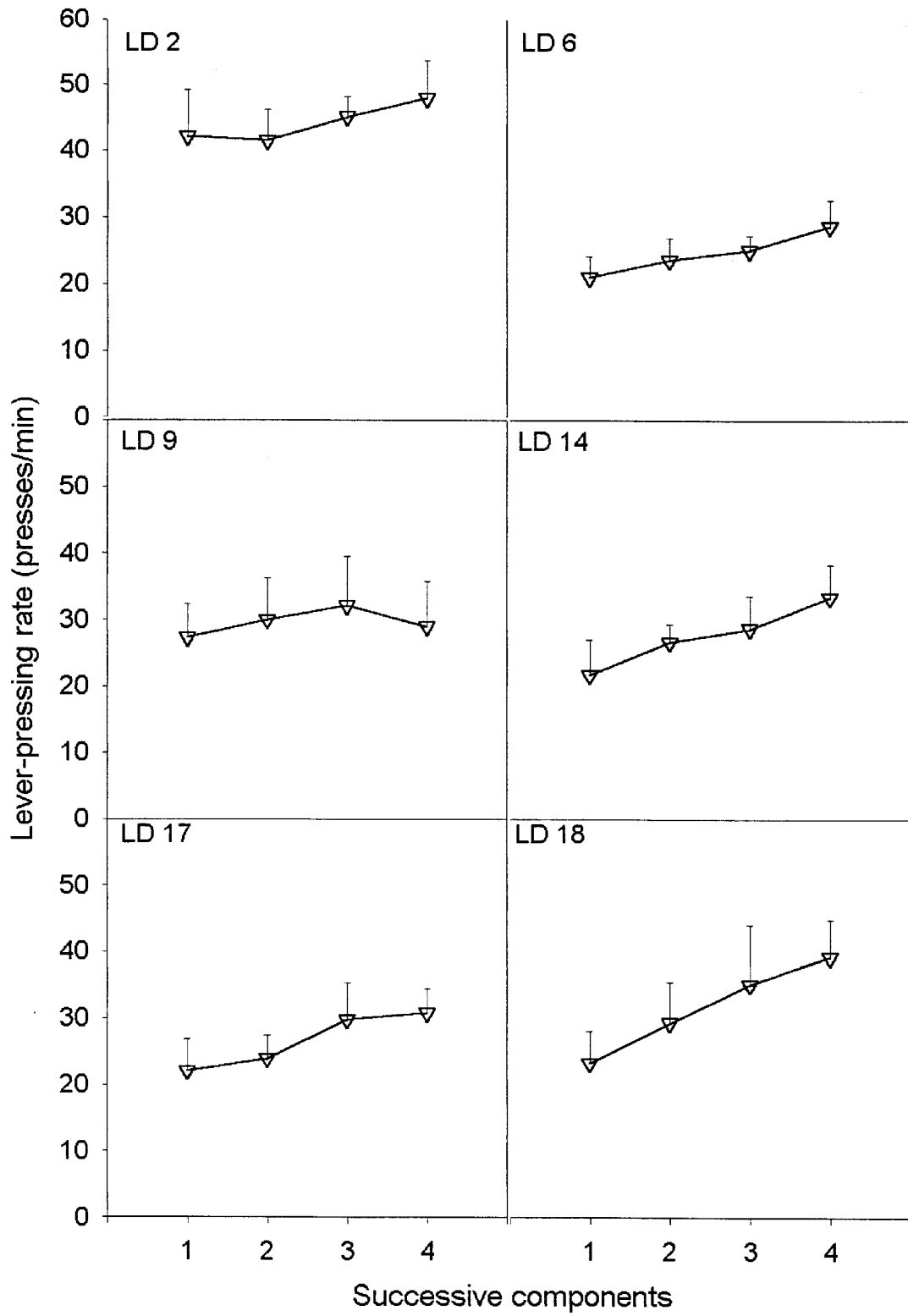


Table 2

Differences in estimates of k and R_O between the increasing and decreasing reinforcement rate orders and the difference in lever-pressing rates between the last and the first components of a session when the programmed reinforcement rate was held constant.

