

*REINFORCER MAGNITUDE (SUCROSE CONCENTRATION) AND  
THE MATCHING LAW THEORY OF RESPONSE STRENGTH*

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This experiment investigated the relationship between reinforcer magnitude (sucrose concentration) and response rate. The purpose was to evaluate the behavior of two parameters of an equation that predicts absolute response rate as a function of reinforcement rate and two free parameters. According to Herrnstein's (1970) theory of reinforced behavior, one parameter of this "response-strength equation" measures the efficacy of the reinforcer maintaining responding and the other parameter measures motoric components of response rate, such as response duration. Seven rats served as subjects. Experimental sessions consisted of a series of five different variable-interval schedules of reinforcement, each in effect for 5 minutes. Within each session, obtained reinforcement rates varied over more than a 30-fold range, from about 20 per hour to 700 per hour. The reinforcer was sucrose solution, and, between sessions, its concentration was varied from 0.0 to 0.64 molar (0 to 21.9%). For sucrose concentrations of 0.16 to 0.64 M, response rate was a negatively accelerated function of reinforcement rate. Increases in sucrose concentration increased response rates maintained by low but not high reinforcement rates. This pattern of changes corresponds to a change in the reinforcement-efficacy parameter of the response-strength equation. In contrast, the motor-performance parameter did not change as a function of sucrose concentration. These findings are inconsistent with the results of a similar study (Bradshaw, Szabadi, & Bevan, 1978) but support Herrnstein's theory of reinforced behavior.

*Key words:* reinforced behavior, reinforcer magnitude, matching law, response-strength equation, behavior theory, sucrose concentration, variable-interval schedule, lever press, rats

Bradshaw, Szabadi, and Bevan (1978) reported an experiment on the relationship between reinforcer magnitude (sucrose concentration) and response rate, designed to test Herrnstein's (1970) theory of response strength. This theory has wide empirical support and has been a major influence on the study of reinforced behavior and choice (e.g., Davison & McCarthy, 1988; Herrnstein, 1990; Staddon, 1991; Williams, 1988). However, Bradshaw et al.'s results failed to support Herrnstein's predictions. This discrepancy has been commented on (e.g., Davison & McCarthy, 1988; Williams, 1988), but not resolved. The purpose of the present experiment was to test the generality of Bradshaw et al.'s findings. First, however, some aspects of the theory and the predictions that Bradshaw et al. tested will be reviewed.

Herrnstein (1970) introduced a simple, two-parameter equation to describe the relationship between response rate and reinforcement rate. This equation is sometimes referred to as a quantitative description of response strength,

because of its generality across species and experimental procedures (e.g., Williams, 1988). The conventional notation is

$$B = kR / (R + R_c), \quad (1)$$

where  $B$  stands for response rate,  $R$  stands for reinforcement rate, and  $k$  and  $R_c$  are fitted constants. In the numerator,  $k$  is the asymptotic response rate. For instance, as reinforcement rate ( $R$ ) increases, response rate approaches  $k$ . In the denominator,  $R_c$  is equal to the rate of reinforcement that maintains one half of the asymptotic response rate. That is, when response rate is equal to  $k/2$ , reinforcement rate is equal to  $R_c$ . These constants need not have any empirical meaning (i.e., the equation could simply provide a convenient summary of the data); however, Herrnstein (1970), on the basis of the matching law, proposed that they measured determinants of reinforced responding.

The key ideas are that  $k$  indexes motoric components of response rate, such as the topography of the response, and  $R_c$  indexes the efficacy of the reinforcer maintaining responding relative to the efficacy of uncontrolled, background reinforcers. For example, in experiments with rats,  $k$  varied as a function of response duration (e.g., Porter & Villanueva,

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1988), and  $R_c$  varied as a function of access to competing reinforcers (Belke & Heyman, 1994; Bradshaw, 1977). An important implication of Herrnstein's interpretation of Equation 1 is that manipulations that affect reinforcement efficacy do not necessarily alter the asymptotic response rate,  $k$ ; conversely, manipulations that affect the asymptotic response rate do not necessarily affect the efficacy of the reinforcer maintaining the operant behavior,  $R_c$ . That is, it is assumed that  $k$  and  $R_c$  measure independent determinants of response rate. In contrast, other theories of reinforced behavior (e.g., Catania, 1973; Killeen, 1981; McDowell & Wood, 1984) imply that the two parameters share common determinants, and will, therefore, covary. Put more generally, Equation 1 is widely accepted as a good approximation of the relationship between reinforcement rate and response rate, but Herrnstein's interpretation of the free parameters of the equation is not as widely accepted.

Bradshaw et al. (1978) tested Herrnstein's interpretation of  $k$  and  $R_c$  by varying the magnitude of the reinforcer maintaining responding. Rats served as subjects, responses were reinforced according to variable-interval (VI) schedules, and there were three different sucrose concentrations: 0.32, 0.05, and 0.0 molar (M). According to Bradshaw et al., Herrnstein's account predicts that changes in sucrose concentration should change  $R_c$  while not affecting  $k$ . However, they found that changes in sucrose concentration systematically altered both  $k$  and  $R_c$ . For instance, the asymptotic response rate was lowest when the reinforcer was water (the rats were not water deprived) and highest when the reinforcer was 0.32 M sucrose. Thus the asymptotic response rate was not independent of reinforcement conditions.

