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REINFORCEMENT AND PUNISHMENT EFFECTS IN CONCURRENT SCHEDULES: A TEST OF TWO MODELS

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The joint effects of punishment and reinforcement on the pigeon's key-peck response were examined in three choice experiments conducted to compare predictions of Farley and Fantino's (1978) subtractive model with those made by Deluty's (1976) and Deluty and Church's (1978) model of punishment. In Experiment 1, the addition of equal punishment schedules to both alternatives of a concurrent reinforcement schedule enhanced the preference exhibited for the more frequent reinforcement alternative. Experiment 2 demonstrated decreases in the absolute response rate for each member of a concurrent reinforcement schedule when increasing frequencies of punishment were added to each alternative. Experiment 3 found that preference for the denser of two reinforcement schedules diminished when the absolute frequencies of reinforcement were increased by a constant factor and conditions of punishment for both alternatives were held constant. Diminished preferences were obtained regardless of whether the frequency of punishment associated with the denser reinforcement schedule was greater or less than that associated with the lean reinforcement alternative. The results from all three experiments uniquely supported Farley and Fantino's (1978) subtractive model of punishment and reinforcement.

Key words: subtractive model of punishment, matching relation, concurrent schedules, key peck, pigeons

Farley and Fantino (1978) recently proposed a simple subtractive integration rule to summarize the effects of punishment and appetitive reinforcement upon choice behavior (cf. similar informal suggestions by de Villiers & Millenson, 1972; Estes, 1969). Punishment of a response directed toward one of two choice alternatives is viewed as subtracting directly from the "absolute reinforcement value" which sustains this response. In the absence of punishment, "absolute reinforcement value" may be regarded as synonymous with absolute rate of reinforcement. This diminished absolute reinforcement value is accompanied by a change in the "relative value" of the punishment alternative as well. These changes in both absolute and relative value produce shifts in absolute as well as relative response rates.

A formal elaboration of this value view of choice behavior (cf. Baum & Rachlin, 1969), when both alternatives are punished, is:

$$\frac{R_1}{R_1+R_2}=\frac{(r_1-cp_1)}{(r_1-cp_1)+(r_2-cp_2)}, \tag{1a}$$

and in the case of absolute response rates,

$$R_1=K\frac{(r_1-cp_1)}{(r_1-cp_1)+(r_2-cp_2)+r_0}. \tag{1b}$$

R_1 and R_2 are the rates of response to the two alternatives under consideration, r_1 and r_2 are the rates of reinforcement contingent upon these responses, and p_1 and p_2 are the rates of punishment contingent on R_1 and R_2. The parameters r_0 and K are conventionally interpreted as follows: all other alternative sources of reinforcement within the given experimental context, and the asymptotic amount of responding possible for a given subject (cf. Herrnstein, 1974), respectively. The scalar c is intended to reflect the value of punishment in terms of negative food units. I assume $0 \leq c < q$, where q is a positive constant. c cannot be specified a priori; its value depends on the reinforcement and punishment parameters used in any given experiment and presumably varies for different individuals. The upper limit q, however, can in principle

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be determined. It is defined here as the rate of reinforcement which is just incapable of sustaining consistent responding for the minimally severe combination of punishment parameters examined in a given experiment (i.e., the reinforcement schedule which produces a net value of zero for a given alternative). This definition of a q deliberately precludes Equations 1a and 1b from being either negative or indefinite. Moreover, it establishes appropriate boundary conditions for Equations 1a and 1b so that programmed schedule conditions which are physically unrealizable (e.g., a subject failing to collect reinforcers because of complete suppression) are not to be viewed as conditions which this model is intended to address.

A different combination rule for punishment and reinforcement has recently been offered by Deluty (1976) and Deluty and Church (1978). In this model, punishment of a response can be interpreted as diminishing the relative value of associated events in an indirect manner, through an increase in the absolute value for alternative responses. More formally:

$$\frac{R_1}{R_1+R_2}=\frac{(r_1+cp_2)}{(r_1+cp_2)+(r_2+cp_1)}, \qquad (2a)$$

and in the case of absolute response rates,

$$R_1=K\frac{(r_1+cp_2)}{(r_1+cp_2)+(r_2+cp_1)+r_0}. \qquad (2b)$$

Here, all variables and parameters are defined as in Equations 1a and 1b. Although the initial statement of this model did not explicitly include c (i.e., c was implicitly assumed to equal 1.0), it is introduced here so as to equate the two sets of equations for the number of parameters assumed by each.

How do Equations 1a and 1b and Equations 2a and 2b compare in their predictions of the salient characteristics of reinforcement and punishment interactions in concurrent schedules? It can be seen that when punishment is added to alternative 1 ($p_1 > 0$), Equation 1b predicts R_1 suppression because of a proportionally greater decrease in its numerator (i.e., the absolute value of alternative 1). In contrast, Equation 2b predicts R_1 suppression because of an increase in its denominator; more specifically, that portion of the denominator which comprises the absolute value of alternative 2. An additional consequence of this suppression of R_1 for both sets of equations is an increase in response rate to the no-punishment alternative (i.e., punishment-contrast: Azrin & Holz, 1966; Deluty, 1976). This can be appreciated by considering the analogous equations for R_2:

$$R_2=K\frac{(r_2-cp_2)}{(r_2-cp_2)+(r_1-cp_1)+r_0}, \qquad (1c)$$

$$R_2=K\frac{(r_2+cp_1)}{(r_2+cp_1)+(r_1+cp_2)+r_0}. \qquad (2c)$$

In the current example, when $p_1 > 0$, both Equation 1c and Equation 2c predict R_2 enhancement. This occurs in Equation 1c because of a decrease in the denominator. A change in the relative value of alternative 2 is effected by a decrease in the absolute value of alternative 1 events. Equation 2c, however, predicts decreases in R_2 because of a proportionally greater increase in the numerator, i.e., a direct increase in the absolute, and relative, value of alternative 2 events.

The divergent predictions made by the two sets of equations are of greater interest. These are most conspicuous in concurrent schedules which provide for reinforcement and punishment for *both* alternatives. Since the development of these predictions is complex in some instances, they are simply enumerated here. More detailed expositions of each are given in subsequent sections of this report.

One straightforward difference between the two sets of equations arises when the same schedule of punishment is added to both alternatives of a concurrent reinforcement schedule. As long as $r_1 \neq r_2$, Equation 1a predicts the pattern of overmatching: a more extreme preference for the denser reinforcement schedule than is predicted by the relative frequency of reinforcement. Equation 2a predicts undermatching: a less extreme preference for the denser reinforcement schedule than is predicted by the relative frequency of reinforcement. A second difference between the two sets of equations concerns the predicted changes in absolute response rates in concurrent schedules under the following conditions: reinforcement conditions are held constant, punishment for both alternatives is introduced, and subsequently increased in frequency across conditions. Equation 1b predicts decreased absolute response rates; Equation 2b predicts increased absolute response rates. A third difference between the equations obtains in certain concurrent schedule combinations in which the frequencies of punishment for both alternatives are held constant, but the rates of reinforcement for each are increased. Equation 1a predicts that preferences should become less extreme; Equation 2a predicts that preferences should become more extreme.

The following experiments examined these different predictions and therefore permit a choice between Equations 1a and 1b and Equations 2a and 2b as to which is the more accurate description of how punishment and reinforcement combine to determine performance in concurrent schedules.

EXPERIMENT 1

Experiment 1 examined the changes in choice behavior which occur when the same variable-interval (VI) schedule of punishment is added to both members of a two-key concurrent schedule of reinforcement. Consider first the predictions made by Equation 1a. Since

$$\frac{(r_1-cp)}{(r_1-cp)+(r_2-cp)} > \frac{r_1}{r_1+r_2}, \qquad (3)$$

when $r_1 > r_2$ $(c > 0)$, and this inequality is reversed when $r_1 < r_2$, the predicted effect of adding equal frequencies of punishment to both alternatives is that of overmatching. Preference for the more frequent schedule of reinforcement should be enhanced.

Equation 2a predicts the opposite pattern, since

$$\frac{(r_1+cp)}{(r_1+cp)+(r_2+cp)} < \frac{r_1}{r_1+r_2}, \qquad (4)$$

when $r_1 > r_2$ $(c > 0)$, and the inequality is reversed when $r_1 < r_2$. Equation 2a predicts a pattern of undermatching. Preference for the more frequent schedule of reinforcement should be less than predicted by the relative frequency of reinforcement.

