On the Temporal Control of Behavior

Peter Killeen
Arizona State University

A series of experiments ranging over a number of animal species, several classes of behavior, and a variety of experimental conditions provided the foundation for a mathematical model of the temporal control of behavior. The initial research explored the general activity of pigeons during the interval between food deliveries; most of the variance in that data was accounted for by the algebraic sum of two exponential functions. Parameters of the model were interpreted as indices of arousal level and inhibitory processes which detracted from that level. The parameters changed in ways appropriate to those interpretations when behavior was modified by the action of various drugs, reinforcement contingencies, and competing behaviors. The model was mapped onto a series-latency mechanism and extended to account for various schedule-induced, operant, and respondent behaviors.

Perhaps the most basic control procedure in the study of conditioning is the periodic presentation of the reinforcer—or unconditioned stimulus—independent of the organism's behavior and in the absence of any associated stimulus change. Such procedures have given rise to a number of theoretically important discoveries. Pavlov (1960) found conditioning to occur readily under such circumstances and called the process temporal conditioning because of the inferred temporal conditioned stimulus. Skinner (1948) found that walking and other gross movements increased in frequency under such circumstances. He called the process superstitious conditioning, citing the fortuitous contiguity between various responses and the periodic reinforcer. Campbell and Sheffield (1953) employed the paradigm to study the increase in spontaneous activity that was said

to occur with deprivation. They found that the increased activity of rats actually reflected a hyper-reactivity to normal stimuli; the effect of hunger "is to augment the normal activity responses to novel stimuli and to greatly augment the activity to stimuli associated with the performance of the consummatory response" (Sheffield & Campbell, 1954, p. 99). Amsel and Work (1961), Slivka and Bitterman (1966), and Zamble (1967) have also shown that the presentation of stimuli that have been paired with a reinforcer increases general activity. Such studies have contributed impetus to the recent movement away from drive-reduction theories and toward incentive-motivation accounts of behavior (cf. Bindra, 1970; Bolles, 1967; Cofer & Appley, 1967). Recent studies of autoshaping (e.g., Brown & Jenkins, 1968) are the logical extensions of this line of enquiry.

Not all activity during periodic feeding schedules is associated with stimuli occurring prior to reinforcement; hyperreactivity to stimuli occurring after reinforcement has

also been observed. "Schedule-induced" polydipsia, wheel running, gnawing, aggression, and pica (Falk, 1972; Segal, 1972) exemplify this type of "adjunctive" activity. Staddon and Simmelhag (1971) have also reported unreinforced sequences of behavior recurring throughout the interval between feedings.

Activity has been variously taken as an *integral part* of the normal conditioning process (Sheffield, 1966), as an *adventitious by-product* of conditioning by contiguity (Skinner, 1948), as a sign of *frustration* (cf. Scull, 1973), and as an *adjunctive* behavior induced by a schedule of reinforcement (Levitsky & Collier, 1968). Most of these evaluations have been made within the context of one or another theoretical paradigm; few have incorporated extensive parametric measurements of activity; none have adduced an adequate quantitative description of the course of activity over time. The following experiments demonstrate that an increase in activity level is as fundamental a consequence of reward as is the acquisition of learned responses; that activation is not reducible to the law of effect; and that activity increases to a maximum soon after a signal of impending reward and then decreases as a function of interference by competing responses. These and other implications are drawn from an empirically derived model of activation. An extension of the model adequately describes the temporal course of typical operant and respondent behaviors and of schedule-induced behaviors such as polydipsia.

ACTIVITY AS A FUNCTION OF INTERFOOD INTERVAL

Experiment 1

Method. Four White Carneaux pigeons, all with previous histories of experimentation, served as subjects. The wooden experimental chamber was 46 cm wide, 31 cm deep, and 34 cm high. A feeder that dispensed *mixed grain* was *centrally located* on the widest wall, and a houselight was located directly above it near the ceiling. This chamber was placed in a sound-resistant enclosure, which itself was located in a room separate from the control and recording equipment. The floor of the chamber consisted of six movable panels, three hinged at the rear of the chamber and three hinged at the front. Microswitches under these panels

indicated when the animal moved from one part of the chamber to another or shifted its weight while staying in one part of the chamber. Each activation of a microswitch counted as a single "activity response." Data from the six switches were pooled with no account taken of where in the chamber a response occurred.

The pigeons were reduced to 80% of their free-feeding weight and exposed to various feeding schedules. On these schedules the food hopper was activated for 3 sec at various interfood intervals (25, 60, 120, 200, and 400 sec). Half of the animals experienced the intervals in an ascending series, and half in a descending series. To preclude adventitious reinforcement of pacing, food was delivered *no sooner than 5 sec after the last recorded activity in the chamber* (5-sec Differential Reinforcement of Other Behavior, or DRO). Ten daily sessions were conducted at each interfood interval. Each session lasted for 60 feedings, except at the longer intervals where sessions were terminated after 3 hours. A stepper distributed responses to one of nine counters as a function of the time since the last delivery of food.

In a second experiment (1b) four naive pigeons experienced interfood intervals of 5, 10, 15, and 30 sec, according to a Latin square design. For these animals no DRO contingency was employed.

Results

The average response rate for each animal in each condition may be found in Table 1. Figure 1 shows the rate of activity as a function of the time since the last delivery of food. The data are averages (geometric means) over four animals, averaged over the last five sessions at each condition of Experiment 1a. The abcissa has been normalized for convenience in presenting the data.