However, in contrast to Bradshaw et al.'s (1978) results, other studies showed systematic changes in  $R_c$  while  $k$  remained approximately constant. There were three sorts of experiments: those in which deprivation level was manipulated (e.g., Heyman & Monaghan, 1987; Logan, 1960); those in which some aspect of the reinforcer, such as its magnitude or quality, was manipulated (e.g., Conrad & Sidman, 1956; de Villiers & Herrnstein, 1976; Guttman, 1954; Hamilton, Stellar, & Hart, 1985; Petry & Heyman, 1994); and those in which the background reinforcement context was manipulated (e.g., Belke & Heyman,

1994). Moreover, some of these studies were quite similar to Bradshaw et al.'s experiment. For example, working in the same laboratory, Bradshaw, Ruddle, and Szabadi (1981) reported that  $R_c$  but not  $k$  varied as a function of sucrose volume. It is not obvious why sucrose volume and sucrose concentration would have such different behavioral effects. In an effort to resolve this apparent inconsistency, we tested the generality of the sucrose-concentration results.

Our procedure had the following basic elements. During daily sessions, rats were presented with a series of five different VI reinforcement schedules. This permitted collection of five pairs of response and reinforcement rates. Equation 1 was fitted to these results, so that each session provided an estimate of  $k$  and  $R_c$  for each subject. The reinforcer was sucrose solution, and its concentration varied from 0.0 M (tap water) to 0.64 M between sessions. Thus, between-session estimates of  $k$  and  $R_c$  were used to determine if changes in sucrose concentration affected only  $R_c$  or both  $k$  and  $R_c$ .

## METHOD

### *Subjects*

Seven experimentally naive male Wistar rats from Royal Hart breeders served as subjects. At the start of the experiment, the rats were approximately 3 months old and weighed about 350 g. They were housed one to a cage, and the colony room was illuminated 12 hr a day (lights on at 6:30 a.m.). The rats obtained sucrose during the experimental session, and after each session they were given rat chow (Purina), typically about 12 to 15 g, to keep them at 85% of their preexperimental weights. There was free access to water in the home cage.

### *Apparatus*

The experiments were conducted in seven standard chambers (Coulbourn Instruments, Modular Test Cage, Model E10-10: 28.5 cm wide, 29.5 cm long, and 24 cm high), equipped with a single lever, 6.5 cm from the floor. The lever was operated by a force of about 0.25 N. In the middle of the front panel, to the left of the lever, was an opening that allowed access to a 0.02-mL dipper of sucrose solution. On

the left and right sides of the front panel, about 10.0 cm from the floor, were stimulus lights (28 V, 0.04 A, No. 1819), and behind the panel was a clicker (standard coil relay). The two lights and clicker were used to signal different phases of the experimental session. The chambers were enclosed in plastic, sound-attenuating, ventilated outer boxes. A PDP® 11 computer controlled and recorded experimental events.

### Procedure

Daily sessions consisted of a series of five different VI schedules of reinforcement. The series of intervals in each schedule approximated a Poisson distribution, and was based on the list of times derived by Fleshler and Hoffman (1962). The mean intervals were 5 s, 10 s, 30 s, 45 s, and 100 s, which correspond to rates of 720, 360, 120, 80, and 36 reinforcers per hour. Each schedule was in effect for 5 min, and between schedules there was a 15-min period during which the schedules were not available and stimulus lights were off. Schedules were presented in a random order without replacement so that each schedule appeared no more than once per session. A reinforcer consisted of a series of three 0.02-mL dipper presentations of sucrose solution (concentrations described below). The first dipper presentation lasted 2 s, and the two following presentations were 1 s each. A 3-s blackout period followed each reinforcement. During reinforcement and the blackout, the VI timer did not run and the stimulus lights remained off. The stimulus lights and clicker signaled which of the five schedules was in effect. The patterns, from the leanest schedule to the richest, were: (a) stimulus lights on continuously, (b) stimulus lights flashing on for 2 s and off for 2 s, (c) stimulus lights flashing on for 1 s and off for 1 s, (d) clicker on for 0.1 s and off for 5 s plus stimulus lights on continuously, and (e) clicker on for 0.1 s and off for 2 s plus stimulus lights flashing on for 2 s and off for 1 s. In other experiments, different patterns of stimuli were used (e.g., Heyman & Monaghan, 1987), and more recently, the different reinforcement rates were not distinguished by distinctive stimuli (e.g., Heyman, 1992).

Sucrose solution was the reinforcer, and during the course of the study its concentration was varied from 0.0 M (tap water) to 0.64 M.

Table 1  
Order of conditions and number of sessions.

Sucrose concentration (molar)	Sessions
0.32	13
0.05	10
0.16	30
0.64	9
0.32	17
0.64	23
0.00	8
0.16	44

Table 1 lists the order and number of sessions for which each concentration was in effect. The 0.16 M (5.5%), 0.32 M (10.9%), and 0.64 M (21.9%) concentrations were presented twice to control for time-course and order effects. Tap water (0.0 M) and the 0.05 M solutions were presented just once, because neither reliably maintained lever pressing. The 0.16 to 0.64 M conditions remained in effect until the parameters  $k$  and  $R_c$  appeared to be stable. The criteria were absence of an extreme value and absence of a strictly decreasing or increasing trend over the last five consecutive sessions.

A weighted least squares method was used to fit Equation 1 to the response and reinforcement rates. The technique was developed by Wilkinson (1961) for fitting the Michaelis-Menten equation to enzymatic reactions.