A test of Equations 1a and 2a was therefore arranged by comparing choice behavior in concurrent reinforcement schedules in conditions where punishment was present vs. those where it was absent. Equation 1a predicted a trend toward overmatching in punishment conditions, and Equation 2a predicted undermatching. The results of this comparison are reported below.

METHOD

Subjects

Three adult male White Carneaux pigeons, maintained at approximately 75% of their free-feeding weights, served. All three subjects had previous training with concurrent reinforcement schedules.

Apparatus

Three standard two-key operant conditioning chambers for pigeons were used. Each was enclosed within a light- and sound-attenuating shell. Side and rear walls and roof were constructed of clear Plexiglas so as to yield inner chamber dimensions of 32 by 30 by 38 cm. The circular translucent response keys, illuminated by 28-V dc stimulus projectors (Industrial Electronic Engineers, #1820), were mounted 31 cm from the floor and 12 cm apart. A force of .14 *N* resulted in response key closure. Illumination in two of the chambers was provided by white 28-V dc lights located in the rear. In the third chamber, a single 110-V ac houselight was mounted in the rear. A 110-V ac solenoid-operated grain hopper, centrally located between the two response keys, provided 3-sec access to mixed grain.

In this experiment, as well as in subsequent ones, brief (35 msec) deliveries of electric shock served as punishers. Shock presentations were accomplished by switching the output of the constant-current shock generator (Lafayette Instrument Co., #A615-B) through a harness arrangement to stainless steel electrodes implanted around the pigeon's pubic bones (Azrin, 1959). Appropriate voltage and resistance combinations were selected to ensure that variations in the pigeons' resistances contributed negligibly (<1%) to the obtained current value of 6 ma. Electrodes were periodically checked and cleaned to ensure good electrical continuity between bird and electrodes.

Procedure

Each bird was exposed to the five pairs of concurrent reinforcement schedules which are listed in Table 1. The no-punishment conditions provided a standard of choice behavior, against which the effects of superimposing a VI 2-min punishment schedule on each alternative could be evaluated. Punishers and reinforcers were precluded from occurring within 3 sec of one another. In addition, a

Table 1

Description of training conditions and results of Experiment 1. For each subject the order of training conditions and the number of sessions conducted in each (parenthetical numbers) are given. Also listed are the absolute response and reinforcement rates to both alternatives for each subject, obtained from the last three days of training. In all punishment conditions, the schedule of punishment was VI 2-min.

Experimental conditions			*LK*			*RK*		
LK	*RK*	*Order*	*R/min*	*S^R/min*	*Pun/min*	*R/min*	*S^R/min*	*Pun/min*
			Bird 1					
VI 6-min	VI 1-min	1(7)	15.4	.15	—	94.6	1.10	—
VI 6-min + pun	VI 1-min + pun	2(10)	6.3	.09	1.65	83.2	1.01	2.03
VI 3-min	VI 1-min	9(6)	27.5	.31	—	82.5	.97	—
VI 3-min + pun	VI 1-min + pun	10(7)	11.7	.30	2.03	78.1	.98	1.99
VI 2-min	VI 2-min	5(7)	46.5	.47	—	49.8	.53	—
VI 2-min + pun	VI 2-min + pun	6(7)	40.0	.51	2.10	46.9	.51	1.96
VI 2-min	VI 4-min	7(8)	57.3	.46	—	30.1	.27	—
VI 2-min + pun	VI 4-min + pun	8(7)	56.2	.49	1.98	23.0	.27	2.10
VI 1-min	VI 4-min	3(10)	81.9	.94	—	18.0	.23	—
VI 1-min + pun	VI 4-min + pun	4(7)	71.3	1.01	1.99	7.9	.26	1.95
			Bird 2					
VI 6-min	VI 1-min	1(8)	7.8	.16	—	52.1	.93	—
VI 6-min + pun	VI 1-min + pun	2(10)	4.2	.10	1.74	42.4	.98	1.97
VI 3-min	VI 1-min	9(6)	13.9	.34	—	44.0	1.05	—
VI 3-min + pun	VI 1-min + pun	10(6)	9.2	.33	1.95	36.5	.96	2.03
VI 2-min	VI 2-min	3(6)	29.9	.52	—	35.7	.51	—
VI 2-min + pun	VI 2-min + pun	4(6)	23.1	.52	1.92	22.8	.49	1.94
VI 2-min	VI 4-min	5(7)	42.1	.45	—	15.3	.24	—
VI 2-min + pun	VI 4-min + pun	6(7)	36.7	.43	2.01	9.3	.29	1.98
VI 1-min	VI 4-min	7(6)	46.4	.97	—	12.1	.27	—
VI 1-min + pun	VI 4-min + pun	8(6)	44.9	1.03	1.97	6.1	.23	1.89
			Bird 3					
VI 6-min	VI 1-min	1(7)	7.4	.18	—	45.0	1.03	—
VI 6-min + pun	VI 1-min + pun	2(10)	6.5	.17	2.05	36.7	.98	1.99
VI 3-min	VI 1-min	3(9)	13.3	.34	—	39.4	1.00	—
VI 3-min + pun	VI 1-min + pun	4(11)	9.6	.32	1.98	30.2	.96	2.01
VI 2-min	VI 2-min	9(7)	26.3	.53	—	23.2	.51	—
VI 2-min + pun	VI 2-min + pun	10(7)	19.2	.49	2.02	21.3	.50	1.96
VI 2-min	VI 4-min	7(6)	30.2	.48	—	19.6	.28	—
VI 2-min + pun	VI 4-min + pun	8(7)	28.7	.51	1.97	14.1	.23	2.02
VI 1-min	VI 4-min	5(7)	34.5	.97	—	19.4	.27	—
VI 1-min + pun	VI 4-min + pun	6(7)	35.1	.98	2.01	4.9	.11	1.90

3-sec changeover delay contingency (COD) was included in all conditions so that transitions from one key to another were neither immediately reinforced nor punished.

Training in a given condition continued until the choice proportions for three consecutive sessions deviated by no more than .07 about their mean. Each daily session was 100 min in duration, and was conducted 6 or 7 times a week. The order of training conditions and the number of sessions in each are given in Table 1. The interevent intervals of all reinforcement and punishment schedules were constructed according to Segal's (1964) method. In all conditions, the left response key was illuminated red; the right was illuminated green. Standard relay-operated programming and recording equipment was located in an adjacent room.

RESULTS AND DISCUSSION

Figure 1 presents the relative rate of response to the left key for each subject. These choice proportions are plotted as a function of the relative rate of obtained reinforcement for the left key. Each point represents the mean choice proportion from the last three days of training in each condition. Birds 1 and 2 show good conformity to the matching relation in the absence of punishment (circles). Bird 3's preferences for the more frequent reinforcement schedules were less extreme than

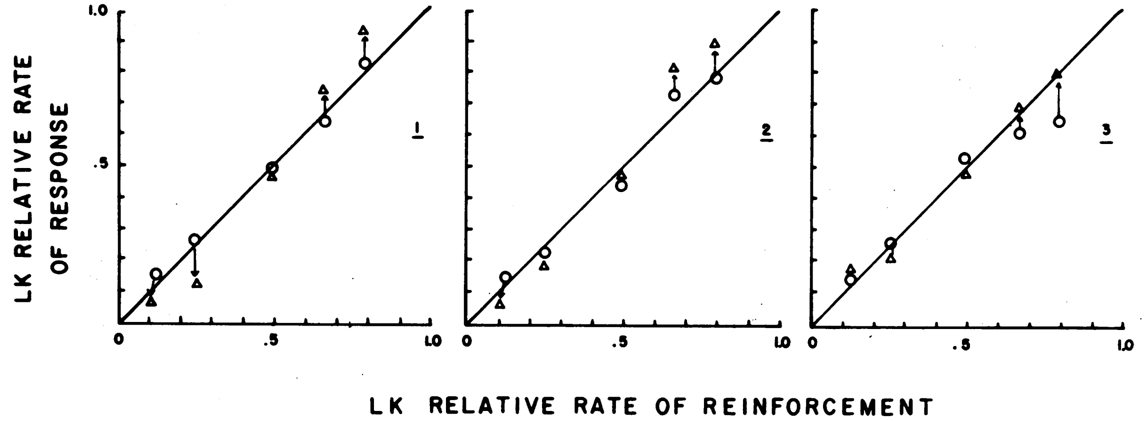

Fig. 1. Relative rate of key pecking to the left key plotted as a function of relative rate of obtained reinforcement for this key. Each point represents an average obtained from the last three days of training in each condition. Circles represent data from no-punishment conditions; triangles represent data from punishment conditions.