The data for the three shorter interfood intervals all show a pronounced increase in activity after feeding, an increase that is maximal one-fifth of the way through the interval. The overall rate of activity is greatest for the shortest interfood intervals and decreases monotonically with increasing interfood intervals.

Response rates were substantially higher in Experiment 1b, but the time-course of activity through the interfood interval was similar. Activity was maximal one-quarter of the way into the interval and was minimal immediately after feeding. The decrease in activity before feeding was not nearly so marked as in Experiment 1a, presumably because no DRO contingency was employed.

TABLE 1

INTERFOOD INTERVAL, RESPONSE RATE, AND
PARAMETER VALUES FOR EQUATION 1 IN
EXPERIMENTS 1a AND 1b

Interfood interval (sec)	Responses per minute	A	C	I	n[a]
Experiment 1b					
5	61.2	600	.37	.24	76
10	63.6	318	.46	.20	80
15	58.4	185	.57	.16	75
30	55.1	130	.86	.16	89
Experiment 1a					
25	21.0	134	.30	.13	24
60	15.6	47	.44	.07	18
120	10.7	32	.46	.07	12
200	7.1	10	1.63	.02	16
400	5.7	7	3.42	.00	22

[a] Number of parallel processes necessary to account for the data if they are assumed to derive from a series latency mechanism.

Discussion

A surprising amount of general activity occurred in this feeding situation despite contingencies that reinforced quiescence. Other investigators have also noted the difficulty of getting animals to stand still using food as a reward (Blough, 1958; Breland & Breland, 1966). The situation is the inverse of that dealt with by Bolles (1970b) and Keehn (1972), who noted the ease of getting rats to "freeze" in the context of occasional electric shock. Bolles proposed the existence of various "species-specific defense reactions," such as freezing, fleeing, and fighting, which were especially easy to condition with aversive stimuli. It may well be that the floor panels of the chamber used in these experiments provide a gross measure of "species-specific appetitive reactions," behaviors that are either induced by the recurring food deliveries, or are easily conditioned through adventitious pairing with food. The latter notion is suspect, however, since the 5-sec DRO was specifically designed to minimize superstitious behaviors.

It is curious that in both experiments activity decreased before the delivery of food. This decrease was arranged by the DRO contingency of the first experiment, but in Experiment 1b there was no such contingency. It is possible that the motivation

generated by food is simply exhausted by the end of the interfood interval. This is unlikely, however, for all of the curves peak at the same relative time after food delivery and fall to the same level before the next delivery. Were these changes coincident on an absolute time scale, the exhaustion of a reserve would be a plausible explanation. Their coincidence on a relative time scale denotes a greater dependence on the *schedule* of food delivery than on the aftereffect of any *single* delivery.

A more likely explanation for the decrease in activity is that competing behaviors, incompatible with general activity, are elicited by the temporal proximity of food. These activities might include consistent orientations to the front of the chamber, pecking at the front wall, and investigation of the magazine aperture. Such behaviors have been observed at the end of a free-food interval by Staddon and Simmelhag (1971), and at the end of a conditioned stimulus by Zamble and Kirkwood (1969); they would clearly
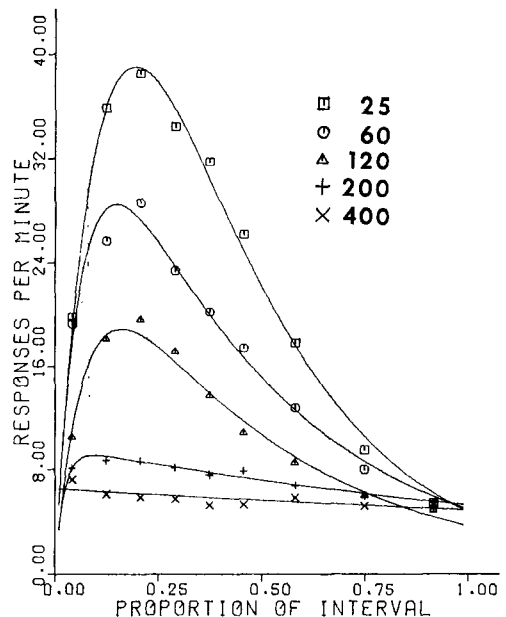

FIGURE 1. Rate of panel activation as a function of the time since reinforcement. (Interfood interval is the parameter; the abcissa is normalized to range between 0 and 1. Data, from Experiment 1a, are averages over four pigeons. The curves are derived from Equation 1.)
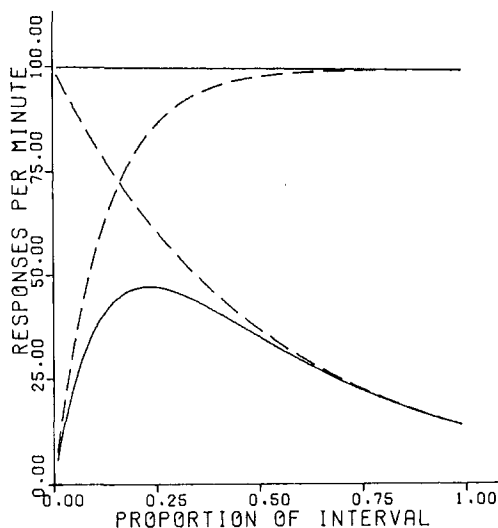
FIGURE 2. Hypothetical curves representing: A constant asymptotic rate of A responses per minute (solid horizontal line), general activity with no competing terminal behaviors (rising dashed curve, from Equation 3), terminal behaviors suffering no inhibition by reinforcement (falling dashed curve, from Equation 4), and the time course of general activity (bitonic solid line, from Equation 1).

interfere with general activity as measured in the present experiment. A more careful analysis of prefood behaviors is conducted in the second series of experiments.