## RESULTS

Figure 1 shows the relationship between response rate and reinforcement rate for the second presentation of the 0.16, 0.32, and 0.64 M sucrose concentrations for each subject. The rates were obtained by averaging over the last five sessions of a condition. The results for the sessions in which tap water and 0.05 M sucrose served as the reinforcers were not included, because it was not possible to obtain stable levels of responding in these conditions. When the reinforcer was tap water, all but 2 rats responded at less than one response per minute, independently of the schedule (the rats were not water deprived), and when the reinforcer was a 0.05 M sucrose concentration, 4 subjects responded sporadically or not at all in the three lower reinforcement rate schedules, and 3 rats responded at less than 10 re-

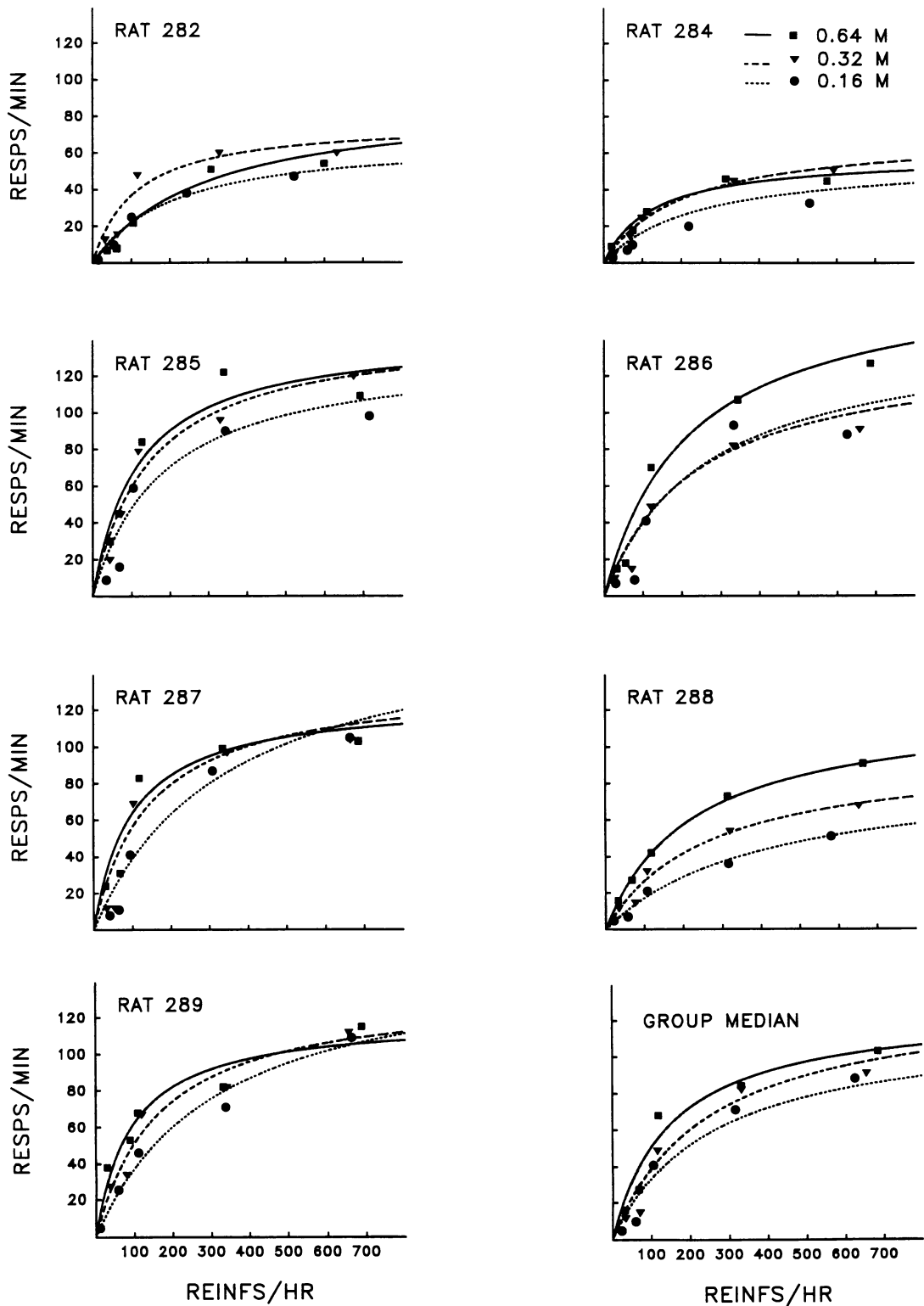


Fig. 1. Mean response rates for each subject and the median rates for the group, calculated over the last five sessions of each condition. Response rates are plotted as a function of obtained reinforcement rates. The smooth curves were obtained by fitting Equation 1 to the data.

Table 2

A summary of the values of parameters  $k$  and  $R_c$  in Equation 1, obtained by a weighted least squares method (Wilkinson, 1961). Also shown is the percentage of variance accounted for (VAC) by Equation 1. The equation was fitted to the average response and reinforcement rates, calculated over the last five sessions of each condition.