predicted by the relative frequency of reinforcement in the conc VI 2-min VI 4-min and conc VI 1-min VI 4-min conditions. In other words, this bird occasionally undermatched in the absence of punishment. Nevertheless, the addition of punishment to both alternatives produced an enhancement of preference for the more frequent reinforcement schedule (triangles) for all subjects. That is, all birds tended to overmatch, relative to baseline. This appears as a downward deflection of choice behavior for points plotted to the left of .50 on the abscissa, and an upward deflection for points to the right of .50. The contribution of punishment per se to overmatching was confounded by deviations of obtained, from programmed, reinforcement rates for the leaner reinforcement alternative in three instances (see Table 1): conc VI 6-min VI 1-min (Birds 1 and 2) and conc VI 1-min VI 4-min (Bird 3). Even here, however, choice for the denser schedule exceeded the relative rate of obtained reinforcement. These equivocal results are more than outweighed by the nine other possible comparisons which clearly demonstrate overmatching when no deviation of obtained, from programmed, reinforcement rates occurred. The entire pattern of results is consistent with the Farley and Fantino (1978) subtractive model of punishment (Equation 1a) and directly contradicts the predictions of Equation 2a.

A comparison of these results with those of an unpublished experiment described by de Villiers (1977) and an earlier report by Todorov (1971) is worth comment. de Villiers also reported consistent overmatching for two of three pigeons responding on a single pair of concurrent VI food schedules when equal VI punishment schedules were added, and punishment intensity was systematically increased. Earlier, Todorov also obtained an increase in preference for the more frequent member of a pair of concurrent VI schedules when punishment was added to both. In Todorov's experiment, however, only changeover responses were punished; his results appear to reflect a direct decrease in the rate of changeover responses. In the present experiment, changeover responses were deliberately never immediately punished. This does not imply, of course, that changeover responses continued unabated. Since they were not recorded in this experiment, it is impossible to determine how much of the obtained overmatching is due to their decrease. Although punishment of both changeover responses and "postchangeover" responses can be accommodated by Equation 1a, it is important to realize that these two classes of behavior are in all probability functionally distinct. A more complete version of Equation 1a would make this explicit.

A report by Holz (1968), which stated that matching continued to occur when punishment was added to both alternatives of a conc VI 1.9-min VI 7.5-min schedule, also merits discussion since this appears to contradict the overmatching obtained here. This discrepancy is more apparent than real, however, since each response was punished in Holz's experiment. Thus, the obtained frequency of punishment for each alternative equaled the associated rate of response. In other words, each alternative was associated with punishment in a manner commensurate with its initial ability to sustain responding. This set of conditions can be formulated in terms of Equation 1a as follows:

$$\frac{R_1}{R_1+R_2}=\frac{(r_1-cp'_1)}{(r_1-cp'_1)+(r_2-cp'_2)}, \tag{5a}$$

where p'_1 and p'_2 are the obtained frequencies of punishment. Assuming Equation 1b to be correct, p'_1 and p'_2 will be proportional to $(r_1/r_1+r_2+r_0)$ and $(r_2/r_1+r_2+r_0)$, respectively. Substituting these terms into Expression 5a yields matching, as the following demonstrates:

$$\frac{R_1}{R_1+R_2}=\frac{r_1-(r_1c/r_1+r_2+r_0)}{r_1-(r_1c/r_1+r_2+r_0)+r_2-(r_2c/r_1+r_2+r_0)} \tag{5b}$$

$$=\frac{r_1(1-c/r_1+r_2+r_0)}{(r_1+r_2)(1-c/r_1+r_2+r_0)}$$

$$=\frac{r_1}{r_1+r_2}. \tag{5c}$$

Holz's findings are therefore consistent with Equations 1a and 1b.

EXPERIMENT 2

Equations 1b and 2b can be further contrasted with each other by examining the predicted changes in *absolute* response rates in concurrent schedules of reinforcement and punishment. Suppose that r_1 and r_2 are held constant, but both p_1 and p_2 are increased. How should absolute response rates change?

An intuitive appreciation of the complexity of this situation can be gained by noting that changes in both the absolute and relative values associated with each alternative undergo changes. Moreover, these changes tend to offset one another. In the case of Equation 1b, an increase in p_1 results in a decrease in the absolute value of events associated with alternative 1. In the absence of any change in p_2, this should reduce R_1. However, the increase in p_2 results in alternative 2s events decreasing in absolute value as well. This should increase R_1. For Equation 2b, an increase in p_1 results in an increased absolute value of alternative 2, which should result in R_1 decreases; but an increase in p_2 should offset this decrease. Clearly, a means of determining how these changes in absolute and relative reinforcement value interact to determine net output is needed.

A technique which is useful in the analysis of the behavior of multivariable functions, in circumstances such as these, involves the examination of directional derivatives. As used here, this method permits an assessment of how Equations 1b and 2b should change when r_1, r_2, and r_0 are held constant, but p_1 and p_2 are increased. For example, if the sign of the directional derivative for Equation 1b or Equation 2b is positive, this implies that the absolute response rate—R_1—is increasing. If the sign of this derivative is negative, this implies that R_1 is decreasing. If the signs of the directional derivatives of Equations 1b and 2b are reversed in some given set of conditions, then a decisive test of the models can be arranged. Two such sets of conditions are described below.

Case 1: $r_1 = r_2$; $p_1 = p_2$.

Set $r_1 = r_2$ and $p_1 = p_2 = 0$. Hold r_1 and r_2 constant. Increase p_1 and p_2 equally. Assuming Equation 1b to be true, the directional derivative can be shown (see Appendix) to be of the form:

$$\frac{-cp_1r_0kh}{(2r_1+r_0)^2}. \tag{6}$$

Here, k is the constant factor by which punishment frequency is increased, and h is a positive constant (see Appendix for definition and interpretation). Equation 6 will always be either zero, in the special case where r_0 equals zero, or more generally, negative. This implies that R_1 will either remain constant or decrease as p_1 and p_2 increase.

Assuming Equation 2b to be true, the directional derivative takes the form (see Appendix):

$$\frac{cp_1r_0kh}{(2r_1+r_0)^2}. \tag{7}$$

Here, all terms are defined as in Expression 6. The value of this expression will always be either zero, when r_0 equals zero, or positive. Therefore, Equation 2b implies that R_1 will either remain constant or increase as p_1 and p_2 increase.

Case 2: $r_1 < r_2$; $p_1 < p_2$.

Set $r_2 = mr_1$ (e.g., $m = 2$ in the experimental conditions here) and $p_2 = mp_1 = 0$. Hold r_1,

r_2, and r_0 constant and increase p_1 and p_2 proportionally. Under this set of conditions, unlike Case 1, stimulus control over responding to each alternative can be directly checked since $r_1 \neq r_2$ for Equations 1b and 2b. Assuming Equation 1b to be true, the directional derivative is:

$$\frac{r_1 r_0(j-1) - c p_1 r_0 m j}{(3r_1 + r_0)^2}. \tag{8}$$

The scalar m is defined as before, and j is a positive constant—analogous to h in Equations 6 and 7. Expression 8 will be either zero ($r_0 = 0$) or negative, since $0 < j < 1.0$. Therefore, R_1 should remain constant or decrease as p_1 and p_2 are increased proportionally.

Assuming Equation 2b to be true, the directional derivative is given by:

$$\frac{c p_1 m j(3r_1 + 2r_0)}{(3r_1 + r_0)^2}. \tag{9}$$

All terms are as defined in Equation 8. This expression will be either zero or positive. Therefore, R_1 should remain constant, or increase, as p_1 and p_2 are increased proportionally.