Rat	Difference in		Lever-pressing rates
	k	R_O	
LD2	20.87	60.42	5.74
LD6	16.46	78.30	7.82
LD9	7.54	15.56	1.64
LD14	28.24	65.29	11.69
LD17	17.98	47.91	8.69
LD18	58.26	142.65	15.96

all rats displayed fairly systematic increases in mean revolutions per reinforcer across components. A repeated measures ANOVA revealed a significant effect of component, $F(3, 15) = 22.62$, $p \leq .001$, and Dunnett t -test comparisons revealed that wheel-running rate in the first component was significantly lower than that in the remaining components, $t^d(15) = 5.32, 6.71$, and 7.44 , all p s $\leq .01$. Furthermore, analysis for linear trend revealed a significant linear trend in the running rates in this condition, $F(1, 5) = 22.81$, $p \leq .01$.

In contrast to the decreasing rate order, changes in wheel running in the increasing reinforcement-rate condition were more varied. Rats LD2 and LD17 had higher running rates in the first than the last component, and Rat LD9 had almost the same rate at the beginning and the end of the session. The remaining 3 rats had lower rates in the first component relative to those in the subsequent components. Mean revolutions per reinforcer across successive components were 10.91, 12.39, 12.16, and 11.68. A repeated measures ANOVA revealed no effect of component, $F(3, 15) = 2.53$, $p = .10$.

DISCUSSION

The results from the present study show that the hyperbolic curves describing the re-

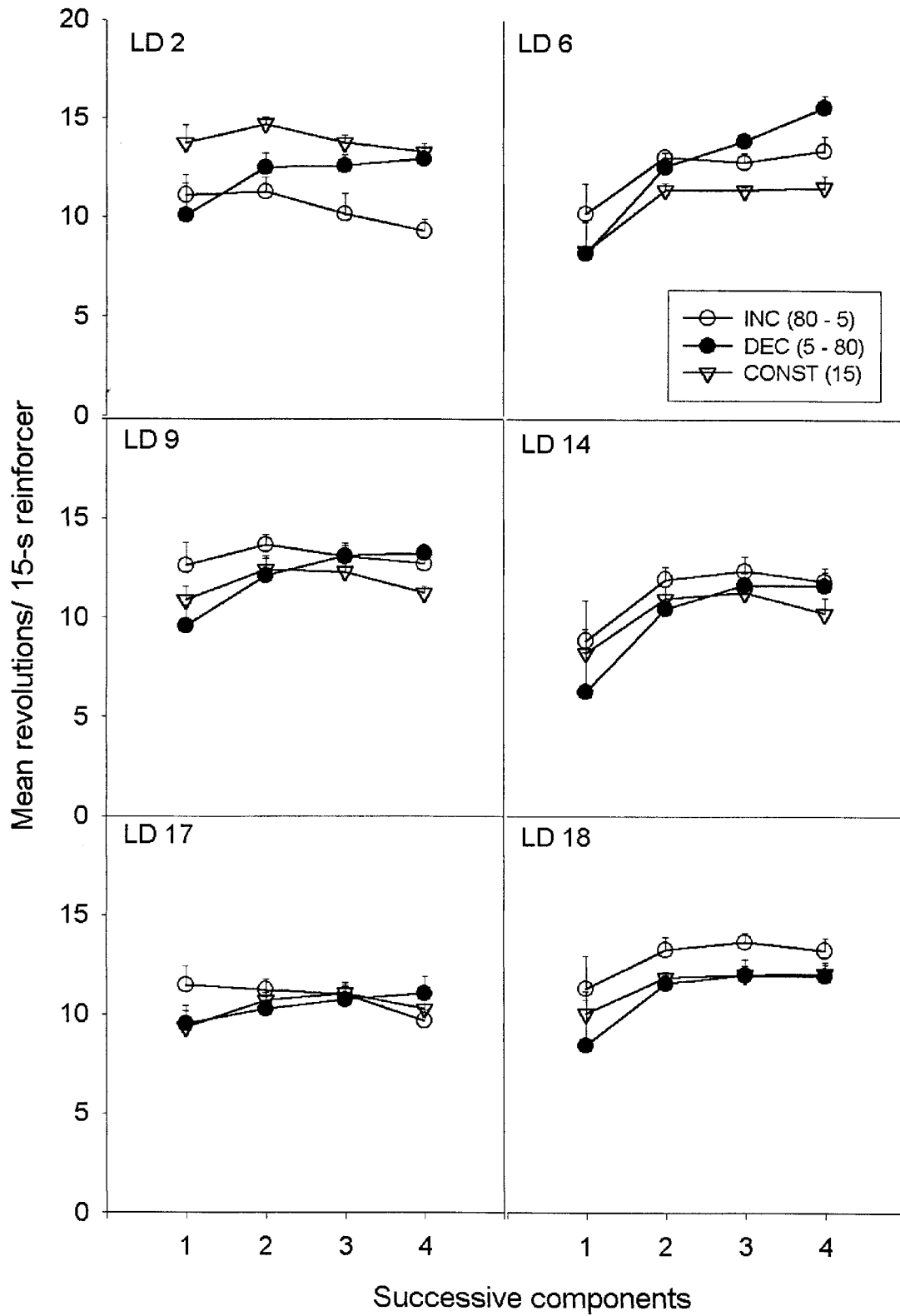
sponse-reinforcer relation differed systematically with schedule order. Specifically, the hyperbolic curves displayed in Figure 1 rose more rapidly to a lower asymptote when reinforcement rates were arranged in a decreasing order and rose less rapidly toward a higher asymptote when reinforcement rates occurred in an increasing order. Consequently, estimates of the response-rate asymptote (k) and the reinforcement rate that maintains half the asymptotic response rate (R_O) were higher when reinforcement schedules were arranged in order of increasing reinforcement rate. Also related to these differences between the curves is the observation that there was less variation of response rates with reinforcement rate when the schedules were presented in an order of decreasing reinforcement rate.