Sucrose concentration (molar)	$k$	$R_c$	VAC (%)	$k$	$R_c$	VAC (%)	$k$	$R_c$	VAC (%)
	Rat 282			Rat 284			Rat 285		
0.16	97	412	97	57	239	94	137	185	97
0.32	120	259	97	110	255	98	247	181	96
0.64	81	160	97	52	155	99	170	100	99
0.16	68	207	97	58	414	99	134	180	89
0.32	77	109	88	71	206	98	146	146	93
0.64	90	304	94	59	128	97	143	117	90
	Rat 286			Rat 287			Rat 288		
0.16	207	621	98	183	356	98	95	433	98
0.32	348	733	98	194	261	95	70	111	88
0.64	126	213	93	163	167	95	99	212	99
0.16	145	261	85	171	341	94	87	404	98
0.32	136	234	96	136	142	87	97	265	97
0.64	176	219	96	126	98	87	122	225	99
	Rat 289			Group M					
0.16	171	330	96	135	368	97			
0.32	216	317	99	186	302	96			
0.64	145	129	99	119	162	97			
0.16	155	314	98	117	303	95			
0.32	135	163	94	114	181	93			
0.64	120	92	90	119	169	93			

sponses per minute, independently of the schedule. The Appendix lists the response and reinforcement rates for each subject in each schedule component for both presentations of the 0.16 to 0.64 M sucrose concentrations.

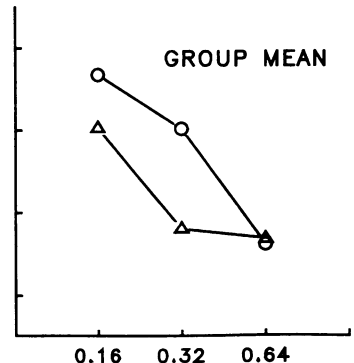
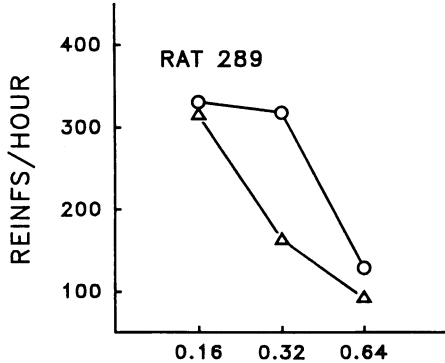
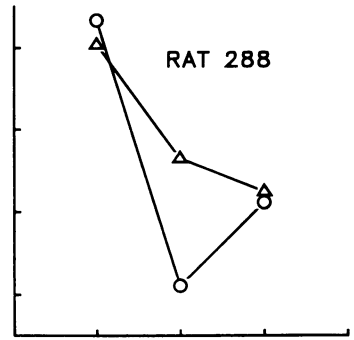
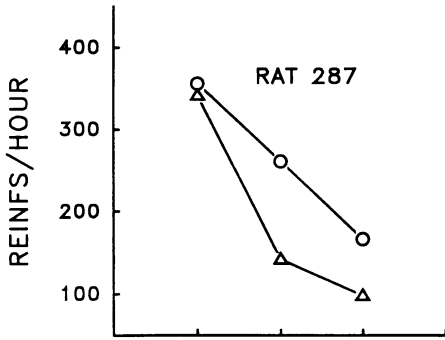
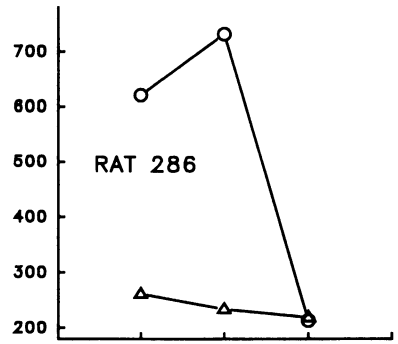
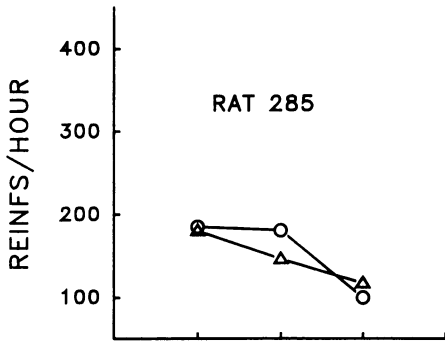
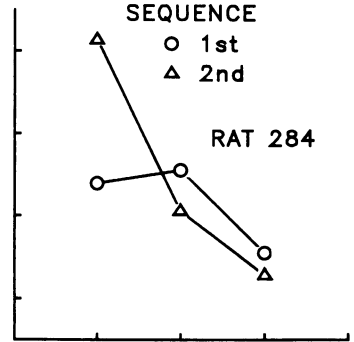
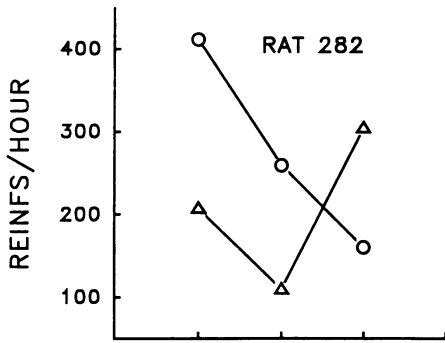
Figure 1 shows that response rate was a negatively accelerated function of reinforcement rate at each of the three sucrose concentrations. The range of obtained reinforcement rates was about 20 to 700 per hour, and the corresponding range of response rates was about 5 to 105 responses per minute. As expected, higher sucrose concentrations usually maintained a higher response rate at a given reinforcement rate. For instance, under each schedule, median response rates (for the group) were ranked by concentration. Figure 1 also shows that individuals differed in overall level of responding. For example, Rat 286 typically responded about twice as fast as did Rats 282 and 284 (holding reinforcement rate approximately constant).