Equations 1b and 2b make opposite predictions about the changes in absolute response rates in various concurrent schedule combinations of punishment and reinforcement. In the first case considered, the two alternatives are equated for reinforcement and punishment frequency. Subsequently, punishment frequency is increased. Equation 1b predicts that absolute response rates will decrease.[1] Equation 2b predicts that absolute response rates will increase. These two equations make the same divergent predictions in cases where $r_1 < r_2$ and $p_1 < p_2$, when p_1 and p_2 are increased proportionally. These predictions were examined in Experiment 2.

METHOD

Subjects

Six adult male White Carneaux pigeons were maintained at 75% of their free-feeding weights. All were experimentally naive.

Apparatus

The same as in Experiment 1, with one exception. The deliveries of punishing stimuli were accompanied by brief (1-sec) flashes of cue lights. Punished responses to the left key were cued by amber. Punished responses to the right key were cued by blue. These cue lights were 28-V dc lights, covered by appropriately colored plastic caps, mounted at the top of the front and rear panels of the chamber.

Procedure

Preliminary training. The six birds were initially magazine trained until each subject ate reliably from the hopper. They were then exposed for four sessions to a discrete-trial procedure designed to ensure responding to both response keys. This procedure involved two types of trials. The first involved the illumination of the right key by a red hue for 10 sec, the termination of which was followed by 3-sec access to mixed grain. The second trial type involved the illumination of the left key by a green hue for 10 sec, also followed by 3 sec of reinforcement. The mean intertrial interval (ITI) was 1 min, and the two trial types were strictly alternated. A session terminated after 60 trials. All birds were then exposed, for five sessions, to simultaneous and constant illumination of the response keys, each of which was associated with its own VI reinforcement schedule. In the first session, a VI 15-sec schedule was associated with both keys. In the subsequent four sessions, a VI 30-sec schedule was in effect. During the third session, a 1-sec COD was added; this was increased to 3 sec in the fourth and subsequent sessions.

Concurrent reinforcement and punishment training. The birds were then split into two groups of three and were exposed to the two sets of conditions described in Table 2. Birds 1, 2, and 3 were exposed to the nondifferential reinforcement and punishment conditions of Table 2. Birds 4, 5, and 6 were exposed to the differential-reinforcement and punishment conditions. Relatively dense reinforcement

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[1] In Case 1, the directional derivative for R_2 is the same as that for R_1, regardless of whether Equations 1a and 1b or Equations 2a and 2b are assumed to be correct. In Case 2, the derivatives are different. Assuming Equation $1\bar{b}$ to be true, the directional derivative for R_2 is $-2c^2 r_0 j l p_1/(3r_1 + r_0)^2$. This expression is either zero or negative. Analysis of Equation 2c yields the following derivative: $c^2 j l p_1(r_0 - 3r_1)/(3r_1 + r_0)^2$. This may be either positive, negative, or zero, depending on the magnitude of r_0 relative to $3r_1$. Because of this indeterminancy of r_0 (it is a parameter to be estimated from the data), Equations 1a and 1b and Equations 2a and 2b cannot be meaningfully discriminated between on the basis of R_2 data.

Table 2

Description of training conditions and results of Experiment 2. For each subject the order of training conditions and the number of sessions conducted in each (parenthetical numbers) are given. Absolute response, reinforcement, and punishment rates for each alternative also appear. All values are averages from the last three training sessions in a given condition.

Experimental Conditions									
LK	*RK*		*LK*				*RK*		
Reinf. + Pun.	*Reinf. + Pun.*	*Order*	*R/min*	*S^R/min*	*Pun/min*	*Choice*	*R/min*	*S^R/min*	*Pun/min*
Nondifferential reinforcement, punishment				Bird 1					
VI 30-sec	VI 30-sec	1(15)	42.7	2.10	—	.51	40.9	2.00	—
		5(13)	47.1	1.97	—	.52	44.3	2.00	—
VI 30-sec +	VI 30-sec +	2(17)	31.2	1.89	.96	.46	33.0	1.95	.89
VI 60-sec	VI 60-sec	8(7)	32.8	1.97	.95	.51	31.9	1.88	.97
VI 30-sec +	VI 30-sec +	3(10)	25.8	2.03	1.98	.50	25.3	1.99	1.96
VI 30-sec	VI 30-sec	7(8)	29.1	1.89	1.95	.51	27.9	2.04	2.00
VI 30-sec +	VI 30-sec +	4(7)	23.0	1.91	3.84	.49	24.2	1.98	3.91
VI 15-sec	VI 15-sec	6(7)	26.1	2.00	3.87	.52	23.9	1.96	3.90
				Bird 2					
VI 30-sec	VI 30-sec	1(10)	63.9	1.96	—	.51	60.2	1.92	—
		5(10)	67.2	2.03	—	.51	63.7	2.03	—
VI 30-sec +	VI 30-sec +	2(15)	41.3	1.98	1.03	.53	37.2	1.91	.97
VI 60-sec	VI 60-sec	8(6)	35.8	1.97	.99	.49	36.9	2.01	.98
VI 30-sec +	VI 30-sec +	3(13)	29.8	1.93	2.10	.51	28.8	1.98	2.07
VI 30-sec	VI 30-sec	7(7)	26.9	2.07	2.01	.53	23.9	1.91	1.98
VI 30-sec +	VI 30-sec +	4(10)	19.3	1.74	3.95	.48	21.2	1.80	4.10
VI 15-sec	VI 15-sec	6(9)	25.2	1.98	4.06	.49	26.1	2.01	3.99
				Bird 3					
VI 30-sec	VI 30-sec	1(11)	93.4	1.98	—	.50	91.7	1.89	—
		5(8)	91.2	2.03	—	.50	92.0	2.00	—
VI 30-sec +	VI 30-sec +	2(13)	88.1	1.96	1.05	.51	84.3	1.94	1.03
VI 60-sec	VI 60-sec	8(8)	91.5	1.95	.94	.51	89.1	1.97	.98
VI 30-sec +	VI 30-sec +	3(9)	73.6	1.91	1.95	.51	70.7	2.02	1.93
VI 30-sec	VI 30-sec	7(7)	79.6	2.01	2.06	.50	78.1	1.95	2.00
VI 30-sec +	VI 30-sec +	4(7)	64.5	2.07	4.03	.49	67.1	1.97	3.96
VI 15-sec	VI 15-sec	6(6)	73.5	1.98	3.98	.53	65.2	2.04	4.02
Differential reinforcement, punishment				Bird 4					
VI 30-sec	VI 15-sec	1(11)	85.9	1.93	—	.41	121.7	3.96	—
		5(10)	82.1	1.95	—	.38	132.3	4.02	—
VI 30-sec +	VI 15-sec +	2(13)	75.4	2.05	.97	.39	119.2	3.98	1.01
VI 60-sec	VI 60-sec	8(7)	73.2	1.91	1.03	.37	124.3	4.05	1.02
VI 30-sec +	VI 15-sec +	3(10)	69.7	1.81	2.03	.41	100.1	4.01	1.99
VI 30-sec	VI 30-sec	7(8)	64.1	1.97	1.95	.38	102.9	3.96	2.01
VI 30-sec +	VI 15-sec +	4(6)	54.0	2.02	3.98	.36	94.1	3.89	4.01
VI 15-sec	VI 15-sec	6(7)	43.2	1.90	3.91	.33	87.2	3.91	3.97
				Bird 5					
VI 30-sec	VI 15-sec	1(12)	92.1	1.88	—	.38	147.3	1.98	—
		5(13)	87.5	2.01	—	.39	139.2	2.03	—
VI 30-sec +	VI 15-sec +	2(19)	86.0	1.94	1.01	.39	137.1	1.95	.96
VI 60-sec	VI 60-sec	8(9)	84.1	1.99	1.03	.40	127.2	2.01	1.03
VI 30-sec +	VI 15-sec +	3(18)	73.5	1.97	1.98	.37	123.8	1.91	1.99
VI 30-sec	VI 30-sec	7(9)	69.7	2.02	2.00	.39	109.7	2.09	2.02
VI 30-sec +	VI 15-sec +	4(15)	64.5	1.97	3.95	.34	121.3	1.97	3.98
VI 15-sec	VI 15-sec	6(14)	58.1	1.99	4.02	.33	117.4	1.98	4.01
				Bird 6					
VI 30-sec	VI 15-sec	1(13)	67.1	2.03	—	.36	119.1	3.85	—
		5(11)	69.1	2.04	—	.40	105.3	4.04	—
VI 30-sec +	VI 15-sec +	2(10)	61.2	1.98	.97	.40	91.1	4.10	1.00
VI 60-sec	VI 60-sec	8(8)	58.7	2.01	1.03	.37	104.1	3.91	1.01
VI 30-sec +	VI 15-sec +	3(9)	43.7	1.97	1.98	.34	84.7	3.95	2.00
VI 30-sec	VI 30-sec	7(7)	50.3	2.02	1.95	.33	98.2	4.02	1.93
VI 30-sec +	VI 15-sec +	4(8)	23.1	1.93	4.10	.33	47.9	3.97	4.01
VI 15-sec	VI 15-sec	6(7)	24.7	1.97	3.97	.29	59.1	4.00	3.99

schedules and a "fading" procedure for the introduction of punishment were used to minimize the likelihood that these punishment-naive birds would stop responding in high-frequency punishment conditions.

