# Effects of Changes in Response Requirement and Deprivation on the Parameters of the Matching Law Equation: New Data and Review

Gene M. Heyman and Michael M. Monaghan American Cyanamid Company, Lederle Laboratories, Pearl River, New York

The relation between response rate and reinforcement rate is described by the matching law equation. For an experiment in which there is just one explicit source of reinforcement, the equation has two parameters. The magnitude of one is equal to the response rate asymptote; the magnitude of the other is equal to the rate of reinforcement that maintains a one-half asymptotic response rate. This report describes experimental manipulations that affect these two parameters. Rats were trained on a series of variable-interval reinforcement schedules that provided reinforcement rates ranging from about 20 to 700 reinforcements per hour. The response was a lever press, and the reinforcer was water. In Experiment 1, the duration of the deprivation period was varied. Response rates maintained by the lower reinforcement rates showed the largest changes, and, accordingly, the parameter that is equal to the reinforcement rate for a one-half asymptotic response rate changed. In Experiment 2, the weight of the lever was varied. Response rates changed independently of reinforcement rate, and, as a result, the parameter that is equal to the asymptotic response rate changed. In Experiment 3, manipulations from Experiments 1 and 2 were combined. The results replicated those of Experiments 1 and 2, and there was no evidence of interactions. Our interpretation is that the asymptote of the matching law equation is a measure of motor performance and that the reinforcement parameter is a measure of the efficacy of the reinforcer maintaining the response.

The matching law describes the relation between measures of reinforcement, such as amount and delay, and measures of behavior, such as rate and latency. The relations are described mathematically, with the terms and operations depending on such factors as the number of reinforcement sources, whether reinforcers are available simultaneously or sequentially, and the delay from response to reinforcement. Applications have varied, and they include social psychology experiments in which the frequency of conversations was the dependent variable (Conger & Killeen, 1974) and ethological studies in which the amount of time spent foraging was the measure of interest (Houston, 1986). The most elementary matching law equation applies to a situation in which there is just one measured reinforcement source, just one measured behavior, and no delay. This equation was introduced by Herrnstein (1970), and it is written as follows:

$$B = \frac{B_{max}R}{R + R_{half}},\tag{1}$$

where B is response rate, R is reinforcement rate, and  $B_{\rm max}$  and  $R_{\rm half}$  are parameters whose magnitudes are obtained by fitting Equation 1 to the data. In words, Equation 1 says that response rate depends on three factors: reinforcement rate (R) and the

We thank Carmela Nardella and Mary Wilfred for their excellent technical assistance in preparing the manuscript, Kenneth DeCanio and Alphonso Thurman for help in running the experiments, and Marika Iwane and Paul Gallo for their able help with the statistics.

Correspondence concerning this article should be addressed to Gene M. Heyman, American Cyanamid Company, Lederle Laboratories, CNS Research, Pearl River, New York 10965.

variables that are represented by the parameters  $B_{\rm max}$  and  $R_{\rm half}$ . These two parameters and what they represent have been the subject of a number of empirical and theoretical articles (e.g., Bradshaw, Ruddle, & Szabadi, 1981; de Villiers & Herrnstein, 1976; Herrnstein, 1974; Staddon, 1977). Our purpose in this article is to describe the kinds of experiments that affect  $B_{\rm max}$  and  $R_{\rm half}$  and, thereby, to provide these quantities with empirical interpretations.

Figure 1 shows a graph of Equation 1. Response rate is a negatively accelerated function of reinforcement; it approaches but does not exceed  $B_{\rm max}$ . The magnitude of  $B_{\rm max}$ , therefore, is equal to the asymptotic response rate, and, accordingly,  $B_{\rm max}$  is measured in the same units as B, for example, responses per minute. The parameter  $R_{\rm half}$  is measured in the same units as the reinforcer (R), for example, reinforcers per hour, and if response rate is set equal to one-half the asymptotic response rate (that is, set  $B = B_{\rm max}/2$ ), it can be seen that the magnitude of  $R_{\rm half}$  is equal to the rate of reinforcement that would maintain exactly a one-half asymptotic response level. Note that Figure 1 shows the curve-fitting definitions of  $B_{\rm max}$  and  $R_{\rm half}$ . These are inherent to the structure of Equation 1 and do not imply any particular interpretation of what the parameters represent.

There are two competing interpretations of the matching law parameters. One is that  $B_{\rm max}$  is a measure of the motor component of the reinforced response, such as its duration, and  $R_{\rm half}$  is a measure of the efficacy of the reinforcer (see, e.g., Herrnstein, 1974, 1979; Heyman, in press). In this account, features of the experiment that affect the topography of the response, such as the response requirement, can affect  $B_{\rm max}$  without influencing  $R_{\rm half}$ , and, conversely, manipulations that affect the strength of the reinforcer, such as deprivation, can affect  $R_{\rm half}$  without influencing  $B_{\rm max}$ . The other view is that one or both of the parameters.

eters are affected by determinants of both motor performance and reinforcement efficacy (e.g., Catania, 1973; Killeen, 1981; McDowell, 1980; Staddon, 1977). These theories predict that changes in the response requirement and/or the conditions of reinforcement will affect both parameters simultaneously. For example, in Staddon's (1977) threshold derivation of Equation 1, a term representing response topography is found in both the  $B_{\text{max}}$  and  $R_{\text{half}}$  slots of Equation 1. Consequently, the derivation predicts that a treatment that alters response topography, such as a change in the response requirement, will necessarily change both matching law parameters.

In the Results section of this article, we describe the effects of changes in the response requirement and the duration of the deprivation period on the parameters. In the General Discussion section we compare our results with those of similar studies. If  $B_{\rm max}$  measures response topography and  $R_{\rm half}$  measures reinforcement efficacy, it should be possible to find a set of experiments that altered  $B_{\rm max}$  but not  $R_{\rm half}$  and, conversely, a second set that altered  $R_{\rm half}$  but not  $B_{\rm max}$ . However, if the parameters share common referents, then it will not be possible to find two distinct collections of studies.

#### General Method

# Subjects

Eight, experimentally naive, male Wistar rats from Royal Hart (Kingston, New York) served as subjects. At the start of the experiment, the rats were about 3 months old and weighed between 250 and 340 g. The rats were housed two to a cage and were maintained on a water-deprivation regime, as described in the *Procedure* section. Throughout

the study, they had free access to food (Purina Rat Chow). The colony room was illuminated 12 hr a day (lights on at 6:00 a.m.).