A MATHEMATICAL MODEL

The theoretical curves accompanying the data are derived from the equation

$$R = A(e^{-t/C} - e^{-t/I}). \qquad [1]$$

The dependent variable, R, is rate in responses per minute, and e is the base of the natural logarithms. Values for the parameters A, C, and I, which were derived by an iterative least-squares program, may be found in Table 1. The proportion of the interfood interval measured by t ranges between 0 and 1.0. The parameter A is a scale factor, affected by the units of measurement and the sensitivity of the system. Of greater theoretical importance, A provides a measure of the maximum level of activity engendered by the feeding schedules. In the absence of competing behaviors or inhibitory stimuli, Equation 1 would predict a constant rate of A panel activations

per second (cf. top solid line, Figure 2). If from that constant rate we subtract

$$R = Ae^{-t/I}, \qquad [2]$$

we obtain

$$R = A(1 - e^{-t/I}), \qquad [3]$$

whose locus is traced by the rising dashed line in Figure 2. Parameter I governs the rate at which the response curve approaches maximum (A); the smaller I, the steeper the ascending part of the curve. Parameter I is interpreted as a measure of the inhibition of activity by food delivery which is believed due to the role of food in signaling a period during which the next food delivery is unlikely (cf. Jensen & Fallon, 1973; Siegel & Domjan, 1971; Staddon, 1974).

Consider now the equation

$$R = Ae^{-t/C}, \qquad [4]$$

which is traced as the falling dashed line in Figure 2. This curve accurately represents the right tail of the activity curve, approaching 0 as t grows large. The decrease in activity before the delivery of food (at $t = 1.0$) is presumed to be due to the presence of competing behaviors which occur toward the end of the interfood interval and which interfere with general activity. In Experiment 2, the rate of some terminal behaviors is modified directly by reinforcement, and the predicted changes in C are witnessed.

When these two basic processes are joined —the fast acting inhibition of Equation 2 being subtracted from the slower decay of general activity modeled by Equation 4— Equation 1 and its curve at the bottom of Figure 2 result. Equation 1, which was empirically derived, has close relatives in at least two other formal systems, control theory and stochastic latency models.

Control, or cybernetic, systems are those which employ some form of feedback to moderate the output of the system (cf. McFarland, 1971; Milsum, 1966). Examples range from servo-mechanisms to thermostats, and in humans include the gamma-efferent control of limb movement and the mechanisms which govern pupil aperture. Random impulses to such homeostatic systems will cause momentary disruption, followed by asymptotic return to the set-point.

One of the simplest models of this asymptotic return is provided by the exponential function. The impulse carries the system to some level A, and this is followed by a return to the reference level whose course is described by an equation such as 4. Immediately after the impulse ($t = 0$) the system is at Level A, and as t grows large the function approaches 0. The rate of return to reference level (0) is governed by C, which is called the "time-constant" of the system. When $t = C$, the system has completed 63% of its return to equilibrium.

Equation 1 models a more complicated system in which the disruption is not maximal until some time after the impulse. An analogue is found in the striking of a very elastic ball. The energy of the impulse is first absorbed in deforming the ball, and only moments later is effective in propelling the ball through space. Equation 1 represents a second-order control system with two time constants, C and I. If the restoring force, 1/C, were 0 (cf. Equation 3), the system would some to rest at Level A and would be 63% of the way to that level after a time equal to I. For Cs less than infinity, one contends with the difference between two exponential curves, one tending to carry the system asymptotically to Level A and the other tending to carry it asymptotically back to the reference level. The form of the resultant curves depends on the values of the time constants, with those found in Figure 1 being typical examples.

The reciprocal of the geometric mean of C and I defines the "resonant," or "natural" frequency (ω) of a control system. This index remained approximately constant at 5.4 in Experiment 1a and at 3.2 in Experiment 1b. The value of ω reflects the responsiveness of the system; since the obtained values are "faster" than the input frequency (i.e., the rate of feeding, here given a value of 1), the level of activity should rise to its maximum and drop back to equilibrium relatively quickly. In the normalized coordinates of Figure 1, the constancy of ω indicates that the natural frequency of the system is a linear function of the actual interfood interval —the organism "stays in-tune" with its feeding schedule. The cybernetic interpretation

of Equation 1 will be further examined later in the General Discussion section.