Table 2 and Figures 2 and 3 summarize the

parameter values and statistics obtained from fitting Equation 1 to the averaged response and reinforcement rates (listed in the Appendix). Equation 1 accounted for 88% to 99% of the variance in obtained response rates, and the median standard error of the parameter estimates was less than 5% of the mean (see Table 2). On the y axis of Figure 2, the values of  $R_c$  are given in reinforcers per hour, and on the y axis of Figure 3, the values of  $k$  are given in responses per minute. (Recall that  $R_c$  is the rate of reinforcement that maintains one half the asymptotic response rate, and  $k$  is the asymptotic response rate.) In both graphs, the scale of the x axis is logarithmic.

Figure 2 shows that  $R_c$  decreased as a function of sucrose concentration. This means that at higher sucrose concentrations, lower reinforcement rates maintained a given proportion of asymptotic responding. Most subjects showed this pattern. For example, in all but two instances (of 14 possible cases), the lowest sucrose concentration was associated with the

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highest value of  $R_c$ ; similarly, in all but two instances, the highest sucrose concentration was associated with the lowest value of  $R_c$ . Statistical analysis supported these observations. Repeated measures analysis of variance revealed a statistically significant relationship between concentration and  $R_c$ ,  $F(2, 12) = 13.08$ ;  $p < .002$ , and contrast tests showed a statistically significant linear relationship between increases in sucrose concentration and decreases in  $R_c$ ,  $F(1, 6) = 47.04$ ,  $p < .0001$ . The values of  $R_c$  tended to be lower during the second presentation of each concentration, but this relationship was not statistically significant,  $F(1, 6) = 2.07$ ;  $p < .25$ .

Figure 3 shows that  $k$  remained relatively constant in the second presentation of the three sucrose concentrations but not in the first presentation. In the first presentation, the 0.32 M concentration was associated with markedly higher values of  $k$  than either the lowest or highest sucrose concentrations. This was probably an order effect. The 0.32 M concentration was presented first, and during the first sequence,  $k$  decreased as a function of the order in which the concentrations were presented. For example, the order was 0.32, 0.16, and 0.64 M, and the respective values of  $k$  were 186, 135, and 119 responses per minute. Put in terms of sessions, the average value of  $k$  declined from 186 to 135 responses per minute over the first 53 sessions and then remained within a range of 114 to 119 responses per minute for the remaining 101 sessions and across the three sucrose concentrations.

Analysis of variance shows a concentration effect,  $F(2, 12) = 4.01$ ;  $p < .05$ , and a sequence effect,  $F(2, 12) = 8.14$ ;  $p < .05$ . However, as suggested by Figure 3, the concentration effect was due to the difference between the first condition and the five subsequent conditions. That is, there was no statistically significant relationship between  $k$  and sucrose concentration when the data from the initial condition (0.32 M) were removed from the analysis,  $F(4, 24) = 1.35$ ;  $p < .30$ .

## DISCUSSION

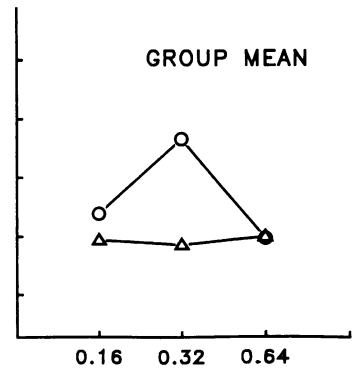
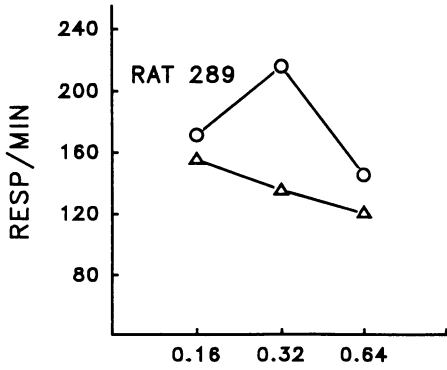
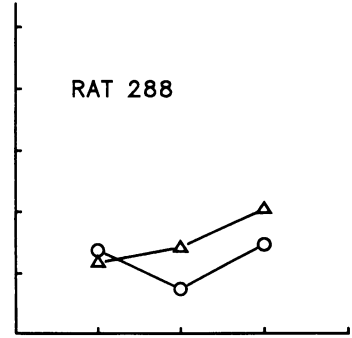
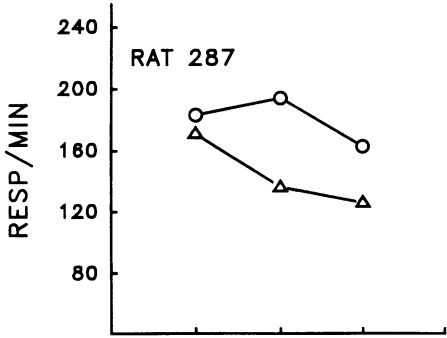
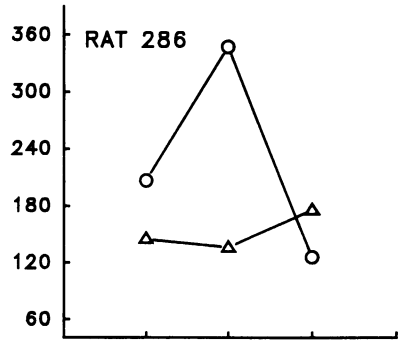
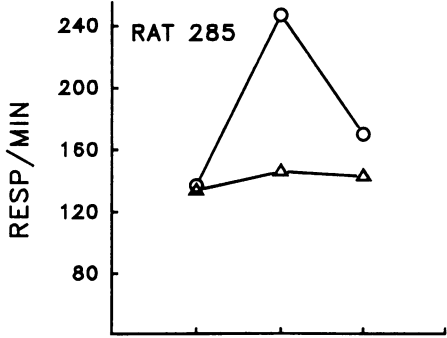
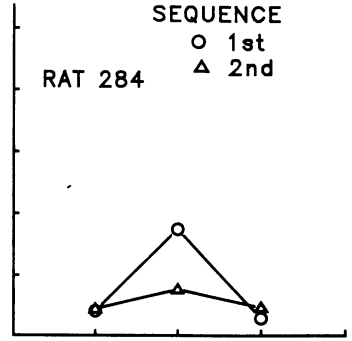
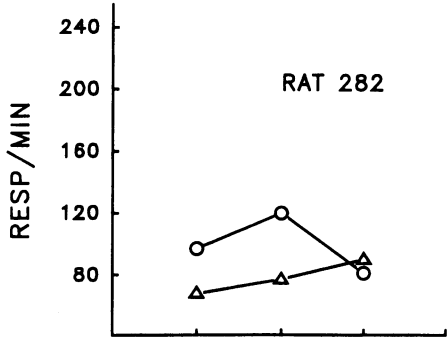
The basic finding in this study was that the parameter  $R_c$  of Equation 1 was systematically related to reinforcement magnitude, whereas the parameter  $k$  was not. Put in terms of the curve-fitting definitions of these parameters, the rate of reinforcement that maintained one half the asymptotic response rate varied as a function of sucrose concentration, but the asymptotic response rate was independent of sucrose concentration. These findings support the conclusions that (a)  $R_c$  measures the efficacy of the reinforcer maintaining responding, (b)  $R_c$  and  $k$  measure independent determinants of reinforced responding (Herrnstein, 1970), and (c) the motivation to engage in reinforced behavior is independent of motoric features of the behavior (at least those measured by  $k$ ).