#### Apparatus

The experiments were conducted in eight standard, two-lever chambers (Coulbourn Instruments, Modular Test Cage, Model E10-10: 28.5 cm, 29.5 cm, 24 cm). The right but not the left lever was functional. It was set into the front wall, 6.5 cm above the floor and operated by a force of about 0.30 N. The force requirement was adjustable. A weight of either 25, 50, or 75 ( $\pm$  0.2) g could be attached to the end of the lever that was outside the chamber. A small aluminum cup (7 g) held the weight. To the left of the lever was a recessed opening that allowed access to a 0.025-ml dipper of water. The dipper sat in a trough of water and was raised into the recessed opening when the subject had fulfilled the reinforcement requirement. Left and right stimulus lights and a clicker were set into the front wall. These were used to signal different phases of the experimental session. The lights were illuminated with miniature bulbs (28 V, .04 amp, #1819), and the clickers were standard coil relays (Coulbourn Instruments). The experimental chambers were enclosed in sound-attenuating, ventilated boxes. Experimental events were controlled and recorded by a PDP 8-a computer. The programs were written in SKED (Snapper, Stephens, Cobez, & Van Haaren, 1976).

#### Procedure

Experimental sessions consisted of a series of five variable-interval (VI) reinforcement schedules (a five-component multiple schedule). In each session, each schedule was available for 540 s. A 300-s time-out period separated consecutive schedules, and the schedule order was random, without replacement (thus each subject was exposed to each of the five schedules in every session). The programmed interreinforcement intervals approximated an exponential distribution (following the list of

# MATCHING LAW: CURVE FITTING DEFINITIONS

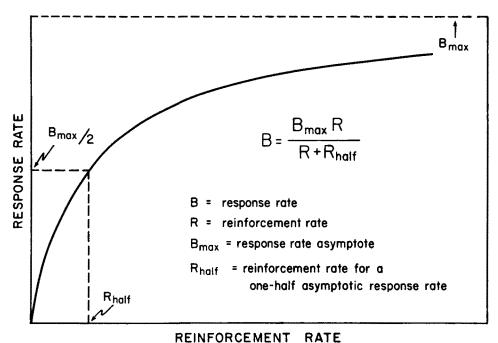


Figure 1. The matching law equation along with the curve fitting definitions of the parameters.

Table 1
Order of Conditions and Number of Sessions

Deprivation period				
No.	Duration (in hr)	Response requirement	Sessions	
1	23.5	standard	60	
2	6.0	standard	11	
3	47.5	standard	15	
4	23.5	standard	33	
5	23.5	standard + 32 g	6	
6	23.5	standard + 57 g	6	
7	23.5	standard + 82 g	6	
8	23.5	standard	9	
9	23.5	standard + 82 g	17	
10	47.5	standard + 82 g	25	
11	23.5	standard + 82 g	36	
12	6.0	standard + 82 g	8	
13	23.5	standard	13	

intervals derived by Fleshler & Hoffman, 1962), so that the conditional probability of a reinforcement was approximately constant. The mean intervals for the five schedules were 150 s, 75 s, 30 s, 10 s, and 5 s, which corresponds to programmed reinforcement rates of 24, 48, 120, 360, and 720 per hour. The reinforcer was 2.5-s access to the 0.025-ml dipper. For this period and the immediately following 1.5 s, the interval timer and stimuli were inoperative. The session began with a "warm-up" period in which the subject earned five reinforcers according to a fixed-ratio 5 or a fixed-time 10-s schedule, whichever occurred first. A 2-min time-out period separated the warm up from the first variable-interval schedule component. (The identical procedure was used in several previous studies, e.g., Heyman, Kinzie, & Seiden, 1986.)

The different reinforcement rates were signaled by combinations of the left and right stimulus lights and the clicker. From low to high reinforcement rates, the combinations were as follows: left stimulus light continuously on; left stimulus light continuously on and right stimulus light flashing (2.5-s interval and 0.2 s on); left stimulus light continuously on and clicker clicking (2.5-s interval and 0.2 s on); left stimulus light continuously on, right stimulus light flashing (1.5-s interval) and clicker clicking (1.5-s interval); left stimulus light continuously on, right stimulus light flashing rapidly (0.25-s interval). During the time-out periods, the stimuli were off, and responses had no experimentally arranged consequences but were recorded.

Table 1 lists the order of the conditions and the number of sessions each was in effect. The criteria for a change of condition were at least three consecutive sessions in which the parameter estimates (a) did not take on extreme value and (b) did not show a strictly increasing or decreasing trend. We used three sessions because previous research (e.g., Heyman et al., 1986) indicated that parameter estimates based on samples of 15 or more data points (5 data points per session) had standard errors that were not especially large: typically about 10% of the magnitude of the parameter, with a range of about 5% to 20%. However, three sessions was a minimum criterion. Deprivation affected the variability in response rate and parameter estimates, with shorter periods producing greater variability. Larger sample sizes reduce the parameter standard errors (Draper & Heyman, 1983; Wilkinson, 1960). Consequently, the sample sizes for the 6.0-hr, 23.5-hr, and 47.5-hr deprivation periods were seven sessions, five sessions, and three sessions, respectively. This led to approximately equal errors in the parameter estimates for the three different deprivation periods.

The parameter estimates were obtained by a weighted least-squares analysis (Wilkinson, 1960). The approach was developed for modeling enzyme reactions (an equation like Equation 1 describes their rates) and

is described in detail by Wilkinson (1960) and Draper and Heyman (1983).

# Experiment 1

The purpose of Experiment 1 was to determine if changes in the length of the deprivation period would affect only  $R_{half}$  or both  $R_{half}$  and  $B_{max}$ . A recent derivation of Equation 1 (Heyman, in press) predicts that just  $R_{half}$  will change, whereas other approaches call for changes in both parameters (e.g., Killeen, 1981). There were three different deprivation periods (Conditions 1 to 3): 6.0 hr, 23.5 hr, and 47.5 hr. The 6.0-hr period was arranged by allowing the subjects access to a water bottle for 5 min at 6 hr before the start of the session. At the end of each session the rats had access to a water bottle for 30 min in their home cage (where food pellets were also available). Consequently, sessions that were preceded by a 47.5-hr deprivation had to be conducted on alternate days. The parameters and response rates were calculated from the last three sessions for the 47.5-hr condition, from the last five for the 23.5-hr condition, and the last seven for the 6.0-hr condition. As pointed out in the General Method section, different sample sizes were used to offset the increase in response rate variability that accompanied the decrease in deprivation.

### Results

Figure 2 shows the effect of deprivation on response rate. In the top panel, the points represent the median response rate for the 8 subjects, and in the bottom two panels, the points represent the median response rates for 2 representative subjects. The graphs show that changes in response rates depended on two factors: deprivation period and reinforcement rate. The longer deprivation periods produced higher response rates, and the changes were an inverse function of reinforcement rate. Thus, increases in deprivation produced larger relative increases in response rate in the lower reinforcement rate components. For example, for Rat 155 there was more than a 1,000% increase in response rate in the lowest reinforcement rate component but increases of no more than 7% in the highest rate component (reinforcement rates varied from about 13 to 700 per hour). This pattern was typical. Consequently, the median percentage changes in response rate, as calculated from the 8 subjects, held a strictly inverse relation with reinforcement rate. This is shown in Table 2.