Equation 1 is also found in the analysis of stochastic latency mechanisms (McGill, 1963), as one instance of a "general-gamma distribution" (McGill & Gibbon, 1965). If an event such as "Response A" has a fixed probability of occurring in any small unit of time, then the probability that the response will occur by time t, $f(t)$ has a geometric distribution that is approximated by the exponential:

$$f(t) = \lambda\, e^{-\lambda t}. \qquad [5]$$

Consider now a series latency mechanism wherein the response latency has two components,

$$t = t_1 + t_2. \qquad [6]$$

The values t_1 and t_2 are random delays associated with the two components which must be completed in sequence before a response is recorded, and

$$f(t_1) = e^{-t_1/I}/I, \qquad [7]$$

$$f(t_2) = e^{-t_2/C}/C. \qquad [8]$$

Then

$$f(t) = \frac{1}{C - I}(e^{-t/C} - e^{-t/I}). \qquad [9]$$

Equation 9 resembles Equation 1, although each describes a quite different set of data— the former changes in response rate, the latter a probability density function. The curves may be made congruent by assuming that each panel activation is the outcome of a unique two-component series latency mechanism (Equation 9) and that many such mechanisms operate in parallel. The random completion of each of the two-step processes throughout the interval will result in a single measured response; the curves of Figure 1 result from the completion of many such processes. The first event in this two-step process, specified by Equation 7, need not be an observable response or any sort of response as those are normally construed. It may be conceived as the timing-out of an internal clock which signals the end of a quiescent period. There ensues a second period of time terminated by a recorded response.

One of the quick returns on an investment in stochastic latency mechanisms is an esti-

mate of the number of parallel processes necessary to account for the data. Since each process will generate a function with a coefficient of $1/(C - I)$, n processes are necessary to generate a function with a coefficient of A, where $n = A(C - I)$. Values of n are listed in Table 1. It can be seen that the estimates of n range around 80 for Experiment 1b and around 18 for Experiment 1a. Because A incorporates a scale factor, the estimates are unique up to a multiplicative constant. The estimates show no dependence on interfood interval but do show a large increase in Experiment 1b, where activity was no longer suppressed by a DRO contingency. The correlation of the hypothetical gamma processes with observed behaviors and their employment as minimal units of behavior are the types of potential benefits which might justify the assumptions of underlying series latency mechanisms.

If an additional step is added to the series latency mechanism, Equation 10 results:

$$R = N\left(\frac{Ce^{-t/C}}{(C - I)(C - B)} + \frac{Ie^{-t/I}}{(I - C)(I - B)} + \frac{Be^{-t/B}}{(B - C)(B - I)}\right). \quad [10]$$

It can be seen that as B (the time constant of the third step) approaches zero, Equation 10 reduces to Equation 9. In the system modeled by Equation 10, each recorded response is the outcome of a three-step chain. This equation is especially useful as a model for behaviors occurring during brief periods of time—interfood intervals or conditioned stimulus durations of less than 15 sec. The consumption of grain or the orientation to the conditioned stimulus may extend several seconds into the interval; where longer intervals are under consideration, the error attributable to such spillover behaviors is negligible. For shorter intervals it becomes worth incorporating an additional step (and parameter) into the model. Whereas Equation 1 accounted for 95% of the data variance of the two shortest intervals in Experiment 1b, Equation 10 accounted for over 98.5% of that variance.
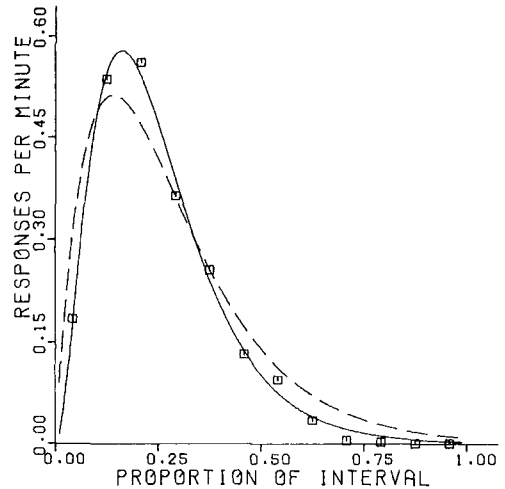

FIGURE 3. The probability of pigeons emitting some interim behavior. (Based on data from Staddon & Simmelhag, 1971; the dashed curve was derived from Equation 1, the solid curve from Equation 10.)

Additional data for which Equation 10 is a useful model were collected by Staddon and Simmelhag (1971), who monitored the activities of pigeons that were given access to grain every 12 sec. Staddon and Simmelhag dichotomized those activities into a set occurring just before food delivery ("terminal behaviors") and a set consisting of all other activities ("interim behaviors"). I have combined their data to reflect the probability that any interim behavior occurs during each second of the interval. These data are displayed in Figure 3, along with curves derived from Equation 1 (dashed) and Equation 10 (solid). Although the value of B was quite small (.05, implying that 63% of the spillover behaviors were completed within the first .6 sec), it improved the proportion of variance accounted for from .935 to .995.

As additional steps are added to the series latency mechanism, the probability density functions quickly become unmanageable. At the same time, however, those functions converge on the normal distribution:

$$R = He^{-(\frac{t-M}{S})^2}, \quad [11]$$

where M is the midpoint of the curve, S is proportional to the standard deviation (S = $\sqrt{2}\,\sigma$), and H is the height of the curve at

$t = M$.   Equation 11 will subsequently be used to describe the time course of various adjunctive and terminal behaviors.

CONCURRENT AND COMPETING OPERANT BEHAVIORS

The parameter C has been identified as descriptive of behavior occuring predominantly near the end of the interval. The smaller C, the more quickly activity subsides to near-zero levels. In the first experiment, a concurrent operant response—key pecking—is established. Insofar as this response is incompatible with general activity, a further suppression of responding should occur near the end of the interval and should be reflected in a decrease in C. In the second experiment, general activity is first suppressed with increasingly severe DRO contingencies and then is reinforced with a positive contingency between activity and feeding.