The general plan of training was to first establish stable choice behavior for a given pair of reinforcement schedules in the absence of punishment. Punishment was then introduced for two sessions, according to the prescribed schedule, at a relatively low intensity (2 ma). A single session of training with a moderately intense (4-ma) punisher was followed by training to stability with a 6-ma punisher in effect. Punishment frequency was then increased in an ascending series of training conditions, and redeterminations of relative and absolute response rates were made under a descending series of punishment frequency conditions. A return to a no-punishment condition separated the ascending and descending series. The exact sequence of training conditions and the number of sessions in each condition are listed in Table 2. The stability criterion used was the same as in Experiment 1; training in each condition continued until the choice proportions for three consecutive sessions deviated by no more than .07 about their mean.

RESULTS AND DISCUSSION

Figure 2 presents the absolute response rates in the punishment and no-punishment conditions of Experiment 2. Each data point is the average response rate obtained from the last three sessions of training in a given condition. The results are clear: an increased frequency of punishment results in an increased suppression of responding. No deviations from the programmed rates of reinforcement occurred (see Table 2). Birds 2 and 6 exhibited somewhat more suppression in the descending series of punishment conditions (triangles); Bird 1 exhibited greater suppression in the ascending series of conditions (circles). The response rate decreases observed here when punishment *frequencies* are increased have also been reported when punishment *intensity* has been increased for concurrent responses (Todorov, 1977). These rate decreases would appear, therefore, to be a general consequence of any parametric change which, on a priori grounds, would be expected to increase the aversiveness of the punishment schedule.

The relative response rates to the left key in all conditions also appear in Table 2 for each bird. In the differential reinforcement and punishment conditions, increases in the frequency of punishment enhanced the degree of preference exhibited for the denser (right key) reinforcement schedule (see columns labeled *Choice*). This pattern is consistent with Equation 1a and confirms and extends the results of Experiment 1.

EXPERIMENT 3

The differences between Equations 1b and 2b are not limited to cases in which punishment frequency is varied. Additional sets of contrasting predictions arise under circumstances in which punishment frequency is held constant but reinforcement frequency is increased. Two such cases are described below.

Case 1: $r_1 > r_2$; $p_1 < p_2$.

Set $r_1 = 2r_2$ and $p_2 = 2p_1$. Holding constant the conditions of punishment, increase r_1 and r_2 by the same factor (k). Assuming Equation 1a to be correct, the directional derivative of the relative response rate function is of the form (see Appendix):

$$\frac{5cp_1n(p_1 - r_1)}{(5r_1 - 5p_1)^2}, \tag{10}$$

where all variables are as defined previously, and n is a positive constant analogous to h in Equations 6 and 7. By fixing the initial values $r_1 > p_1$, Equation 10 can be seen to be negative. This implies that preference for alternative 1 will diminish as the absolute frequencies of reinforcement are increased by a constant factor.

Assuming Equation 2a to be correct, the directional derivative is of the form:

$$\frac{r_1p_1n(5c - 3n) + 4p_1^2cn}{(5r_1 - 5p_1)^2}. \tag{11}$$

Under the same experimental conditions (i.e., initial values $r_1 > p_1$) outlined above, this equation is positive, since $3nr_1p < 4p_1^2cn$. This outcome implies that preference for alternative 1 will increase as the absolute frequencies of reinforcement are increased by a constant factor.

Case 2: $r_1 > r_2$; $p_1 > p_2$.

For example, set $r_1 = 2r_2$ and $p_1 = 2p_2$. Holding constant the conditions of punish-

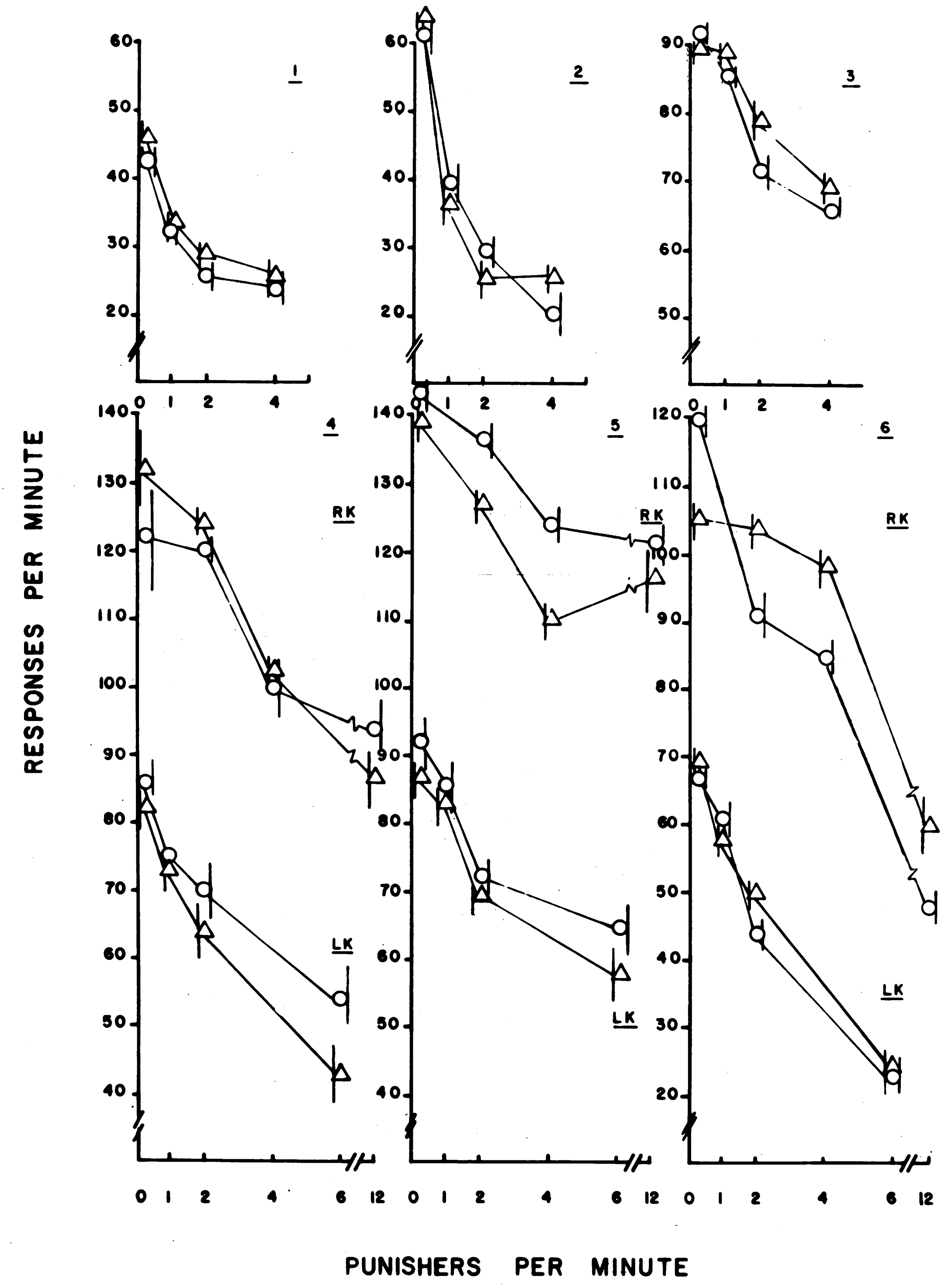

Fig. 2. Absolute rates of key pecking to the left and right keys plotted as functions of the frequency of punishment for each. Each point represents an average obtained from the last three days of training in each condition. For Birds 1, 2, and 3, the results for left and right keys have been combined. Vertical lines denote standard deviations. Circles represent data obtained from ascending series of punishment conditions in which punishment frequencies were increased; triangles represent data from descending series of punishment conditions.

ment, increase r_1 and r_2 by a constant factor. Assuming Equation 1a to be correct, the directional derivative of the relative response rate function is:

$$\frac{8cp_1n(p_1 - r_1)}{(3r_1 - 3p_1)^2}. \tag{12}$$

When $r_1 > p_1$, this expression is negative. When $r_1 < p_1$, this expression is positive.