Table 3 and the left panel of Figure 3 summarize the effects of deprivation on the matching law parameters. The summary shows the median values. These were obtained by fitting Equation 1 to the results from each subject and then locating the midpoint between the fourth and fifth ranking values. Figure 3 shows large decreases in  $R_{\rm half}$  as a function of deprivation (in other words, when the deprivation period was longer, a fixed proportion of behavior was maintained by a lower reinforcement rate). In contrast, changes in  $B_{\rm max}$  were small and did not show signs of a relation with deprivation. A repeated measures design, 3 (deprivation)  $\times$  8 (subject) analysis of variance (ANOVA), was performed on  $B_{\rm max}$  and  $R_{\rm half}$  (Winer, 1971, chap. 4). As suggested by Figure 3, the relation between deprivation and  $R_{\rm half}$  was significant: F(2, 14) = 35.06, p < .01. Post hoc, pair

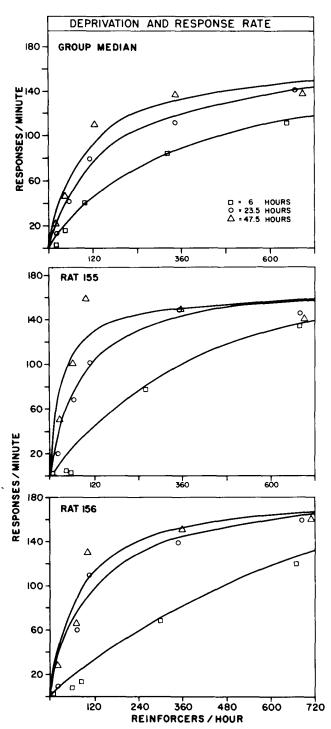


Figure 2. The effect of deprivation on response rate. (In the top panel are the median response rates for the group. For example, in the 23.5-hr condition of Experiment 1, the median is based on a population of 40 because the sample size for this condition was five sessions. In the bottom two panels are the results for 2 representative subjects.)

wise comparison F tests, which used estimates of variance from the ANOVA (Winer, 1971, pp. 257–258), indicated that in both the 23.5- and 47.5-hr conditions, the value of  $R_{half}$  was smaller

than it was in the 6.0-hr condition: F(1, 14) = 40.71, p < .01, and F(1, 14) = 62.21, p < .01, respectively. In contrast, there was no indication of a relation between deprivation and  $B_{\text{max}}$ : F(2, 14) = .04, p > .95.

# Experiment 2

The purpose of Experiment 2 was to determine if changes in the weight of the lever would affect just  $B_{\text{max}}$  or both  $B_{\text{max}}$  and  $R_{\text{half}}$ . Theories such as Staddon's (1977) threshold derivation of Equation 1 predict changes in both parameters, whereas other approaches (e.g., Herrnstein, 1974) predict that only  $B_{\text{max}}$  will change. There were four different lever weights (Conditions 4 to 7 in Table 1): the standard lever (which required a force of 0.30 N to operate), standard plus 32 g, standard plus 57 g, and standard plus 82 g (each weight includes the 7-g aluminum cup that held the weight; see General Method section). The deprivation period was set at 23.5 hr throughout the study. The weight increments were introduced in order of magnitude, and each was in effect for six sessions. The response rates and parameters were calculated from the last five sessions for the standard lever setting (Condition 4, which served as baseline) and from the last three sessions at each weight increment. The subjects were the ones used in Experiment 1.

Figure 4 summarizes the effects of different lever weights on response rate. As in Figure 2, the top panel shows the median response rates for the group, and the two bottom panels show the median response rates for Rats 155 and 156. The graphs show that increasing the weight of the lever decreased response rate, and the greater the weight, the greater the decrease. For example, as a function of lever weight, the median decreases in response rate for the 8 rats were as follows: -54%, -61%, and -68%. However, unlike the results in Experiment 1, the changes did not covary with reinforcement rate. For example, in the 57g weight conditions, the changes in response rate for Rat 156, as ordered by reinforcement rate, were -58%, -47%, -57%, -40%, and -45%. Similarly, the group results (listed in Table 2) show a narrow range of changes and no particular relation with reinforcement rate. Thus, changes in the response requirement produced a similar pattern of parameter shifts for the 8 subjects.

Table 3 and the middle panel of Figure 3 summarize the effects of different lever weights on  $B_{\rm max}$  and  $R_{\rm half}$ . Increases in the lever weight invariably decreased  $B_{\rm max}$  (i.e., the heavier the lever, the lower the estimated asymptotic response rate). In contrast, the relation between  $R_{\rm half}$  and lever weight was not systematic. There was, however, a large increase in  $R_{\rm half}$  at the 57-g weight setting. Three subjects showed unusually high values, but for the other 5 subjects  $R_{\rm half}$  was near or below baseline. The factors that may have affected  $R_{\rm half}$  are not clear because this parameter did not change at either a lower or a higher weight.

A repeated measures design, 4 (weight)  $\times$  8 (subject) ANOVA, was performed on  $B_{\text{max}}$  and  $R_{\text{half}}$  (the same approach as in Experiment 1). As suggested by Figure 3, there was a significant relation between the magnitude of  $B_{\text{max}}$  and the weight of the lever: F(3, 21) = 9.85, p < .01. Post hoc, pair-wise, comparison F tests confirmed that in each of the weighted lever conditions  $B_{\text{max}}$  was lower than it was with a standard lever (Condition 4): at 32 g, F(1, 21) = 14.39, p < .01; at 57 g, F(1, 21) = 12.14, p < .01

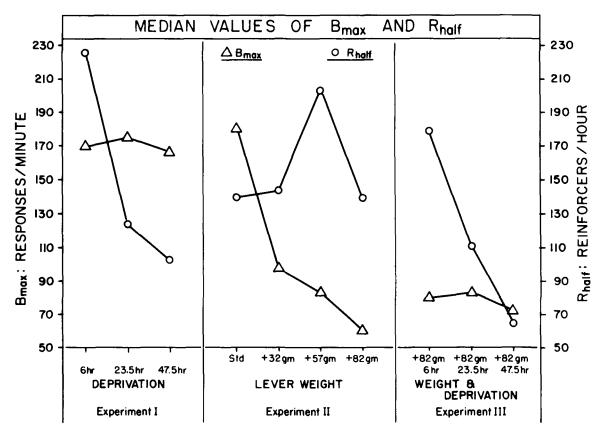


Figure 3. The median values of  $B_{\text{max}}$  and  $R_{\text{half}}$ . (The data points are based on the individual subject results. Thus, the graph shows the values that were midway between the fourth and fifth ranking values. Std standard.)

.01; and at 82 g, F(1, 21) = 27.31, p < .01. In contrast, it was not possible to find a relation between the weight of the lever and  $R_{\text{balf}}$ : F(3, 21) = 2.0, p > .10.