Why then did Bradshaw et al. (1978) find that changes in sucrose concentration were correlated with changes in  $k$  as well as  $R_c$ ? The major methodological difference between the two studies was in how the reinforcement schedules were arranged. Bradshaw et al. presented each of five schedules alone for either 12 or 30 sessions and then fitted Equation 1 to the between-session response and reinforcement rates. In contrast, in the current study, five schedules were presented in each session, in random order, and Equation 1 was fitted to within-session response and reinforcement rates. Although the two methods are quite different, previous results show similar findings regarding the behavior of  $k$  and  $R_c$ . First, in both methods, response rate was a negatively accelerated function of reinforcement rate, as described by Equation 1. Second, in both methods,  $k$  changed as a function of response requirements (see Bradshaw, Szabadi, & Ruddle, 1983; Hamilton et al., 1985; Heyman & Monaghan, 1987; McSweeney, 1978), whereas  $R_c$  changed as a function of deprivation and reinforcement conditions (e.g., Bradshaw et al., 1981; Conrad & Sidman, 1956; de Villiers & Herrnstein, 1976; Hamilton et al., 1985; Hey-

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 Fig. 2. The relationship between  $R_c$  (in reinforcements per hour) and sucrose concentration for each subject. The parameter estimates were obtained by fitting Equation 1 to the average response and reinforcement rates for each subject (listed in the Appendix).

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man & Monaghan, 1987). Third, in both methods, there was no evidence that the order in which schedules were presented affected the behavior of either  $k$  or  $R_c$ . For instance, in the within-session method, similar findings were obtained when reinforcement rates were presented in a strictly increasing order (Heyman, 1983; Petry & Heyman, 1994), in a strictly descending order (Heyman, 1983), in a random order (Heyman & Monaghan, 1987), and in an ascending-descending order (Heyman, 1992). This is not to say that schedule order may not affect the absolute magnitudes of  $k$  and  $R_c$ , but rather that it did not affect their relationship to the experimental conditions.

Thus, the manner in which the schedules were presented does not seem a likely basis for the different findings. We find two other accounts more plausible. First, in Bradshaw et al.'s (1978) study, the sucrose concentrations were 0.32, 0.05, and 0.0 M. It seems natural to think of this as variation in reinforcer magnitude. But what if the reinforcing effects of 0.05 M sucrose are more like those of water than of 0.32 M sucrose? For instance, in a study that used a sham-feeding procedure, rats consumed about the same amount of 0.034 M sucrose as they did water (Nissenbaum & Sclafani, 1987). Thus, it may be more reasonable to classify Bradshaw et al.'s experiment as a study of changes in reinforcer quality rather than reinforcer amount. This distinction is relevant because there is evidence that qualitatively different reinforcers support different response topographies. For instance, in pigeons (Wolin, 1968) and rats (Hull, 1977), water and food maintained topographically distinct operants even though there had been no change in response requirement. Thus, the changes in  $k$  reported by Bradshaw et al. may reflect changes in reinforcer quality.