Assessment of within-session changes in response rate with the programmed reinforcement rate held constant, as displayed in Figure 2, revealed that response rates increased from the beginning to the end of the session. This pattern of increasing lever-pressing rates is consistent with that previously observed by Belke (1997). The possibility that the within-session change in response rates may be related to the differences in the hyperbolic curves is suggested by the strong positive correlation between the magnitude of the within-session increase in lever-pressing rates and the magnitude of the difference in the estimates (k and R_O) between the two schedule orders (Table 2).

For example, when reinforcement rates increased throughout the session, so that the effect of reinforcement rate on response rate coincided with the within-session increase, response rates changed more and the asymptote was higher. When, however, reinforcement rates were arranged to decrease throughout the session so that the effect of reinforcement rate on response rate opposed the within-session increase, response rates changed less and the asymptote was lower. The data in Table 2 show that the magnitude of these effects appears to be related to the

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Fig. 3. Mean revolutions per 15-s reinforcer across successive components for the increasing reinforcement-rate order (inc, open circles), the decreasing reinforcement-rate order (dec, filled circles), and the constant reinforcement rate (const, open inverted triangles). Vertical lines indicate standard deviations.



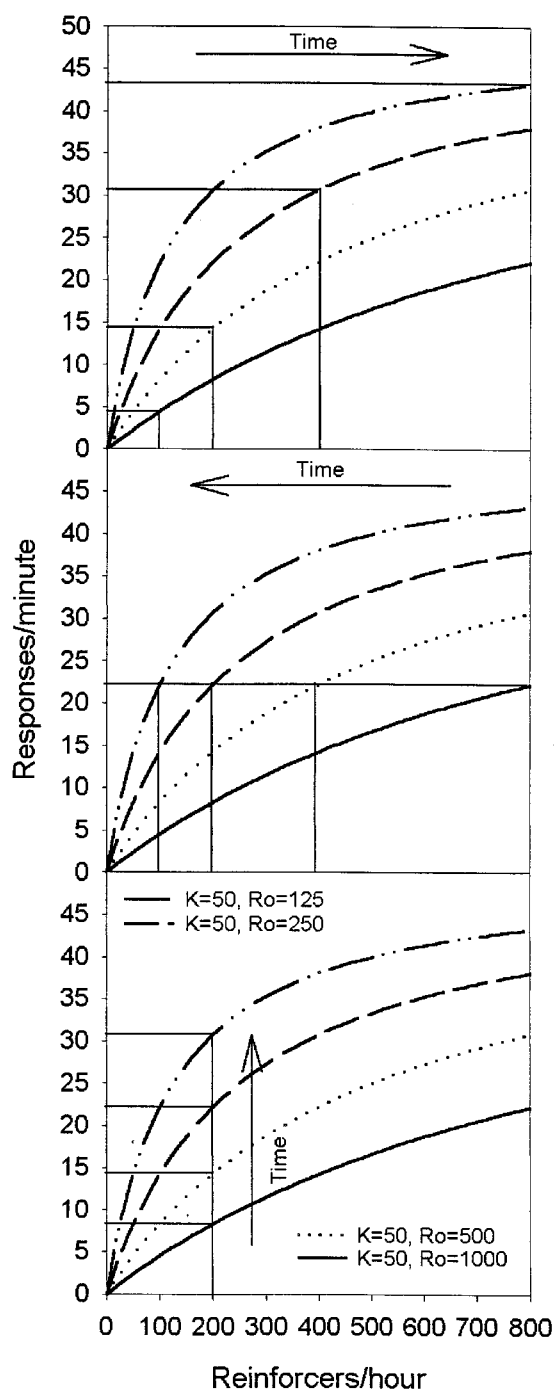


Fig. 4. Sets of hyperbolic curves with k constant and R_O varied. The intersections of the horizontal and vertical lines with the curves show the response rates that would be predicted for successive components. The arrows show the direction of time from the beginning to the end of the session. The top panel shows the response rates that would be predicted if reinforcement efficacy increased throughout the session and reinforcement sched-

magnitude of the within-session increase in responding.

This correlation appears to support McSweeney et al.'s (1995) assertion that the fit of Equation 1 can be affected by within-session patterns of responding. However, unlike previous studies that assessed within-session patterns of operant responding maintained by food or water reinforcement, wheel-running reinforcement provides the opportunity to observe changes in both operant and consequent behavior. As previously observed (Belke, 1997), wheel-running rates increased within a session (Figure 3), although not as strongly or as systematically as lever-pressing rates (Figure 2). This observation suggests a possible explanation for both the differences in the hyperbolic functions and the within-session response pattern. The increase in revolutions per opportunity to run suggests that the efficacy of the reinforcer increased from the beginning to the end of the session. The effect of a change in the efficacy of the reinforcer can be modeled using