# Experiment 3

Experiment 3 tested the generality of a finding reported by McDowell and Wood (1984, 1985). In an experiment in which

Table 2
Median Percentage of Change in Response Rate

	Variable interval (in s)					
Experiment & condition	150	75	30	10	5	
Experiment 1 <sup>a</sup>		-				
23.5 hr	+294	+166	+91	+43	+26	
47.5 hr	+536	+186	+166	+62	+22	
Experiment 2 <sup>b</sup>						
+32 g	-43	-56	-42	-59	-54	
+57 g	-64	-56	-63	-53	-61	
+82 g	-54	-63	-69	-76	-68	
Experiment 3°						
23.5 hr	+150	+185	+56	+17	+8	
47.5 hr	+285	+789	+130	+21	+15	

<sup>&</sup>lt;sup>a</sup> Relative to 6.0-hr deprivation. <sup>b</sup> Relative to standard lever. <sup>c</sup> Relative to 6.0-hr deprivation plus 82 g.

the subjects were humans, changes in reward magnitude (money) affected  $B_{\text{max}}$  if the response requirement was made more effortful (by increasing the weight of the manipulandum). We tried to approximate these conditions by increasing the weight of the lever and then varying deprivation. The weight was increased in steps (Condition 9) up to 82 g. Rat 158, however, could not be pushed beyond 57 g (although this subject had performed reliably at 82 g in Experiment 2). Consequently, in order to keep this subject in the study, we left its response requirement at +57 g (whereas the other 7 subjects were at +82g, and for verbal convenience, we refer to the response requirement in this condition as "standard + 82 g"). Once the sessionto-session parameter estimates stabilized (five consecutive sessions in which there was not an extreme parameter value or strictly monotonic trend), deprivation was varied. The order was 23.5 hr, 47.5 hr, 23.5 hr, and 6.0 hr (Conditions 9, 10, 11, and 12). The parameter estimates from the two exposures to the 23.5-hr deprivation period (Conditions 9 and 11) were not significantly different from one another. Consequently, for comparison with the 6.0- and 47.5-hr deprivation conditions, we based the 23.5-hr parameter values on a pooled sample of the last five sessions from each 23.5-hr period (Conditions 9 and 11). The sample sizes for the 6.0-hr condition was seven, and for the 47.5-hr conditions it was three, as in Experiment 1.

Experiment 1 and Experiment 3, then, had identical deprivation conditions but different response requirements: standard

Table 3
Median Matching Law Parameters and Goodness-of-Fit Scores

Condition	Deprivation period (in hr)	Response requirement	$B_{ m max}$		$R_{ m half}$			
			Resp/min	Range	Reinf/hr	Range	%VAC*	Range
1	23.5	standard	174	77-295	123	58-215	96	93-99
2	6.0	standard	170	76-291	215	124-288	98	95-99
3	47.5	standard	166	73-251	100	53-164	98	84-99
4	23.5	standard	180	83-234	138	78-348	96	83-97
5	23,5	standard + 32 g	97	45-159	143	67-566	96	75-99
6	23.5	standard + 57 g	83	43-265	204	54-361	94	13-99
7	23,5	standard + 82 g	58	30-156	147	42-355	95	63-99
8 <sup>b</sup>	23.5	standarð						
9	23,5	standard $+82 g$	82	44-130	166	78-351	94	57-97
10	47.5	standard + 82 g	71	55-95	64	28-273	92	77-99
11	23.5	standard + 82 g	82	40-121	105	51-351	96	72-99
12	6.0	standard + 82 g	88	55-172	254	56-722	97	87-98
13	23.5	standard	159	76-211	158	56-290	94	72-98

Note. Resp/min = responses per minute; reinf/hr = reinforcers per hour; % VAC = percentage of variance accounted for  $(r^2)$  score.

versus standard + 82 g. Consequently, by combining the two data sets we were able to evaluate a Weight  $\times$  Deprivation interaction on the matching law parameters (and also evaluate the effect of the two weights, thus replicating two of the conditions from Experiment 2).

# Results

Figure 5 shows group and individual results from the Experiment 3. The format is the same as in Figures 2 and 4. The effects of deprivation on response rate were similar to those in Experiment 1. Longer deprivation periods typically produced higher response rates, and the relative magnitude of the changes was usually an inverse function of reinforcement rate. Rat 156 (see Figure 5) did not fit this pattern in the two richest reinforcement rate schedules, but this, as indicated by the median results, was atypical. Comparison of Figure 5 and Figure 2 also shows that with the 82-g weight, response rates were lower than with the standard weight, as in Experiment 2.

The right panel of Figure 3 shows the effect of deprivation on  $B_{\text{max}}$  and  $R_{\text{half}}$ . There were decreases in  $R_{\text{half}}$  but no apparent change in  $B_{\text{max}}$ , just as in Experiment 1. A repeated measures design, 3 (deprivation) × 8 (subject) ANOVA, was performed on  $B_{\text{max}}$  and  $R_{\text{half}}$ . The analysis indicated a relation between  $R_{\text{half}}$  and deprivation: F(2, 14) = 13.09, p < .01. Post hoc, pair-wise comparison F tests indicated that the 23.5- and 47.5-hr conditions produced smaller values of  $R_{\text{half}}$ : F(1, 14) = 5.10, p < .05 and F(1, 14) = 11.31, p < .01, respectively. In contrast, there was no evidence of a relation between deprivation and  $B_{\text{max}}$ : F(2, 14) = 1.65, p > .20.

Next, we combined the results from Experiments 1 and 3 to examine the effects of varying deprivation at two different response requirements. A repeated measures design, 3 (deprivation)  $\times$  2 (weight)  $\times$  8 (subject) ANOVA, was performed on  $B_{\text{max}}$  and  $R_{\text{half}}$ . First, the heavier response requirement reduced  $B_{\text{max}}$ : F(1, 7) = 28.75, p < .01, but had no apparent effect on  $R_{\text{half}}$ :

F(1, 7) = .28, p > .60. This replicates results from experiment 2. Second, there was no evidence of a Weight  $\times$  Deprivation interaction. The results for  $B_{\text{max}}$  and  $R_{\text{balf}}$  were, respectively: F(2, 14) = 2.45, p > .10 and F(2, 14) = 1.13, p > .35.

# General Discussion

The major findings were that the parameters of the matching law equation systematically changed and did so independently of one another. In Experiment 1, in which deprivation was manipulated, there was a significant decrease in  $R_{\rm half}$ , whereas changes in  $B_{\rm max}$  were small, statistically insignificant, and not systematic. In Experiment 2, in which the response requirement was manipulated, there were significant decreases in  $B_{\rm max}$ , whereas changes in  $R_{\rm half}$  were not statistically significant nor systematic. In Experiment 3 the manipulations entailed in Experiments 1 and 2 were combined: an 82-g weight was added to the lever, and deprivation was varied. The change in the response requirement did not influence the effects of deprivation on the parameters:  $R_{\rm half}$  systematically changed, just as in Experiment 1. In sum, the parameters of the matching law bore a simple and orderly relation to the experimental conditions.

Other researchers have used the matching law to quantify and interpret behavioral changes. We organized these results in terms of studies that altered just  $B_{\rm max}$ , and  $R_{\rm half}$ , and both  $B_{\rm max}$  and  $R_{\rm half}$ . In all cases the parameter estimates are based on experiments in which there were five or more data points.