Experiment 2a

Two pigeons were trained to peck at a Gerbrands response key centrally located above the hopper in the experimental chamber, the first key peck to occur 60 sec after the last reinforcement activated the hopper for 3 sec.

The introduction of a contingency requiring a key-peck response appeared to have had little effect on the pattern of general activity, although the overall level of responding was lower than that obtained for the same animals during Experiment 1a. But examination of the parameters leads to a different conclusion. A and I did not change from control values (54 and .09) when the concurrent response was introduced,[1] but C decreased from .38 to .24. The lowering of activity level was attributable solely to a change of the parameter governing the rate of return to equilibrium.

Experiment 2b

Three naive pigeons were maintained at 80% of their free-feeding weights. Three seconds of access to grain, normally occur-

ring every 60 sec, could be delayed by panel activations occurring during the last few seconds of the interval: DRO contingencies of 0, 5, and 12 sec were employed in ascending order.

In the last condition of this experiment, the DRO was replaced with a fixed-ratio schedule. After 55 sec had elapsed, each panel activation would count toward reinforcement, which was delivered after 10 activation responses. The purpose of this scheduling was to encourage high response rates while attempting to maintain constant the interfood interval.

Results. For all conditions except fixed ratio, rate was greatest about one-fifth of the way through the interval. Overall rate of responding decreased with increases in DRO length (cf. Table 2). The presence of a DRO contingency affected the shape of the curves, but even without that contingency, activity decreased before reinforcement. The fixed-ratio contingency increased response rates, but the shape of the activity curve was not the familiar "scallop" or the "break and run" usually obtained on ratio schedules. Instead, activity was greatest about halfway through the interval and decreased slightly before reinforcement. These data are essentially identical to those collected in a pilot study with experienced subjects.

Once again the data have been fit with curves derived from Equation 1, with parameters listed in Table 2. The radical changes in terminal contingencies have no effect on I. Changes in the terminal contingencies are correlated with changes in C, which de-

TABLE 2

EXPERIMENTAL CONDITION, OBTAINED INTERFOOD INTERVAL, AND PARAMETERS OF EQUATION 1 FOR EXPERIMENT 2b

Terminal contingency	Inter-food interval (secs)	A	C	I
DRO 0	60	39.7	.87	.05
DRO 5	67	36.6	.68	.05
DRO 12	75	24.1	.52	.05
Fixed ratio 10	98	22.5	7.14	.05

Note. Abbreviation: DRO = Differential Reinforcement of Other Behavior.

---

[1] Parameters were said to remain invariant if, when left free to vary, the data variance accounted for by the model increased by less than 1%.
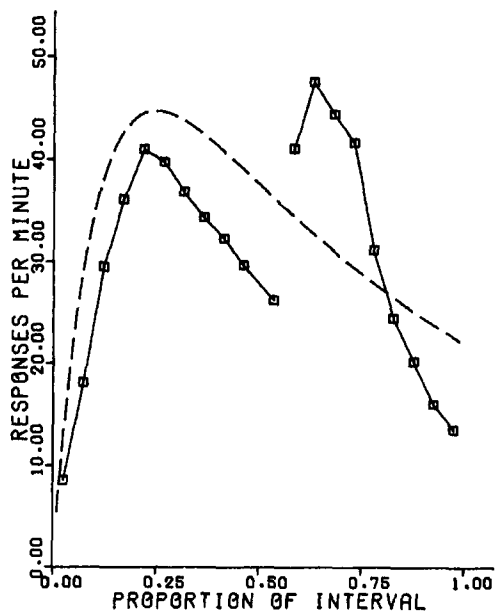
FIGURE 4. Rate of panel activation in Experiment 3a before blackout (.0 to .5) and before reinforcement (.5 to 1.0). (The dashed line represents the locus of the control data.)

creased with increasing DRO requirements, and increased markedly under the fixed-ratio contingency.

In Experiment 2a, although the level of general activity decreased upon introduction of the competing behavior, the theoretical asymptotic level of activity (A) did not change. In the present experiment, the value of A did vary with changes in the terminal contingencies, although the values were not monotonically related to the changes in terminal response rates. It is probable that changes in A were due solely to variations in the obtained interval, for imposition of the DRO contingencies decreased the rate of reinforcement (see Table 2), and a further decrease occurred when the fixed-ratio contingency was introduced.

Discussion. These experiments show that activity may be suppressed, either by the introduction of competing behaviors or by direct punishment of that activity. Equation 1 remains an appropriate model, with the effects of these manipulations primarily manifested in one parameter, C.

EFFECTS OF INTERPOLATED STIMULI

The curves in Figure 1 are reminiscent of curves drawn by Konorski (1967) to depict the "hunger drive" which occurs in anticipation of food, is suppressed during eating, and is "restored with rebound after the [eating] response is over" (p. 46). Their nature is more complex, however, than the simple model proposed by Konorski. The peak "rebound" of these curves does not bear a fixed temporal relationship to the eating response: Instead, the maximum occurs a fixed proportion of the distance until the next feeding. This anticipatory nature of the data seems to rule out a simple reflexive interpretation, such as Konorski's.