a series of hyperbolic curves in which the asymptote remains constant but the efficacy of the reinforcer, as indexed by R_O , varies. Figure 4 shows sets of hyperbolic functions depicting how response-rate functions would change if the response-rate asymptote remained constant (i.e., $k = 50$ presses per minute) but the efficacy of a reinforcer doubled with each successive component (i.e., $R_O = 1,000, 500, 250, 125$). The successive panels represent the sampling of response rates across these curves when (a) programmed reinforcement rates increased throughout the session, (b) programmed reinforcement rates decreased throughout the session, and (c) the programmed reinforcement rate remained constant throughout the session. Arrows denote the direction of sampling from the beginning to the end of the session. The intersection of the horizontal and vertical lines shows the response rate that would

ules were arranged in order of increasing reinforcement rate. The middle panel depicts the response rates that would be predicted if reinforcer efficacy increased throughout the session and reinforcement rates were arranged in decreasing order. The bottom panel depicts how response rates would be predicted to change within a session if reinforcement efficacy increased but reinforcement rate remained constant.

be predicted given the reinforcement rate and current efficacy of the reinforcer. For the top two panels, these would be the response rates predicted across successive curves for reinforcement rates of 100, 200, 400, and 800 reinforcers per hour. For the bottom panel, these would be the response rates predicted across successive curves with a constant obtained rate of reinforcement.

In the top panel, with both reinforcement rates and reinforcer efficacy increasing within the session, predicted response rates sampled across successive curves show greater changes in responding with changes in reinforcement rate than would occur if response rates were sampled along a single curve. That is, for obtained reinforcement rates of 100, 200, 400, and 800 reinforcers per hour, the response rates predicted would be 4.55, 14.29, 30.77, and 43.24, responses per minute, respectively. In contrast, the response rates that would be predicted for these reinforcement rates if the efficacy of the reinforcer remained constant at a level indexed by an R_O of 1,000 reinforcers per hour would be 4.55, 8.33, 14.29, and 22.22 responses per minute. If the efficacy remained constant at a level indexed by an R_O of 125 reinforcers per hour, then the equivalent rates would be 22.22, 30.77, 38.10, and 43.24 responses per minute. The difference in predicted response rates associated with the highest and lowest reinforcement rates is greater if reinforcer efficacy changes within a session than if it does not. The effect on the estimated parameters would be inflation. Estimated values of k and R_O for the predicted response rates sampled across successive curves would be 109 responses per minute and 1,091 reinforcers per hour. The asymptote is more than double the assumed 50 responses per minute.