# B<sub>max</sub> Shifts

In four studies, including the present one, the experimental manipulation led to changes in  $B_{\rm max}$  but not  $R_{\rm half}$  (Bradshaw, Szabadi, & Ruddle, 1983; Hamilton, Stellar, & Hart, 1985; Mc-Sweeney, 1978). These experiments had one feature in common: In each study the experimenter changed the response requirement. In three of the studies, those that used rats, the

<sup>&</sup>lt;sup>a</sup> This column shows the degree of fit between the predicted and obtained response rates. The predictions were compared with the averaged response rates for each subject in each condition.

b It was not possible to obtain reliable estimates for Condition 8 because of equipment failures.

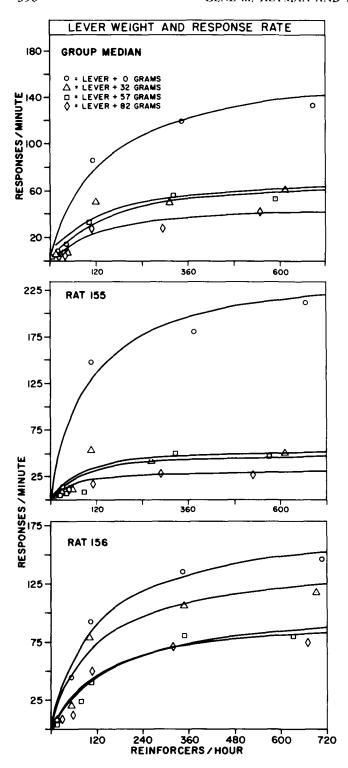


Figure 4. The effect of changes in the response requirement on response rate. (In the top panel are the median response rates for the 8 subjects.) In the bottom two panels are the results for 2 representative subjects.)

change was an increase in the weight of the lever. In the other study (McSweeney, 1978), which used pigeons, the change was the manipulandum itself. A key, which the pigeons pecked, was

replaced by a treadle, which the pigeons kicked. The variable features included species, reinforcer, and manner of schedule presentation. In one experiment the reinforcer was brain stimulation (Hamilton et al., 1985), and in the others it was food or water. In two experiments the different VI schedules were presented together, in a single session (Hamilton et al., 1985, and this report), and in two the different VI schedules were pre-

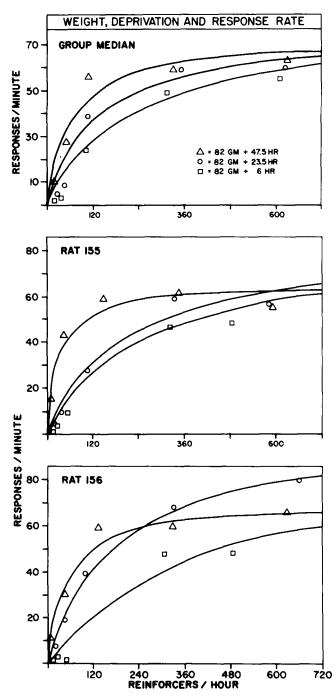


Figure 5. The effect of deprivation on response rate, with the lever set at 82 g. (Note that y-axis is different than in Figure 2 and Figure 4. In the bottom two panels are the results for 2 individual subjects.)

sented singly, with several sessions devoted to each one. The common feature, a change in the response requirement, necessarily altered physical features of the response, such as its duration and/or the subsequent interresponse time. Thus, the evidence suggests that  $B_{\rm max}$  depends of the topography of the response, for example, its duration. The variable features show that this relation holds for quite different species, reinforcers, and procedures.

# Rhalf Shifts

In nine studies, including this report, the experimental manipulation led to a shift in  $R_{half}$  but not  $B_{max}$ . In these studies there was a change in the duration of the deprivation period or in some property of the reinforcer, such as its magnitude (Bradshaw, Szabadi, & Bevan, 1978a; Bradshaw et al., 1981; Bradshaw, Szabadi, Ruddle, & Pears, 1983; Conrad & Sidman, 1956; Guttman, 1954; Hamilton et al., 1985; Kraeling, 1961; Logan, 1960; de Villiers & Herrnstein, 1976, analyzed the results for the studies conducted before 1976). For example, in an experiment with rats, changing the reinforcer from glucose to sucrose (an increase in sweetness, according to humans) decreased  $R_{half}$ by about 35% without affecting  $B_{\text{max}}$  (Guttman, 1954). These nine experiments also varied in important ways. The subjects were either human (Bradshaw et al., 1978a), monkey (Conrad & Sidman, 1956), or rat; the reinforcer was consumable (food or water) or nonconsumable (brain stimulation, in Hamilton et al., 1985, and money, in Bradshaw et al., 1978a); and the different VI schedules were presented together in one session (e.g., Hamilton, et al., 1985; Bradshaw et al., 1978a) or separately in single sessions. Because it is generally understood that a reinforcer's capacity to maintain responding depends on such properties as its magnitude and the subject's degree of deprivation, the common features in these studies indicate that  $R_{half}$  measures reinforcement efficacy. The variable features show that this definition holds for a wide range of species and procedures.

# Generalization of the Matching Law Method

The experiments reviewed above form two nonoverlapping classes: those in which the response requirement was changed and those in which some aspect of the reinforcer or deprivation was changed. This neat dichotomy provides  $B_{\rm max}$  and  $R_{\rm half}$  with clear and distinguishable empirically based definitions. An immediate consequence is that the matching law can be used to quantify and interpret new results. This sort of methodological generalization recently took place in the analysis of the behavioral effects of antipsychotic drugs.

Chlorpromazine was the first widely prescribed antipsychotic drug. Early in its development, it was noted that it attenuated reinforced responding in rats and other species used in laboratory research. This effect was dose dependent and robust, but its interpretation remained unclear. Some researchers claimed that chlorpromazine and similar drugs (called neuroleptics) reduced the subject's sensitivity to reinforcement (e.g., Stein & Ray, 1960; Wise, 1982). Others, however, claimed that the neuroleptics reduced the subject's motor capacity so that the subject's motivation to respond had not changed, but its ability to do so had (e.g., Tombaugh, Tombaugh, & Anisman, 1979). The

debate remained unresolved because the criteria for confirming either theory inevitably proved ambiguous (see, e.g., Heyman et al., 1986; Wise, 1982, and accompanying commentary). A number of investigators turned to the matching law or a similar approach to distinguish motor and reinforcement effects (e.g., Gallistel & Karras, 1984; Hamilton et al., 1985). The results were consistent: At low doses, neuroleptics increased  $R_{\text{ball}}$  (Gallistel & Karras, 1984; Heyman et al., 1986), whereas at intermediate and high doses, these compounds affected both parameters:  $R_{half}$  increased as before, but with larger increments for higher doses, and, in addition,  $B_{\text{max}}$  decreased (Hamilton et al., 1985; Heyman, 1983; Heyman et al., 1986). Thus, the matching law experiments suggested that neuroleptics change both reinforcement efficacy and motor performance, but at different doses. This simple conclusion is consistent with the large literature on the behavioral effects of neuroleptics, and it also explains why the controversy concerning the interpretation of neuroleptics has persisted for so long.