In the first series of experiments two effects of reinforcement were thoroughly confounded. The delivery of food was both the main source of energy or motivation for the subjects, and thereby undoubtedly had direct effects on their behavior, and it was also a signal with a fixed temporal relationship to the subsequent reinforcement, and thereby undoubtedly acquired incentive motivational (Bindra, 1968) or inhibitory (Staddon & Innis, 1969; Staddon, 1970) properties. In the following series of experiments additional stimuli are added in various temporal relations to reinforcement, and are found to have patent inhibitory and excitatory effects upon the course of activity.

Experiment 3a

Method. Four pigeons were exposed to a schedule of free food every 60 sec. After nine sessions, every other feeding was replaced with a 3 sec blackout of the houselight, and an additional nine sessions were conducted. Activity in the chamber had no effect on the scheduling of blackout or food.

Results. Response rates before blackout (0–50% of interval) and after blackout (50–100% of interval) are shown in Figure 4, along with the locus of response rates during the control condition (dashed line). Responding after feeding shows an increase to maximum rate about one quarter of the way through the interval, followed by a slower decrease until the blackout occurs. Activity after blackout begins substantially below the maximum postreinforcement rate, then in-

creases quite dramatically, peaking at a rate higher than that found after food, and even higher than the maximum rate during 60 sec interval pretraining of these subjects.

The present data seem consistent with studies of the "Frustration Effect" (Amsel, 1962) or of the patterning of running in studies of alternate reinforcement in straight alleys (Capaldi, 1966, 1970). In both cases, running speed is greater on the trials after nonreinforcement than after reinforcement. Indeed, the present curves might easily be taken for running-speed data, for they show the characteristic acceleration and deceleration associated with the movement of a rat in the confines of an alley (Amsel, 1972).

The decrease in rate before reinforcement is similar to that found in all of the experiments reported thus far, and, as in those cases, is most likely due to terminal behaviors such as "hopper-tending" that are elicited by the temporal proximity to reinforcement. The decrease in rate before blackout is a more curious affair. Blackout will occur no matter where the animal is in the chamber, and there are no behaviors which might possibly increase the value of that stimulus change, as hopper-tending might increase the amount of food the animals can obtain. Since pigeons tend to "roost" in the dark, it is possible that roosting behavior was conditioned to occur during the preblackout period. A more likely explanation is that the two intervals were confused by the pigeons, and the prereinforcement behaviors generalized to the preblackout period. These hypotheses are examined in the following two experiments.

Experiment 3b

The decrease in responding before blackout in Experiment 3a might have been due to the generalization of prereinforcement behaviors into the preblackout period. To test this possibility, the two periods were made quite discriminable: the houselight was turned off after 60 sec had elapsed since reinforcement and was left off until the end of the next reinforcement. Thus, during the first half of the 120-sec interfood interval the chamber was normally illuminated, and during the second half it was blacked out. The
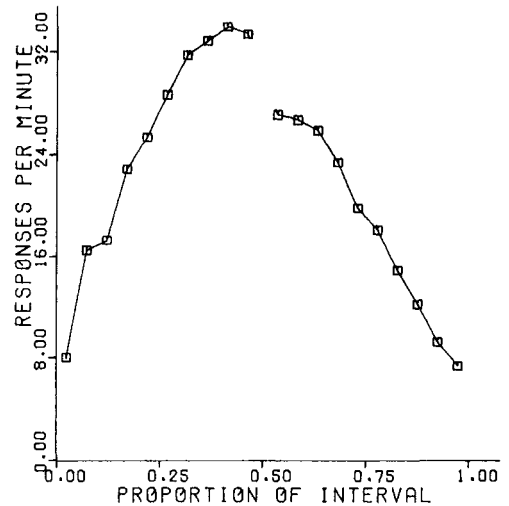

FIGURE 5. Rate of panel activation in Experiment 3b before blackout (.0 to .5) and during blackout (.5 to 1.0).

subjects and apparatus were the same as in the previous experiment.

Results. Figure 5 shows that the clear differentiation of the intervals eliminated the downturn in the postreinforcement activity curve: The animals increased their activity up until the blackout (at 50% of the interval) and then decreased it until the delivery of reinforcement. Note furthermore that the pigeons were not stationary during the blackout, and that this much longer blackout did not elicit preblackout quiescence.

Experiment 3c

In the preceding experiments, blackouts interpolated within the interfood interval appeared to have various facilitative and inhibitory effects on the behaviors preceding and following them. Some of the effects were demonstrated to due to trace-discriminative control or to the generalization of prereinforcement behaviors to the prestimulus period. Whereas there appeared to be an abundance of general activity in these experiments and a facilitation of activity by an interpolated blackout (in Experiment 3a), general activity has always decreased before food delivery. This seems inconsistent with observations that

incentive-motivational stimuli are sufficient to increase general activity . . . [this] activity has all

the marks of anticipatory excitement, such as that seen during classical appetitive conditioning . . . and that described by ethologists as 'appetitive behaviors'. (Bindra, 1968, pp. 3–4)

The present experiment was conducted in an attempt to more clearly demonstrate "anticipatory excitement." A flickering houselight was used to signal the imminent delivery of food. This stimulus was less likely to elicit roosting, was long enough to permit a measure of activity during its occurrence, and was more closely associated with food delivery than were any of the stimuli used in the preceding experiments.

Method. Two of the pigeons from the previous experiments were given 3-sec access to mixed grain every 60 sec. After seven sessions of these control conditions, the basic feeding schedule was continued for an additional seven sessions, but during the last 12 sec of each interval the houselight was pulsed at a rate of 10 Hz.