The middle panel of Figure 4 shows response rates that would be predicted if reinforcing efficacy increased across the session while reinforcement rates decreased. That is, the highest programmed reinforcement rate would occur when reinforcer efficacy within the session was lowest, and vice versa. In this case, the effect of the change in reinforcer efficacy is to diminish the changes in response rates with changes in reinforcement rate. For this situation, with reinforcer efficacy doubling across successive components and reinforcement rate halving, there is no

change in response rates with changes in reinforcement rate. A response rate of 22.22 responses per minute would be predicted for reinforcement rates of 100, 200, 400, and 800 reinforcers per hour. For this particular set of response rates, no estimation of fitted parameters can be made. However, the lower response rate associated with the highest reinforcement rate and the lack of differentiation of response rates suggest that both the response-rate asymptote (k) and the index of efficacy (R_O) estimated from these rates would be lower than that which would be observed under the conditions depicted in the top panel.

Finally, the bottom panel of Figure 4 shows how response rates would be predicted to change within a session when reinforcement rate is held constant but reinforcer efficacy increases within a session. In this case, for an obtained reinforcement rate of 200 reinforcers per hour, response rates of 8.33, 14.29, 22.22, and 30.77 responses per minute would be observed across successive components from the beginning to the end of a session. Thus, an increase in reinforcer efficacy within a session with reinforcement rate held constant should produce a within-session pattern of increasing response rates.

In sum, this analysis suggests that an increase in reinforcer efficacy within a session should be manifested as enhanced variation of response rates as a function of reinforcement rates when reinforcement rates are arranged in increasing order, diminished variation of response rates as a function of reinforcement rates when reinforcement rates occur in decreasing order, and a within-session pattern of increasing response rates when reinforcement rate is held constant. In terms of fitted parameters from Equation 1, the values of k and R_O for a decreasing reinforcement-rate order would be expected to be lower than those obtained with an increasing reinforcement-rate order.

The present analysis calls into question the validity of the estimates from Equation 1 as indexes of the response-reinforcer relation when the efficacy of the reinforcer changes within a session. If the observed response rates are sampled across multiple hyperbolic functions, then the resulting function defined by these response rates would not be representative of the underlying response-re-

inforcer relation. Furthermore, different procedures for generating response-reinforcer relations would differ in their susceptibility to this effect of a within-session change in reinforcer efficacy. The within-session procedure of presenting multiple reinforcement schedules within the same session would be more susceptible to this effect than the between-condition procedure of presenting only a single schedule in a session and multiple schedules across conditions.

Another issue is how to determine whether reinforcer efficacy has changed within a session. Operant response rates provide one index of a change in the efficacy of the reinforcer within a session. A more direct measure may be changes in the consequential behavior, although with conventional reinforcers such as food and water, rates of eating and drinking are not typically measured. With wheel-running reinforcement, systematic changes in wheel-running rates may provide a more direct index of reinforcer efficacy, although the effect of other variables (such as fatigue) may influence this measure. Furthermore, the extent to which changes in wheel-running rate can be taken as an index of the change in reinforcer efficacy may depend on the duration of the reinforcer. That is, changes in reinforcer efficacy may be less apparent with short (e.g., 10 s) as opposed to long (e.g., 60 s) reinforcer durations.

What are the implications of the current findings for previous studies of wheel-running reinforcement using Herrnstein's matching law equation? Belke (1998) compared estimates of k within the same animals for lever pressing reinforced by sucrose solution and by the opportunity to run. Estimates of k for each reinforcer were based on response rates obtained by exposing the animals to a series of reinforcement schedules within each session. For both reinforcer types, reinforcement schedules were arranged in order of increasing reinforcement rates. Response-rate asymptotes were higher for sucrose than for wheel-running reinforcement. The results of the present study suggest that the estimate of k for wheel-running reinforcement may have been inflated by a change in the efficacy of the reinforcer within a session. If so, the difference in response-rate asymptotes between sucrose and wheel-

running reinforcement may be greater than that found in Belke's (1998) study.