We found 16 studies in which the experimental manipulation changed just  $B_{\text{max}}$  or just  $R_{\text{half}}$ . In three the independent variable was a drug treatment (Gallistel & Karras, 1983; Heyman & Seiden, 1985; Heyman et al., 1986). These showed a correspondence between biochemical effects and changes in Rhalf. Amphetamine increased the availability of dopamine at postsynaptic receptor sites in the brain, and at low doses it decreased  $R_{half}$ without affecting  $B_{\text{max}}$  (Heyman & Seiden, 1985). Neuroleptics had the opposite biochemical and behavior effects. They decreased the availability of dopamine at the postsynaptic receptor, and in low doses they increased  $R_{half}$  without affecting  $B_{max}$ (Gallistel & Karras, 1984; Heyman et al., 1986). In the other 13 studies there was a correspondence between response requirement and  $B_{\text{max}}$  and between reinforcement conditions and  $R_{\text{half}}$ . The overall orderliness of these results made definition of  $B_{\text{max}}$ and  $R_{half}$  a straightforward matter.

However, it should be pointed out that our conclusions would not necessarily be contradicted by experiments in which changes in the response requirement or the reinforcer affected both  $B_{\text{max}}$  and  $R_{\text{half}}$ . For example, in experiments in which the response requirement is held constant but the reinforcer is switched between food and water, there is a correlated difference in response topographies for rats (Hull, 1977) and pigeons (Wolin, 1968). The pigeons pecked with "drink-like" responses for water reinforcer and with "eating-like" responses for the grain reinforcer (Wolin, 1968). Thus, we predict that substituting food and water would change both  $B_{\text{max}}$  and  $R_{\text{half}}$  in pigeons, rats, and perhaps other species. Similarly, for some subjects reinforcement efficacy may depend on the net difference between response costs and reinforcement magnitude or quality. The subjects in this study did not appear to integrate costs and benefits in this way (see Experiment 2), but other species or rats in other procedures might. The point is that some conditions, such as high doses of drugs, will alter both reinforcement efficacy and response topography.

# Shifts in $B_{max}$ and $R_{half}$

In addition to high doses of amphetamine and neuroleptics, there are some studies in which changes in deprivation and the reinforcer have produced shifts in both  $B_{\text{max}}$  and  $R_{\text{half}}$ . However,

in these studies, the change in  $B_{\rm max}$  is discrepant with very similar experiments in which only  $R_{\rm half}$  changed. The evidence reviewed below suggests that the discrepancy is due to methodological factors.

Snyderman (1983) manipulated body weight in rats and measured changes in the matching law parameters. He reported small changes in  $R_{\rm half}$  and relatively large shifts in  $B_{\rm max}$ . However, there are four studies, including this report, in which the results are virtually the opposite: Changes in deprivation or body weight produced large changes in  $R_{\rm half}$  without systematically affecting  $B_{\rm max}$  (Bradshaw, et al., 1983; Conrad & Sidman, 1956; Logan, 1960; de Villiers & Herrnstein, 1976, analyzed the studies published before 1976). The different outcomes can be traced to a nonmonotonic relation between response and reinforcement rate in Snyderman's experiment.

Snyderman used six different variable-interval schedules. The reinforcer was a 100-mg food pellet, about twice the size as is normally used. At the 90% body weight the richest schedule (VI 10 s) typically did not maintain the highest response rates, although it did so at the 70% body weight. However, for the five other schedules, the relation between response rate and reinforcement rate was monotonic. We fit Equation 1 to the results for these five schedules: Rhalf decreased as a function of deprivation, whereas  $B_{\text{max}}$  showed no consistent pattern of changes. Thus without the nonmonotonic data point, Snyderman's data replicated the four other studies in which body weight or deprivation was manipulated, and, conversely, the discrepant parameter estimates depended entirely on the schedule that produced a nonmonotonic result. This pattern of findings suggests that the subjects may have become satiated at the 90% body weight and/or that the time base for responding decreased because of time spent eating. For example, in the VI 10-s component the rats were given 6.65 g of food, and 6.65 min were put aside for eating; yet according to Teitelbaum and Campbell's (1958) account of eating in the rat, average meal size is about 1.4 g, and eating rate is equivalent to 6.65 g per 36.9 min.

In an experiment with humans, McDowell and Wood (1984, 1985) found that reward magnitude affected  $B_{\rm max}$  if the response requirement was made more effortful by adding weights to the manipulandum. The present experiments tested the generality of the finding. The results did not replicate those of McDowell and Wood, even though the response requirement was varied over a wider range (relative to the subject's body weight). Other differences between the studies included the species of the subject, the manipulation that was combined with an increase in lever weight, and the range of variation in response rates. Of these, there is some evidence that differences in the range of response rates contributed to the different outcomes.

In Experiments 1, 2, and 3, response rates were a negatively accelerated function of reinforcement rate, the range of variation was wide (about 10–140 responses per minute), and the relation between responding and reinforcement was reasonably approximated by Equation 1 (fits of 90% or better). In contrast, in the McDowell and Wood study, response rates often showed little variation, and in 12 of 20 cases (4 subjects and five conditions) the data were better described by a simple straight line than by Equation 1. Moreover, for two data sets, the straight line relation between responding and reinforcement had a negative slope, and the median slope, across subjects and conditions, was

quite shallow. In sum, the relation between response rate and reinforcement rate often did not conform to the predictions of Equation 1, and under these conditions, conclusions based on Equation 1 may be of questionable value. For example, because McDowell and Wood did not report values of  $R_{\rm half}$ , we fit Equation 1 to the results listed in their tables. Estimates of  $R_{\rm half}$  often turned out to be low, for example, below 0.5 cents per hour. It does not seem plausible that humans would respond at substantial rates for less than a cent an hour, yet because of the narrow range of response rates, McDowell and Wood's data lead to that conclusion. It would be of interest to repeat their study, but with a procedure that maintained a reasonably wide range of response rates.

Bradshaw, Szabadi, and Bevan (1978b) evaluated the effect of changes in sucrose concentration on the matching law parameters in rats. There were 4 subjects, and sucrose was the reinforcer, with the concentration set at either 0.05 or 0.32 M (there was also a condition in which water was the reinforcer, but these data are difficult to interpret because the subjects were not deprived, I subject did not respond at all, and the other 3 responded inconsistently [relatively large standard errors for  $R_{half}$ ). In the high concentration condition, the magnitude of  $R_{\text{half}}$  was, as expected, significantly smaller: t(3) = 4.91, p < .05,based on the percentage change scores. However,  $B_{\text{max}}$  may also have changed. For each of the subjects,  $B_{\text{max}}$  was larger in the higher concentration condition. The changes were not significant at the .05 level, but they were at .10: t(3) = 2.34, p < .10. With a larger sample, it would be possible to determine if the trend in  $B_{\text{max}}$  was related to sucrose concentration.