Results and discussion. Figure 6 shows the experimental (squares and solid line) and control (circles and dashed line) data. The 12-sec conditioned stimulus inhibited activity immediately before reinforcement, but released from inhibition behaviors occurring
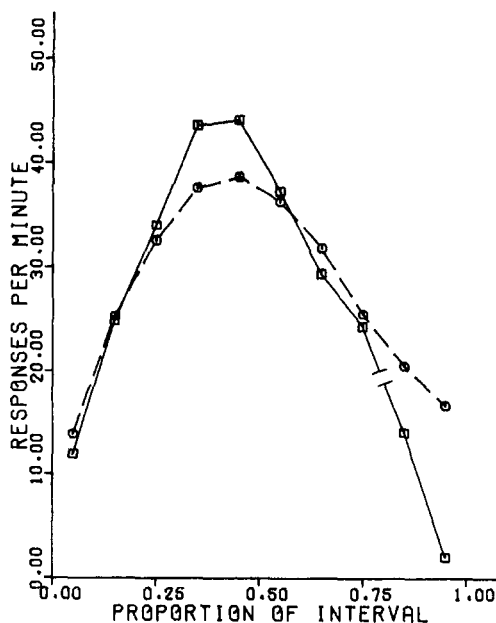

FIGURE 6. Rate of panel activation in Experiment 3c under control conditions (dashed line) and experimental conditions (solid line). The CS began at 0.8.

earlier in the interval. These somewhat paradoxical effects may be understood in terms formulated by Staddon and Simmelhag (1971) in their analysis of "superstitious" behaviors.

Staddon and Simmelhag monitored the behavior of pigeons who were given 3-sec access to food every 22 sec (cf. Experiment 1b of this review). They noted many forms of activity during the interfood interval, some of which followed time courses similar to those found in the present experiment and some of which started later in the interval and increased in rate as the moment of reinforcement neared. The former behavior they termed "interim" responses, the latter "terminal" responses. Staddon and Simmelhag suggested that interim behaviors reflect a set of general activities instigated directly by reward. It is from this set of activities that a few appropriate behavior patterns may later be selected, via a mechanism such as the law of effect. Reinforcement thus has two aspects, "variation"—the generation of diffuse and generalized interim activities—and "selection"—the strengthening of particular behaviors selected by contiguity to reinforcement. Staddon and Simmelhag's analysis and evolutionary model are fundamental to the behavior studied in this article. An analogue may be drawn between the rise of interim behaviors and the parameter I and between their displacement by terminal behaviors and the parameter C.

What terminal behaviors might be expected of a pigeon? Pecking, hopper observation, and other behaviors that have either an innate or learned association with the delivery of food. These behaviors all leave the animal standing in one spot and therefore compete with the explicit dependent variable in the present experiments, general activity. In Experiment 3c, the conditioned stimulus was a less ambiguous predictor of the imminence of reinforcement than whatever temporal cues might have been available to the pigeons, and thus elicited, or was an S^D for, terminal activity. At the same time, the absence of the conditioned stimulus became a predictor of nonreinforcement, and by inhibiting terminal behaviors, it disinhibited interim activity. This

analysis is not inconsistent with Bindra's (1968) theory of incentive-motivation. The terminal behaviors of dogs and rats, Bindra's reference subjects (Bindra & Palfai, 1967; Zener, 1937), were likely to be vigorous coursing or foraging responses that would contribute to measures of general activity. These and subsequent experiments lend confirmation to Bindra's later (1970, 1972) development of incentive-motivation theory.

General activity thus appears too gross a measure to be useful in comparing levels of motivation across species. Indeed, it will not do even for a single species: Levels of activity immediately before reinforcement in Experiment 1a were the same for the 400-sec and 25-sec conditions, but, by most accounts, animals in the former condition would be judged as more highly aroused. This presumed higher level of arousal is reflected in a greater value of A for the shorter interval. Furthermore, while there was little difference in response rates on the 5-, 10-, and 15-sec schedules of Experiment 1b, A continued to show a proportional increase with increases in rate of feeding (A = 3,000/T, where T is the interfood interval), and so provides an index of "arousal" that is unbiased by "ceiling effects" on obtained response rates. It is possible, therefore, that the theoretical asymptote for activity, A, will provide a useful reification of the construct arousal within a species, and, with recalibration, may be of value in cross-species comparisons.

Experiment 3d

By providing a more accurate temporal reference point, signals of forthcoming reinforcement conduce a more intense surge of either interim or terminal behaviors. In Experiment 3a, the blackout permitted a brief disinhibition of activity followed by a more intense suppression. In Experiment 3c, the effects were primarily inhibitory, though a finer analysis of behavior during the first few seconds of the condition stimulus might have uncovered some excitation. This last effect is somewhat curious, since in Experiment 1b, intervals of 5 and 10 sec showed marked patterns of excitation. Judging from those conditions, there was ample time for the

animals to move about the box during the 12-sec conditioned stimulus (CS) in Experiment 3c. Was inhibition predominant in this experiment because the animals had already had an opportunity, during the pre-CS period, to "displace" their energies? Or is the important variable in determining the predominance of interim or terminal behaviors the relative, rather than the absolute, proximity to reinforcement (cf. Jenkins, 1970; Staddon, 1972)? In Experiment 1 the relative proximity of the signal (reinforcement) to reinforcement was zero. Reinforcement was the event most distant from the next reinforcement and thus inhibited the occurrence of both interim and terminal behaviors. In Experiment 3a the relative proximity of the signal (blackout) was .5, and both interim and terminal behaviors were intensified. In Experiment 3c, relative proximity was .8, and only terminal behaviors were observed. In the following experiment, the relative proximity will be set at .8, but the interval will be lengthened to 300 sec. Will a signal with the same relative proximity to reward, but with a much smaller absolute proximity, still incite only terminal behaviors?