Assuming Equation 2a to be correct, the derivative is:

$$\frac{3r_1p_1kn + 5r_1p_1cn + 4cp_1^2n}{(3r_1 + 3p_1)^2}. \tag{13}$$

This expression is always positive.

Equations 10 and 12 and Equations 11 and 13 make opposite predictions when $r_1 > p_1$. Equations 10 and 12 predict that preference for alternative 1 will diminish when the absolute frequencies of reinforcement are increased. Equations 11 and 13 predict that preference will increase. These predictions were examined in Experiment 3.

METHOD

Subjects

Five adult male White Carneaux pigeons were maintained at 75% of their free-feeding weights. Birds 1, 2, and 3 had served in Experiment 2; Birds 4 and 5 also had extensive previous training in a variety of experiments.

Apparatus

The same as in previous experiments. Punishers were accompanied by distinct visual cues, correlated with the key to which the punished response had occurred.

Procedure

Birds 1, 2, and 4 were exposed to three concurrent schedule combinations in which the frequency of reinforcement associated with the left key (red) was twice as great as that associated with the right (green). The schedules associated with the left key were VI 1-min, VI 30-sec, or VI 15-sec in various conditions (see Table 3). The schedules associated with the right key in these same conditions were VI 2-min, VI 1-min, or VI 30-sec, respectively. The frequency of punishment associated with the left key (VI 4-min) was one half that associated with the right key (VI 2-min) in all conditions.

Birds 3 and 5 were also exposed to three concurrent schedule combinations. The association of reinforcement schedules with left and right keys was identical to that for the previous three subjects. The schedules of punishment were reversed, however.

Punishment intensity was 8 ma in all conditions for all subjects, with the exception of Bird 4 for which it was 6 ma. A 3-sec COD was in effect for all conditions. The same stability criterion used in previous experiments was used here. The number of sessions in each condition and the sequence of training for each subject are described in Table 3. Daily sessions were 1 hr in duration and were conducted six or seven times a week.

RESULTS AND DISCUSSION

Figure 3 presents the relative response rate to the denser reinforcement alternative (left key) in all conditions for each bird. Each choice proportion represents the average obtained from the last three days of training in a given condition.

The pattern of data for Birds 1, 2, and 4 clearly indicates that preference for the more frequent reinforcement schedule diminished when the absolute frequencies of reinforcement were increased, despite a constant relative rate of reinforcement. For Birds 3 and 5, the pattern is much the same, although for these subjects the alternative associated with the more frequent reinforcement schedule was also associated with the more frequent punishment schedule. This pattern of results is entirely consistent with Equation 1a but contradicts the prediction of Equation 2a that relative rates should increase. Table 3 indicates that obtained reinforcement rates closely approximated programmed rates.

There are, however, two ambiguities about the interpretation of the results from Experiment 3 which preclude acceptance of these data as unequivocal support for the simple subtractive integration rule. The first concerns the failure of Birds 1, 2, and 4 to exhibit the patterns of strict overmatching which were observed in Experiment 1. Although all three subjects exhibited less extreme preferences as the absolute frequencies of reinforcement were increased, none exhibited left-key choice proportions greater than .67, as required by Equations 1a. It is appropriate to note, however, that a pattern of undermatching appears to be the rule rather than the exception in the matching literature where no punishment is

Table 3

Description of training conditions and results of Experiment 3. For each subject the order of training conditions and the number of sessions conducted in each (parenthetical numbers) are given. Absolute response, reinforcement, and punishment rates for each alternative also appear. All values are averages from the last three training sessions in a given condition.

Experimental Conditions											
LK		*RK*			*LK*				*RK*		
Reinf.	*Pun.*	*Reinf.*	*Pun.*	*Order*	*R/min*	*S^R/min*	*Pun/min*	*Choice*	*R/min*	*S^R/min*	*Pun/min*
Bird 1											
VI 1-min	VI 4-min	VI 2-min	VI 2-min	1(9)	30.1	1.03	.23	.63	17.2	.47	.48
VI 30-sec	VI 4-min	VI 1-min	VI 2-min	2(10)	36.3	1.96	.27	.60	25.9	1.01	.48
VI 15-sec	VI 4-min	VI 30-sec	VI 2-min	3(8)	47.9	3.94	.27	.56	37.3	1.99	.53
Bird 2											
VI 1-min	VI 4-min	VI 2-min	VI 2-min	1(11)	47.1	.97	.25	.67	23.1	.52	.52
VI 30-sec	VI 4-min	VI 1-min	VI 2-min	2(9)	64.7	2.05	.23	.65	42.3	.96	.50
VI 15-sec	VI 4-min	VI 30-sec	VI 2-min	3(9)	67.0	4.10	.26	.55	53.5	1.97	.49
Bird 4											
VI 1-min	VI 4-min	VI 2-min	VI 2-min	3(8)	27.8	.95	.24	.64	15.1	.48	.47
VI 30-sec	VI 4-min	VI 1-min	VI 2-min	2(10)	36.5	1.95	.28	.62	21.7	1.03	.50
VI 15-sec	VI 4-min	VI 30-sec	VI 2-min	1(13)	37.3	3.97	.27	.56	29.1	1.96	.50
Bird 3											
VI 1-min	VI 2-min	VI 2-min	VI 4-min	1(13)	67.2	.96	.47	.60	43.0	.53	.25
VI 30-sec	VI 2-min	VI 1-min	VI 4-min	2(8)	79.3	1.91	.51	.60	51.3	1.05	.22
VI 15-sec	VI 2-min	VI 30-sec	VI 4-min	3(8)	82.3	3.93	.53	.55	67.9	1.94	.27
Bird 5											
VI 1-min	VI 2-min	VI 2-min	VI 4-min	1(11)	31.3	1.03	.45	.53	27.0	.50	.25
VI 30-sec	VI 2-min	VI 1-min	VI 4-min	2(10)	39.3	1.93	.51	.53	34.0	1.02	.21
VI 15-sec	VI 2-min	VI 30-sec	VI 4-min	3(7)	38.6	4.01	.48	.50	38.1	1.93	.24

involved (Myers & Myers, 1977). These birds may, therefore, be quite typical in this regard. It is unfortunate that I failed to conduct a no-punishment baseline condition in Experiment 3 inasmuch as doing so would have indicated the extent of undermatching in the absence of punishment. Nevertheless, the clear tendency for preference for the denser reinforcement schedule to diminish when the absolute frequencies of reinforcement are increased stands in support of Equation 1a. Even here, though, it is uncertain how necessary the presence of punishment is for obtaining the pattern of results observed here. A similar "regression toward indifference" can be seen in "no-punishment" concurrent schedules, with pigeons and the keypeck response, which hold the ratio of reinforcement rates constant and increase the absolute frequencies of reinforcement (e.g., Hunter & Davison, 1978, conditions 1 and 10). However, a study by Norman and McSweeney (1978), using rats in a concurrent lever-press situation, obtained just the opposite results. This study involved a comparison of conc VI 1-min VI 2-min with conc VI 30-sec VI 1-min schedules. The authors reported greater preference for the more frequent reinforcement schedule in the latter combination of schedules. To further confuse matters, a study by McSweeney (1975), using pigeons and a treadle-press operant, involved the comparison of conc VI 2-min VI 4-min with conc VI 1-min VI 2-min. This study found a mixed pattern of results. Some subjects showed more extreme preferences in the latter combination of schedules, while some exhibited less extreme preferences. The reasons for these inconsistencies are not obvious; it is possible that undermatching would have been obtained here if punishment had been absent.