The three studies just reviewed have three common properties: A change in deprivation or reinforcement affected  $B_{\rm max}$  as well as  $R_{\rm half}$ ; the change in  $B_{\rm max}$  is discrepant with very similar studies in which just  $R_{\rm half}$  changed; in each of the three studies the change in  $B_{\rm max}$  was not significant, and/or there was evidence that the change was not due to the nominal independent variable. These common factors suggest that the discrepant results are due to variation in the execution of the experiments rather than variation in the nature of the relation between the experimental manipulations and the parameters.

# Descriptive Adequacy of Equation 1

Figures 2, 4, and 5 indicate that Equation 1 provided a reasonable approximation to the observed response rates. For individual subjects in individual sessions the median fit  $(r^2)$  was .92. If sessions are averaged in three- to seven-session blocks so that some of the between-session variability is decreased, the median fit for individual subjects increases to .96. Larger samples would likely increase the fit. However, the error would not have approached zero, because there was a consistent discrepancy between the observed and predicted response rates that showed up in both the individual and averaged sessions results. In the lowest reinforcement rate schedule, response rates were typically lower than the predicted values. Reinforcement rate interactions among the components of the multiple schedule may have produced this effect. In situations in which there is more than one reinforcement source, the higher reinforcement rate suppresses response rate on the lower reinforcement rate schedule, and, conversely, the lower reinforcement rate schedule enhances responding on the higher reinforcement schedule. This is called *contrast* (Reynolds, 1961), and to check if this phenomenon had caused the discrepancy in the lowest reinforcement rate schedule, we conducted studies in which either the timeout period between reinforcement components was longer or the discriminative stimuli that signaled the different reinforcement rates were removed. Both operations should reduce contrast, and, as expected, both either eliminated or decreased the discrepancy between obtained and predicted response rates in the lowest reinforcement rate component (unpublished data from our laboratory).

Although the experimental manipulations produced orderly shifts in  $B_{\text{max}}$  and  $R_{\text{half}}$  and Equation 1 typically accounted for more than 90% of the variance in response rates, some aspects of the results have not been properly explained. First, as noted in the Results section of Experiment 2, the parameters sometimes showed large and unaccounted for fluctuations. For example, Rat 159 showed a 41% change in  $B_{\text{max}}$ , and Rat 158 showed a 114% change in Rhalf between the first and third exposures to putatively identical conditions: standard lever and 23.5hr deprivation (Conditions 1 and 13). McSweeney (1982) also reported sizeable shifts in  $B_{\text{max}}$  and  $R_{\text{half}}$  under apparently unchanged conditions for some subjects. Second,  $B_{\text{max}}$  may reflect long-term adaptations to the response requirement. For example, in the second exposure to the 82-g weight, response rates were typically higher than they were in the first exposure (see Figure 3), and the rats were slow to return to response levels characteristic of the standard levers after the 82-g weights were removed. Response rates did not immediately spring back or overshoot as might be expected, but instead gradually climbed back to the preweighted level. These observations suggest that  $B_{\text{max}}$  depends on long-term learned behaviors, such as posture. Analogous complexities are likely to obtain for  $R_{half}$ .

Equation 1 is a rectangular hyperbola, and it has been used to describe phenomena in both the physical and biological sciences. In physics, Langmuir (1918) showed the rectangular hyperbola described the rate of adsorption of gases on smooth surfaces, and in physiology, Clark (1933) argued that this equation was the most reasonable model for the amount of drug that will bind to cell membranes. The common link among these and other applications is that there is an equilibrium between two competing actions. For example, the number of bound drug molecules depends on the balance between the rates at which the drug attaches to and detaches from specialized structures (receptors) in the cell membrane. Herrnstein (1970) pointed out that in any operant experiment the subject divided its time between the task arranged by the experimenter and other typically unmeasured activities, such as grooming, resting, and so forth. Elsewhere, it has been shown that on the basis of this elementary observation, it is possible to derive Equation 1 (Heyman, in press). One implication of this derivation was that  $B_{\text{max}}$  measures response topography and  $R_{\text{half}}$  measures reinforcement efficacy. Experiments 1, 2, and 3 and the literature reviewed in this General Discussion section supported the derivation. Thus, the interpretation that  $B_{\text{max}}$  measures the motor component of response rate and  $R_{half}$  measures the efficacy of the reinforcer maintaining the response is consistent with quite general equilibrium principles and the findings of a diverse body of empirical studies.

#### References

- Bradshaw, C. M., Ruddle, H. V., & Szabadi, E. (1981). Relationship between response rate and reinforcement rate in variable-interval schedules: II. Effect of the volume of sucrose reinforcement. *Journal of the Experimental Analysis of Behavior*, 35, 263-269.
- Bradshaw, C. M., Szabadi, E., & Bevan, P. (1978a). Effect of variable interval punishment on the behavior of humans in variable-interval schedules of monetary reinforcement. *Journal of the Experimental Analysis of Behavior*, 29, 161-166.
- Bradshaw, C. M., Szabadi, E., & Bevan, P. (1978b). Relationship between response rate and reinforcement frequency in variable-interval schedules: The effect of the concentration of sucrose reinforcement. *Journal of the Experimental Analysis of Behavior*, 29, 447–452.
- Bradshaw, C. M., Szabadi, E., & Ruddle, H. V. (1983). Herrnstein's equation: Effect of response force requirement on performance in variable-interval schedules. *Behavior Analysis Letters*, 3, 93-100.
- Bradshaw, C. M., Szabadi, E., Ruddle, H. V., & Pears, E. (1983). Herrnstein's equation: Effect of deprivation level on performance in variable-interval schedules. *Behavior Analysis Letters*, 3, 267–273.
- Catania, A. C. (1973). Self-inhibiting effects of reinforcement. Journal of the Experimental Analysis of Behavior, 19, 517–526.
- Clark, A. J. (1933). The mode of action of drugs. London: Edward Arnold.
- Conger, R., & Killeen, P. A. (1974). Use of concurrent operants in small group research. *Pacific Sociological Review*, 17, 399-416.
- Conrad, D. G., & Sidman, M. (1956). Sucrose concentration as reinforcement for lever pressing by monkeys. *Psychological Reports*, 2, 381–384.
- de Villiers, P. A., & Herrnstein, R. J. (1976). Toward a law of response strength. *Psychological Bulletin*, 83, 1131-1153.
- Draper, D., & Heyman, G. M. (1983). On fitting rectangular hyperbolas:

  The effects of random variation. (Tech. Rep. No. 147). Chicago, IL:
  Department of Statistics, University of Chicago.
- Fleshler, M., & Hoffman, H. S. (1962). A progression for generating variable-interval schedules. *Journal of the Experimental Analysis of Behavior*, 5, 529-530.
- Gallistel, C. R., & Karras, D. (1984). Pimozide and amphetamine have opposing effects on the reward summation function. *Pharmacology*, *Biochemistry*, and *Behavior*, 20, 73-77.
- Guttman, N. (1954). Equal reinforcement values for sucrose and glucose solutions compared with equal-sweetness values. *Journal of Comparative and Physiological Psychology*, 47, 358-361.
- Hamilton, A. L., Stellar, J. R., & Hart, E. B. (1985). Reward. performance, and the response strength method in self-stimulating rats: Validation and neuroleptics. *Physiology and Behavior*, 35, 897-904.
- Herrnstein, R. J. (1970). On the law of effect. *Journal of the Experimental Analysis of Behavior*, 13, 243-266.
- Herrnstein, R. J. (1974). Formal properties of the matching law. *Journal of the Experimental Analysis of Behavior, 21,* 159-164.
- Herrnstein, R. J. (1979). Derivatives of matching. Psychological Review, 86, 486–495.
- Heyman, G. M. (1983). A parametric evaluation of the hedonic and motoric effects of drugs: Pimozide and amphetamine. *Journal of the Experimental Analysis of Behavior*, 40, 113-122.
- Heyman, G. M. (in press). How drugs affect cells and reinforcement affects behavior: Formal analogies. In R. M. Church, M. Commons, J. R. Stellar, & A. R. Wagner (Eds.). Biological determinants of reinforcement and memory, Hillsdale, NJ: Erlbaum.
- Heyman, G. M., Kinzie, D. L., & Seiden, L. (1986). Chlorpromazine and pimozide alter reinforcement efficacy and motor performance. *Psychopharmacology*, 88, 346-353.
- Heyman, G. M., & Seiden, L. S. (1985). A parametric description of amphetamine's effect on response rate: Changes in reinforcement efficacy and motor performance. *Psychopharmacology*, 85, 154-161.

- Houston, A. (1986). The matching law applies to wagtails' foraging in the wild. *Journal of the Experimental Analysis of Behavior*, 45, 15–18.
- Hull, J. H. (1977). Instrumental response topographies of rats. *Animal Learning & Behavior*, 5, 207-212.
- Killeen, P. R. (1981). Averaging theory. In C. M. Bradshaw, E. Szabadi, & C. F. Lowe (Eds.), Quantifaction of steady-state operant behavior. Amsterdam: Elsevier/North-Holland Biomedical Press.
- Kraeling, D. (1961). Analysis of amount of reward as a variable in learning. Journal of Comparative and Physiological Psychology, 54, 560–565.
- Langmuir, I. (1918). The adsorption of gases on plane surfaces of glass, mica and platinum. *Journal of the American Chemical Society*, 40, 1361-1403.
- Logan, F. A. (1960). Incentive. New Haven: Yale University Press.
- McDowell, J. J. (1980). An analytic comparison of Herrnstein's equation and a multivariate rate equation. *Journal of the Experimental Analysis of Behavior*, 33, 397-408.
- McDowell, J. J., & Wood, H. M. (1984). Confirmation of linear system theory prediction: Changes in Herrnstein's k as a function of changes in reinforcement magnitude. *Journal of the Experimental Analysis of Behavior*, 41, 183–192.
- McDowell, J. J., & Wood, H. M. (1985). Confirmation of linear system theory prediction: Rate of change of Herrnstein's k as a function of response force requirement. *Journal of the Experimental Analysis of Behavior*, 43, 61–73.
- McSweeney, F. K. (1978). Prediction of concurrent keypeck and treadle-press responding from simple schedule performance. *Animal Learning & Behavior*, 6, 444–450.
- McSweeney, F. K. (1982). Prediction of concurrent schedule performance. Behavior Analysis Letters, 2, 11-20.

- Reynolds, G. S. (1961). Behavioral contrast. *Journal of the Experimental Analysis of Behavior*, 4, 57–71.
- Snapper, A. G., Stephens, K. R., Cobez, R. I., & Van Haaren, F. (1976).
  The SKED Manual 2: OS/8 and Time Share SKED. Kalamazoo, MI:
  The SKED Users Group.
- Snyderman, M. (1983). Bodyweight and response strength. Behavior Analysis Letters, 3, 255-265.
- Staddon, J. E. R. (1977). On Herrnstein's equation and related forms. Journal of the Experimental Analysis of Behavior, 43, 265-277.
- Stein, L., & Ray, O. S. (1960). Brain of stimulation reward "thresholds" self-determined in rat. Psychopharmacologia, 1, 251-256.
- Teitelbaum, P., & Campbell, B. A. (1958). Ingestion patterns in hyperphagic and normal rats. *Journal of Comparative and Physiological Psychology*, 51, 135-141.
- Tombaugh, T. N., Tombaugh, J., & Anisman, H. (1979). Effects of dopamine receptor blockade on alimentary behaviors: Home cage food consumption, magazine training, and performance. *Psychopharmacology*, 66, 219–225.
- Wilkinson, G. N. (1960). Statistical estimates in enzyme kinetics. Biochemical Journal, 80, 324-332.
- Winer, B. J. (1971). Statistical principles in experimental design. New York: McGraw-Hill.
- Wise, R. A. (1982). Neuroleptics and operant behavior: The anhedonia hypothesis. Behavior and Brain Sciences, 5, 39–87.
- Wolin, B. R. (1968). Difference in manner of pecking a key between pigeons reinforced with food and water. In A. C. Catania (Ed.), Contemporary research in operant behavior (p. 286). Glenview, IL: Scott, Foresman and Company.

Received July 14, 1986
Revision received February 2, 1987
Accepted February 17, 1987

# Articles Published in the Most Recent Issue of Journal of Comparative Psychology

#### September 1987

#### Special Issue on Comparative Psychology

Vol. 101, No. 3

- 219 Editor's Introduction Jerry Hirsch
- 221 Comparative Psychology: The Next 100 Volumes Irwin S. Bernstein
- 223 The Journal of Animal Behavior and the Early History of Animal Behavior Studies in America Richard W. Burkhardt, Jr.
- 231 Origins and Accomplishments of Joseph Jastrow's 1888-Founded Chair of Comparative Psychology at the University of Wisconsin *Thomas C. Cadwallader*
- 237 Comparative Psychology and the Study of Animal Learning Michael Domjan
- 242 What Comparative Psychology Is About? Back to the Future Francois Y. Doré and Gilles Kirouac
- 249 Comparative Psychology as the Praxist Views It Robert Epstein
- 254 Compartments and Cohesions in Adaptive Behavior John C. Fentress
- 259 Comparative Psychology Is Dead! Long Live Comparative Psychology Bennett G. Galef, Jr.
- 262 The Developmental Basis of Evolutionary Change Gilbert Gottlieb
- 272 Ethology and Comparative Psychology Glen McBride
- 275 Comparative Psychology as a Search for Invariant Rules Jean Médioni
- 277 Applied Dimensions of Comparative Psychology Greg Moran
- 282 Natural Design and the Future of Comparative Psychology N. S. Thompson
- 287 Comparative Psychology: Is There Any Other Kind? Charles W. Tolman