Second, response rates in Bradshaw et al.'s (1978) sucrose-concentration experiment did not exceed 30 per minute, whereas in the present study, asymptotic response rates were typically close to 80 per minute. If the low rates were due to the difficulty of operating the lever, it is possible that some "responses" went unrecorded. Or, alternatively, when the response

requirement is onerous, asymptotic response rates and reinforcement efficacy may not be independent, as called for by Herrnstein's theory. Thus the correlation between sucrose concentration and  $k$  reported by Bradshaw et al. could simply be a matter of unrecorded behavior, or, more interestingly, it may represent boundary conditions on the independence of motoric and motivational components of reinforced behavior.

Although  $k$  did not vary as a function of sucrose concentration in this study, it declined in 5 of 7 subjects over the first three conditions (in order: 0.32, 0.16, and 0.64 M). It is unlikely that this decline was due to age, because  $k$  remained relatively stable from the third condition on (see Figure 3). Possibly the changes reflect gradual postural adjustments. For example, in a previous study (Heyman & Monaghan, 1987), changes in response requirement (lever weight) did not result in an immediate shift in  $k$ , as would be expected if the response requirement alone determined  $k$ . Instead, changes were gradual, taking place over several sessions. This result, along with the hypothesis that  $k$  may vary as a function of type of reinforcer, suggests that the determinants of the asymptotic response level are not well understood and deserve further research.

Bradshaw et al.'s (1978) experiment was of interest because it appeared to have marked a boundary condition for Herrnstein's (1970) theory of reinforced responding. However, we found that changes in reinforcer magnitude systematically affected response rate, as predicted by Herrnstein's theory. Under what conditions, if any, then, are changes in the efficacy of the reinforcer maintaining the response and changes in the motoric properties of the response not independent? This question seems to us to be useful, because its answer will lead to a yet more general account of the determinants of reinforced behavior.

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Fig. 3. The relationship between  $k$  (in responses per minute) and sucrose concentration for each subject. As in Figure 2, the parameter estimates were obtained by fitting Equation 1 to the average response and reinforcement rates for each subject.

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## APPENDIX

The mean response and reinforcement rates for each subject in each of the five schedules for sucrose concentrations from 0.16 to 0.64 molar. Each concentration was given twice in irregular order, as described in the text. The rates were calculated from the last five sessions of a condition. The parentheses enclose the standard error of the mean.

Rat	Sucrose concentration (molar)		Mean VI interval (s)					
			100	45	30	10	5	
282	0.16	rsp/min	4 (1)	6 (1)	23 (4)	41 (7)	57 (5)	
		rf/hr	23 (4)	60 (3)	107 (7)	308 (13)	623 (15)	
	0.32	rsp/min	10 (3)	14 (5)	43 (3)	66 (5)	85 (4)	
		rf/hr	27 (3)	60 (7)	112 (5)	337 (13)	659 (11)	
	0.64	rsp/min	17 (5)	21 (5)	32 (5)	53 (6)	65 (11)	
		rf/hr	35 (6)	75 (6)	87 (9)	346 (5)	596 (22)	
	0.16	rsp/min	2 (1)	10 (2)	25 (10)	38 (13)	47 (11)	
		rf/hr	15 (3)	55 (8)	100 (12)	244 (53)	523 (101)	
	0.32	rsp/min	13 (3)	16 (3)	48 (6)	60 (6)	60 (1)	
		rf/hr	32 (4)	64 (5)	116 (6)	329 (9)	632 (19)	
	0.64	rsp/min	7 (1)	8 (1)	22 (4)	51 (8)	54 (7)	
		rf/hr	38 (6)	62 (7)	105 (11)	307 (10)	599 (19)	
	284	0.16	rsp/min	6 (1)	10 (1)	41 (2)	88 (6)	129 (8)
			rf/hr	23 (5)	77 (7)	113 (7)	346 (20)	668 (70)
0.32		rsp/min	8 (1)	14 (6)	34 (10)	61 (8)	76 (7)	
		rf/hr	32 (5)	55 (8)	92 (12)	312 (19)	607 (48)	
0.64		rsp/min	12 (2)	15 (5)	18 (5)	34 (9)	41 (6)	
		rf/hr	42 (7)	57 (6)	102 (13)	269 (43)	570 (24)	
0.16		rsp/min	3 (1)	7 (3)	10 (2)	20 (4)	33 (6)	
		rf/hr	24 (5)	61 (8)	75 (8)	219 (10)	530 (70)	
0.32		rsp/min	5 (1)	15 (4)	25 (3)	45 (6)	51 (7)	
		rf/hr	26 (5)	68 (16)	98 (4)	335 (4)	592 (23)	
0.64		rsp/min	9 (3)	18 (3)	28 (3)	46 (5)	45 (6)	
		rf/hr	20 (4)	75 (5)	111 (4)	314 (3)	575 (24)	
285		0.16	rsp/min	11 (3)	24 (8)	59 (10)	87 (21)	101 (21)
			rf/hr	26 (5)	58 (4)	112 (10)	309 (31)	609 (92)
	0.32	rsp/min	26 (3)	49 (7)	113 (7)	167 (10)	190 (2)	
		rf/hr	37 (4)	64 (6)	116 (6)	346 (9)	718 (20)	
	0.64	rsp/min	33 (5)	61 (5)	98 (6)	137 (9)	144 (5)	
		rf/hr	24 (4)	66 (4)	123 (6)	344 (9)	716 (6)	
	0.16	rsp/min	9 (3)	16 (4)	59 (3)	90 (4)	98 (5)	
		rf/hr	35 (8)	69 (7)	105 (6)	334 (13)	672 (16)	
	0.32	rsp/min	20 (4)	45 (6)	79 (4)	96 (4)	120 (11)	
		rf/hr	44 (10)	73 (9)	118 (6)	331 (12)	675 (14)	
	0.64	rsp/min	30 (3)	45 (3)	84 (4)	122 (5)	109 (7)	
		rf/hr	44 (10)	67 (4)	127 (8)	340 (4)	691 (30)	
	286	0.16	rsp/min	4 (1)	10 (1)	30 (6)	77 (11)	102 (11)
			rf/hr	29 (3)	64 (9)	106 (9)	338 (8)	661 (7)
0.32		rsp/min	8 (1)	13 (4)	41 (9)	118 (11)	160 (4)	
		rf/hr	30 (4)	69 (5)	105 (6)	348 (9)	692 (26)	
0.64		rsp/min	11 (3)	19 (3)	47 (8)	85 (7)	87 (7)	
		rf/hr	40 (7)	67 (6)	107 (6)	335 (12)	659 (11)	
0.16		rsp/min	7 (1)	9 (1)	42 (10)	93 (5)	88 (5)	
		rf/hr	30 (5)	78 (13)	108 (12)	333 (8)	626 (13)	
0.32		rsp/min	10 (1)	15 (2)	49 (14)	89 (2)	91 (4)	
		rf/hr	26 (5)	71 (7)	120 (14)	332 (20)	659 (17)	
0.64		rsp/min	15 (4)	18 (5)	70 (9)	107 (4)	127 (2)	
		rf/hr	32 (8)	55 (3)	121 (6)	344 (5)	687 (12)	