GENERAL DISCUSSION

The three experiments reported here directly pitted the predictions of Equations 1a and 1b against those of Equations 2a and 2b and obtained results which clearly support the former. The addition of punishment to both al-

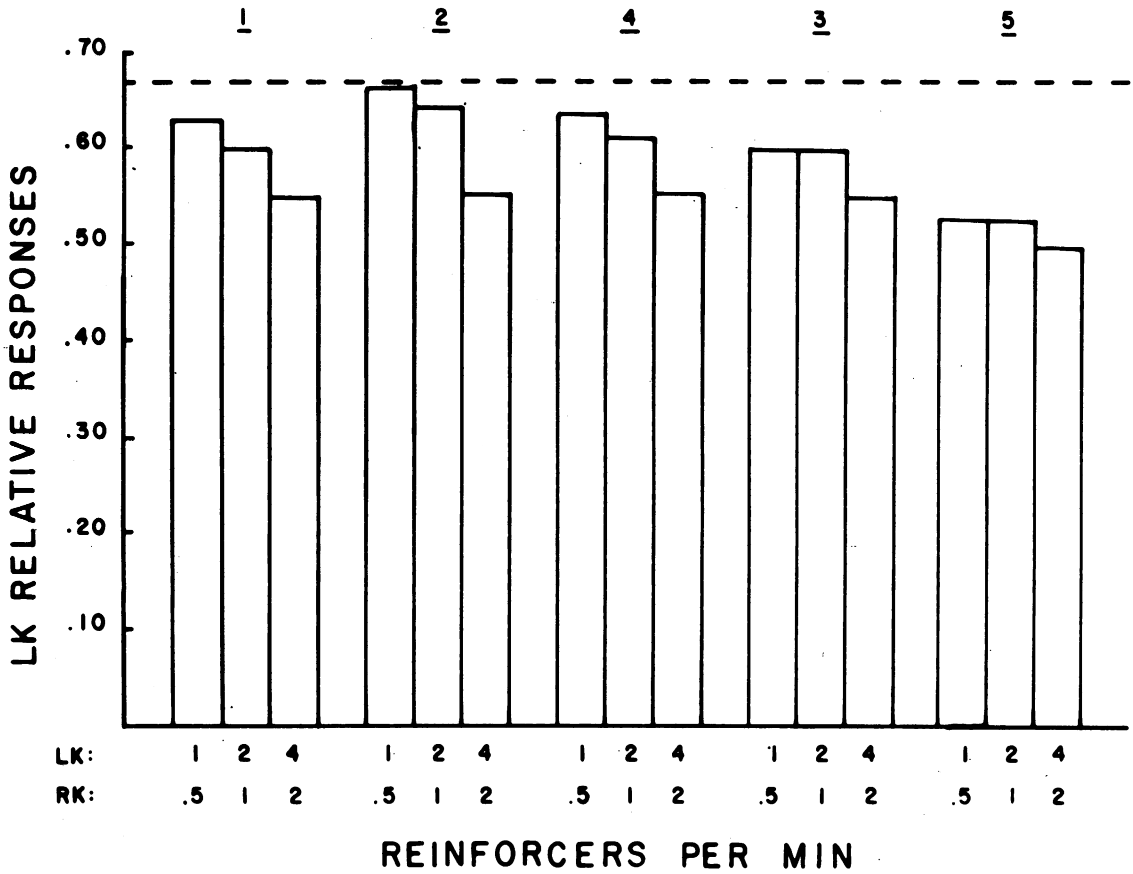

Fig. 3. Relative rate of keypecking to the left key plotted as a function of the absolute frequencies of reinforcement associated with left and right response keys. The ratio of reinforcement rates was constant in all conditions. Each bar represents the average choice proportion obtained from the last three training days in each condition.

ternatives of a concurrent schedule was found, in Experiment 1, to produce the enhancement of preference for the more frequent reinforcement schedule predicted by Equation 1a. Experiment 2 determined that absolute response rates to both alternatives of concurrent reinforcement and punishment schedules diminished when punishment frequencies were increased. This is consistent with Equations 1a and 1b, but not Equations 2a and 2b. Finally, Experiment 3 showed that increased absolute frequencies of reinforcement were accompanied by decreases in preference for the more frequent reinforcement schedule in a concurrent schedule involving a constant ratio of reinforcement schedules and constant punishment conditions.

Although Equations 1a and 1b are certainly preferable to Equations 2a and 2b, is there any additional current formulation which can do as well as, perhaps better than, Equations 1a and 1b? Consider the description of punishment's effects suggested by Bradshaw, Szabadi, and Bevan (1977). On the basis of single response studies with punishment in humans, these authors suggested that punishment acts to reduce K and to increase r_0. Although this suggestion has not yet been formalized in terms of specific rules describing changes in r_0 and/or K as functions of punishment parameters, at least one serious problem can be anticipated. Since neither r_0 nor K appear in the matching relation for choice behavior, it is difficult to see how punishment could ever fail to produce matching. It could, of course, be argued that r_0 is differentially altered, depending on which alternative an organism happened to be responding to. The respective denominators of the equations relating absolute response rates to reinforcement rates (e.g., Equations 1b and 2b) would then be different, and fail to cancel in the derivation of the relation for relative response rates. In this way, a role for r_0—and hence punishment—might be retained. Just what the consequences are of assuming that r_0 can vary across alternatives is difficult to ascertain. At the very least, it complicates the conceptual simplicity of the matching relation as well as the somewhat plausible interpretation which r_0 now has.

A curious parallel between traditional "negative law of effect" vs. "competing response" accounts of response suppression, and the algebraic differences between Equations 1a and 1b and Equations 2a and 2b should be noted. Each of these traditional classes of approach has engendered a variety of distinct accounts (see Mackintosh, 1974, chap. 6, for a thorough discussion), but the essential difference between the two approaches seems to be whether the response suppression occasioned by punishment is best conceptualized as a primary, direct effect of the response-punisher contingency or as an indirect result of an increase in the probability of alternative incompatible responses. Two different views of the behavioral processes responsible for these incompatible responses have been offered. The first stresses an elicitation process (e.g., Bolles, 1967; Guthrie, 1935). The second emphasizes implicit reinforcement of "avoidance" responses (e.g., Dinsmoor, 1977; Solomon, 1964). I suggest that, within the context of the matching relation, the subtractive model of punishment (Equations 1a, 1b, and 1c) is little more than a quantitative and explicit restatement of older "negative law of effect" views, devoid of irrelevant speculation about the weakening of S-R connections (Thorndike, 1913). Response suppression occurs in this model because of a direct decrease in the absolute reinforcement value which sustains the punished response. I also think that Equations 2a, 2b, and 2c are at least one way of formalizing a "competing response" account of punished-response suppression; suppression in this account derives from an increase in the absolute value of the concurrently available response. The occurrence of this response, by definition, is incompatible with the occurrence of the punished response.

A reconsideration of the differences by which response suppression and punishment contrast are inextricably intertwined in Equations 1a and 1c and Equations 2a and 2c highlights this point. Consider a two-alternative concurrent schedule with equal reinforcement conditions but punishment of R_1 only (i.e., $r_1 = r_2$, $p_1 \neq 0$, $p_2 = 0$). Both Equations 1a and 2a predict R_1 decreases and R_2 increases relative to a no-punishment case ($p_1 = p_2 = 0$). Equation 1a requires R_1 to decrease because the absolute value of alternative 1 (the numerator) has decreased proportionally greater than the total reinforcement context (denominator); Equation 2a predicts that R_1 decreases because the total reinforcement context (denominator) has increased in value. More specifically, it is the contribution of the absolute value of alternative 2 ($r_2 + cp_1$) which is responsible. Conversely, R_2 increases occur in Equation 1c because of a decrease in the denominator; specifically, that portion which represents the absolute value of alternative 1 ($r_1 - cp_1$). R_2 increases occur in Equation 2c because of an increase in the numerator, the absolute value of alternative 2 ($r_2 + cp_1$).