In Belke and Heyman's (1994) original study that generalized Herrnstein's (1970) single-operant hyperbolic matching law to lever pressing maintained by the opportunity to run, the order of reinforcement schedules was one of ascending and then descending reinforcement rates (e.g., VI 60 to VI 5 to VI 30 s). The effect of a change in reinforcer efficacy within a session on estimates obtained for this schedule order is unknown. An assessment of the applicability of Herrnstein's equation to wheel-running reinforcement using a between-conditions procedure, however, might help to determine if this effect of a change in reinforcer efficacy on estimation of a response-reinforcer relation can be surmounted.

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APPENDIX B

Estimates of k , R_O , standard errors (SE), and percentage of variance accounted for (%VAC) for the increasing and decreasing reinforcement rates based on response and reinforcement rates averaged over the last 10 sessions of a condition.

Rat	k	R_O	$SE\ k$	$SE\ R_O$	%VAC
Increasing reinforcement rate order (VI 80 s to VI 5 s)					
LD2	45	38	1.9	7.2	97
LD6	53	101	3.1	17.7	98
LD9	35	25	1.4	5.4	95
LD14	52	75	4.9	21.4	94
LD17	50	83	3.1	15.9	98
LD18	77	133	9.7	38.9	93
<i>M</i>	52	76			96
Decreasing reinforcement rate order (VI 5 s to VI 80 s)					
LD2	26	-7	2.7	6.6	29
LD6	34	25	2.9	11.9	80
LD9	24	1	3.3	12.2	0
LD14	20	8	1.8	8.2	38
LD17	32	26	0.7	2.7	99
LD18	24	-8	2.5	6.3	39
<i>M</i>	27	7.5			48

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APPENDIX A

Lever-pressing rates (responses per minute), reinforcement rates (reinforcers per hour), and mean postreinforcement-pause durations (PRP, in seconds) for each tandem FR 1 VI schedule for each subject in the increasing and decreasing reinforcement rate conditions.

Rat	Schedule	Schedule order					
		Increasing rate			Decreasing rate		
		Response rate	Reinforcer rate	PRP	Response rate	Reinforcer rate	PRP
LD2	VI 5	47.50	584.88	9.58	29.86	483.14	13.18
	VI 15	38.59	215.81	10.24	32.13	214.61	13.87
	VI 40	29.08	85.10	9.72	27.84	83.78	9.06
LD6	VI 80	21.48	42.80	13.01	28.51	43.71	10.16
	VI 5	46.08	580.05	7.68	32.41	478.78	21.68
	VI 15	33.24	218.23	9.08	35.74	223.01	13.96
LD9	VI 40	24.16	85.07	12.79	27.38	86.63	11.58
	VI 80	17.74	42.85	32.39	25.18	43.82	11.72
	VI 5	37.21	546.54	13.71	28.30	435.62	11.54
LD14	VI 15	32.15	207.02	16.85	30.95	201.47	10.08
	VI 40	29.03	85.99	16.06	25.96	85.63	14.29
	VI 80	22.77	43.39	15.98	23.01	43.30	11.82
LD17	VI 5	39.85	511.99	14.25	14.98	291.82	25.86
	VI 15	35.99	219.17	16.17	21.88	181.90	27.80
	VI 40	28.30	85.60	16.41	16.85	79.01	23.00
LD18	VI 80	13.72	42.21	31.30	14.19	41.79	23.98
	VI 5	43.56	536.04	14.41	30.34	490.44	12.84
	VI 15	37.82	214.66	15.77	28.23	205.38	13.31
LD18	VI 40	25.33	83.47	26.31	23.90	80.84	19.41
	VI 80	19.79	42.92	29.34	21.23	43.68	22.74
	VI 5	68.03	616.53	8.52	21.91	386.01	17.71
LD18	VI 15	50.34	217.85	9.77	27.92	205.50	13.37
	VI 40	36.98	87.35	11.71	30.71	85.66	13.60
	VI 80	13.91	41.11	23.03	27.17	43.83	15.78