## APPENDIX (Continued)

Rat	Sucrose concentration (molar)		Mean VI interval (s)					
			100	45	30	10	5	
287	0.16	rsp/min	6 (2)	14 (3)	43 (10)	93 (7)	117 (7)	
		rf/hr	15 (3)	57 (11)	95 (12)	343 (11)	687 (12)	
	0.32	rsp/min	11 (2)	19 (4)	63 (7)	116 (7)	132 (7)	
		rf/hr	31 (7)	63 (10)	103 (2)	351 (7)	665 (6)	
	0.64	rsp/min	12 (2)	35 (7)	77 (3)	107 (4)	131 (9)	
		rf/hr	23 (6)	71 (3)	105 (6)	364 (5)	656 (14)	
	0.16	rsp/min	8 (2)	11 (2)	41 (3)	87 (14)	105 (12)	
		rf/hr	42 (7)	65 (4)	95 (8)	309 (26)	663 (13)	
	0.32	rsp/min	12 (3)	12 (2)	69 (6)	97 (7)	104 (4)	
		rf/hr	34 (7)	55 (13)	103 (5)	347 (6)	664 (14)	
	0.64	rsp/min	24 (4)	31 (12)	83 (5)	99 (6)	103 (3)	
		rf/hr	31 (7)	68 (9)	118 (5)	335 (8)	685 (20)	
	288	0.16	rsp/min	7 (1)	7 (2)	22 (3)	36 (7)	57 (4)
			rf/hr	40 (5)	53 (14)	103 (6)	301 (31)	636 (13)
0.32		rsp/min	13 (2)	20 (7)	42 (2)	50 (1)	59 (2)	
		rf/hr	40 (8)	75 (10)	102 (12)	324 (14)	630 (23)	
0.64		rsp/min	14 (2)	19 (1)	39 (1)	62 (2)	73 (2)	
		rf/hr	34 (5)	66 (4)	123 (10)	336 (10)	638 (8)	
0.16		rsp/min	5 (1)	7 (1)	21 (3)	36 (5)	51 (6)	
		rf/hr	21 (2)	58 (10)	108 (10)	316 (8)	581 (25)	
0.32		rsp/min	12 (3)	15 (2)	32 (5)	54 (3)	68 (7)	
		rf/hr	35 (4)	77 (5)	107 (4)	320 (5)	653 (8)	
0.64		rsp/min	16 (2)	27 (3)	42 (4)	73 (5)	91 (5)	
		rf/hr	32 (3)	68 (6)	118 (5)	314 (11)	664 (9)	
289		0.16	rsp/min	10 (1)	15 (5)	50 (6)	82 (8)	115 (6)
			rf/hr	38 (7)	61 (11)	105 (3)	325 (11)	710 (5)
	0.32	rsp/min	19 (3)	36 (4)	58 (3)	113 (7)	145 (6)	
		rf/hr	32 (7)	85 (7)	98 (4)	343 (9)	669 (13)	
	0.64	rsp/min	30 (3)	47 (3)	71 (4)	105 (4)	124 (5)	
		rf/hr	29 (5)	76 (12)	109 (6)	353 (13)	724 (28)	
	0.16	rsp/min	5 (5)	25 (4)	46 (7)	71 (13)	109 (17)	
		rf/hr	11 (2)	58 (3)	111 (8)	337 (14)	663 (11)	
	0.32	rsp/min	27 (4)	34 (4)	67 (8)	82 (10)	112 (11)	
		rf/hr	37 (4)	79 (2)	119 (10)	340 (9)	655 (27)	
	0.64	rsp/min	38 (3)	53 (4)	68 (5)	82 (2)	115 (5)	
		rf/hr	29 (5)	89 (6)	109 (9)	331 (13)	688 (6)	