It is also interesting to consider the Bradshaw, Szabadi, and Bevan (1977) model from this perspective. Since punishment is viewed as diminishing K and increasing r_0, this model would appear to view response suppression as accompanied by both a change in response topography and an increase in alternative sources of reinforcement not under direct experimental control (if Herrnstein's 1974 interpretation of K and r_0 is accepted). This model, therefore, is exceedingly similar to the elicited "competing response" views inasmuch as the class of activities (R_0) sustained by r_0 are viewed as qualitatively distinct from the punished response and are selectively increased by punishment. The success of Equations 1a, 1b, and 1c argues for a conceptualization of response suppression and punishment contrast in terms of a direct decrease in the absolute and relative value of the punishment alternative and an indirect increase in the relative value of alternative 2, respectively.

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APPENDIX

Let $f(r_1, r_2, p_1, p_2, r_0)$ be a function—call it R_1—which describes the absolute response rate to alternative 1 when variables r_1, r_2, p_1, p_2, and r_0 are assigned any particular set of initial values. Let *a, b, e, g,* and *d* represent those initial values. Let vector *P* describe a unit vector which represent the direction of change in any, or all, of the variables appearing in R_1 under some anticipated set of experimental conditions. Evaluation of the following expression allows a determination of whether:

$$Dp \cdot f(a,b,e,g,d) = \text{grad}\, f(a,b,e,g,d) \cdot \text{P} \qquad (14)$$

R_1 is increasing, decreasing, or constant under the anticipated changes in $r_1, r_2 \ldots r_0$. Expression 14 may be paraphrased as follows. It describes the rate of change of R_1 at (a,b,e,g,d), in the direction of the vector *P* (in symbols, this rate of change is: $D_p \cdot f(a,b,e,g,d)$.

The grad R_1 is given by (see any text on multivariable calculus, e.g., Rodin, 1970):

$$\left[\frac{\partial f}{\partial r_1}(I),\ \frac{\partial f}{\partial r_2}(I),\ \frac{\partial f}{\partial p_1}(I),\ \frac{\partial f}{\partial p_2}(I),\ \frac{\partial f}{\partial r_0}(I),\right]. \qquad (15)$$

Here,

$$\frac{\partial f}{\partial r_1}, \frac{\partial f}{\partial r_2} \cdots \frac{\partial f}{\partial r_0}$$

represent the partial derivatives of function *f*, with respect to the variable appearing in the denominator. The vector *I* describes the initial starting values of $r_1, r_2 \ldots r_0$ $[I = (a,b,e,g,d)]$.

Assuming Equation 1a to be true, grad $f(a,b,e,g,d) =$

$$P \cdot \left[\frac{(b - cg + d)}{(a - cb + e - cg + d)^2}, \frac{-(a - ce)}{(a - cb + e - cg + d)^2}, \frac{-c(b - cg + d)}{(a - cb + e - cg + d)^2}, \frac{c(a - ce)}{(a - cb + e - cg + d)^2}, \frac{-(a - ce)}{(a - cb + e - cg + d)^2} \right] \tag{16}$$

Assuming Equation 2a to be true, grad $f(a,b,e,g,d) =$

$$P \cdot \left[\frac{(b + ce + d)}{(a + cb + e + cg + d)^2}, \frac{-(a + cg)}{(a + cb + e + cg + d)^2}, \frac{c(a + cg)}{(a + cb + e + cg + d)^2}, \frac{c(b + ce + d)}{(a + cb + e + cg + d)^2}, \frac{-(a + cg)}{(a + cb + e + cg + d)^2} \right] \tag{17}$$

In Experiment 2, Case 1, initial conditions are: $r_1 = r_2$ $(a = b)$, $p_1 = p_2 = 0$ $(e = g = 0)$, and $r_0 = d$ (unknown). Therefore, $I = (a,a,o,o,d)$. Under the anticipated experimental conditions r_1, r_2, and r_0 are unchanged; p_1 and p_2 are introduced, then increased in frequency. Therefore, $P = (ah, ah, keh, keh, dh)$; where $h = 1/(a^2 + a^2 + e^2 + e^2 + d^2)^{1/2}$.

The solution of Expression 16 is, therefore:

$$\frac{-cedkh}{(2a + d)^2} = \frac{-cp_1r_0kh}{(2r_1 + r_0)^2}. \tag{18}$$

The solution of Expression 17 is:

$$\frac{-cedkh}{(2a + \mathrm{d})^2} = \frac{cp_1r_0kh}{(2r_1 + r_0)^2}. \tag{19}$$

In Experiment 2, Case 2, initial conditions are: $2r_1 = r_2$ $(b = 2a)$, $p_1 = p_2 = 0$ $(e = g = 0)$, $r_0 = d$. Therefore, $I = (a,2a,o,o,d)$. Under the anticipated experimental conditions r_1, r_2, and r_0 are unchanged; p_1 and p_2 are initially introduced with unequal frequencies $(p_2 = 2p_1)$ and thereafter increased by a constant factor (m). Therefore, $P = (aj,2aj,mej,2mej,dj)$; where $j = 1/(a^2 + (2a)^2 + e^2 + (2e)^2 + d^2)^{1/2}$.

The solution of Expression 16 is, therefore:

$$\frac{ad(j - 1) - ecdmj}{(3a + d)^2} = \frac{r_1r_0(j - 1) - cp_1r_0mj}{(3r_1 + r_0)^2}. \tag{20}$$

The solution of Expression 17 is, therefore:

$$\frac{ecmj(3a + 2d)}{(3a + d)^2} = \frac{cp_1mj(3r_1 + 2r_0)}{(3r_1 + r_0)^2}. \tag{21}$$

A similar analysis applies for relative response rate functions (hereafter termed R_1'). Assuming Equation 1b to be correct:
grad $f(a,b,e,g) =$

$$P \cdot \left[\frac{r_2 - cp_2}{(r_1 - cp_1 + r_2 - cp_2)^2}, \frac{-(r_1 - cp_1)}{(r_1 - cp_1 + r_2 - cp_2)^2}, \frac{-c(r_1 - cp_1 + r_2 - cp_2)}{(r_1 - cp_1 + r_2 - cp_2)^2}, \frac{-c(r_1 - cp_1)}{(r_1 - cp_1 + r_2 - cp_2)^2} \right] \tag{22}$$

Assuming 2b to be correct:
grad $f(a,b,e,g) =$

$$P \cdot \left[\frac{(r_2 + cp_1)}{(r_1 + cp_1 + r_2 + cp_2)^2}, \frac{-(r_1 + cp_2)}{(r_1 + cp_1 + r_2 + cp_2)^2}, \frac{c(r_1 + cp_2)}{(r_1 + cp_1 + r_2 + cp_2)^2}, \frac{c(r_2 + cp_1)}{(r_1 + cp_1 + r_2 + cp_2)^2} \right] \tag{23}$$

In Experiment 3, Case 1, initial conditions are $r_2 = 2r_1$ $(b = 2a)$, and $p_2 = 2p_1$ $(g = 2e)$. Therefore, $I = (a,2a,e,2e)$. Under the anticipated experimental conditions, p_1 and p_2 are held constant, while r_1 and r_2 are increased by a constant factor. Therefore, $P = (akn, 2akn, en, 2en)$ where $n = 1/(5a^2 + 5e^2)^{1/2}$.

The solution of Expression 22 is:

$$\frac{5ecn(e - a)}{(5a - 5e)^2} = \frac{5cp_1n(p_1 - r_1)}{(5r_1 - 5p_1)^2}. \tag{24}$$

The solution of Expression 23 is:

$$\frac{aek(5c - 3n) + 4e^2cn}{(5a + 5e)^2} = \frac{r_1p_1k(5c - 3n) + 4p_1^2cn}{(5r_1 + 5p_1)^2}. \tag{25}$$

In Experiment 3, Case 2, the initial conditions are: $r_2 = 2r_1$, $p_1 = 2p_2$. Therefore, $I = (a,2a,2e,e)$ and $P = (akn,2akn,2en,en)$. The solutions, assuming Equations 1b and 2b to be correct, are:

$$\frac{8ecn(e - a)}{(3a - 3e)^2} = \frac{8cp_1n(p_1 - r_1)}{(3r_1 - 3p_1)^2}, \tag{26}$$

and

$$\frac{3aekn + 5aecn + 4e^2cn}{(3a + 3b)^2} = \frac{3r_1p_1kn + 5r_1p_1cn + 4cp_1^2n}{(3r_1 + 3p_1)^2}, \tag{27}$$

respectively.