Method. The subjects had served in Experiment 1b. Food delivery was scheduled to occur every 300 sec and was independent of the behavior of the pigeons. The houselight was on and was constant until 60 sec before food delivery, at which time it was pulsed at a frequency of 10 Hz. After 10 sessions, 10 control sessions were conducted in which food was delivered every 60 sec with the houselight constantly on. Finally, 10 additional sessions were conducted during which the houselight was off until 60 sec before food delivery and then was turned on and pulsed.

Results and discussion. In Experiment 3c, the houselight was pulsed during the last 20% of the interval and during that time general activity was minimal. In the present experiment the houselight was on during the last 20% of the interval, during which time a familiar bitonic trend of general activity through the interval was observed (see Figure 7, squares). An average of 15 panel activations occurred during the 60-sec conditioned stimulus, half of the rate under the control condition (dashed line). While the response rate during the conditioned stimulus
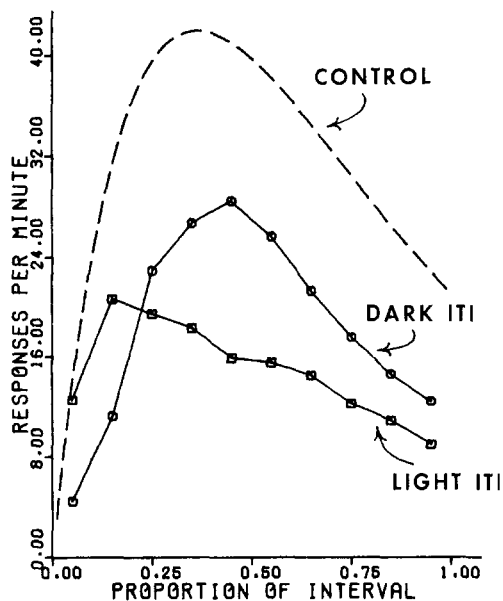
FIGURE 7. Rate of panel activation in Experiment 3d under control conditions (dashed line), first experimental condition (houselight on – pulsed; light ITI, squares), and second experimental condition (houselight off – pulsed; dark ITI, circles).

was greater than the rate immediately preceding the conditoned stimulus, it was lower than the average rate of activity during the 240 sec preceding CS onset (21 responses per minute).

When the houselight was turned off during the intertrial interval, responding was completely suppressed until the onset of the conditioned stimulus, and then it increased to a peak of 28 responses per minute approximately halfway through the CS period (Figure 7, circles). The shapes of the curves differed, with post blackout responding showing the slowest rise to its peak.

Discussion

Relatively more activity was elicited by the conditioned stimulus in Experiment 3d than was the case in Experiment 3c. While the conditioned stimulus elicited more activity than might otherwise be expected during this segment of a 300-sec interfood interval, rate did not exceed the average rate throughout the rest of the interval. A more dramatic effect was obtained when the chamber was darkened during the 240-sec intertrial in-

terval, whereupon rate during CS increased substantially.

Evaluation of the present data in terms of average rates would leave the most important aspects unseen. A signal of forthcoming reinforcement is neither wholly inhibitory nor excitatory but has the now familiar multiphasic effect on activity. Whether the signal is the shift to a flickering houselight or the delivery of food, immediately thereafter activity is suppressed. This suppression occurs whether the conditioned stimulus is of 12-sec or 60-sec duration. An increase in activity may occur after the inhibition; such an increase was noticeable for the 60-sec CS—especially when the conditioned stimulus was the transition from houselight-off to houselight-on—but might have occurred unmeasured for the shorter duration CS. In all cases there was a decrease in activity immediately before reinforcement, presumably due to the evocation of competing terminal activities.

The present series of experiments demonstrate that the course of general activity is strongly affected by the presence and nature of signals within the interfood interval. General activity is not a simple reflexive response to food delivery, for it is modified by signals of impending food—inhibited by signals with close proximity to food, disinhibited and then inhibited more intensely by signals with moderate proximity to food. The last experiment generated activity curves during a conditioned stimulus that resembled the curves obtained in Experiment 1 where the only conditioned stimulus was food delivery. An adequate discussion of these effects will require a vocabulary that includes "words" such as Equation 1, for verbal description of such phenomena will otherwise be ponderous and will omit important information, such as the time constants of the component processes.

DRUG EFFECTS

The parameters of Equation 1 have a relatively straightforward interpretation and summarize effectively various aspects of performance. In the following experiments, the robustness of the basic model is tested. Pigeons will be subjected to various drugs

and deprivation levels. To the extent that these perturbations have selective effects on response systems as modeled by Equation 1, they will be reflected in selective changes in the parameters of that model. To the extent that new processes are introduced by the experimental operation, Equation 1 will fail.

Method. Four White Carneaux pigeons served as subjects. They received 3-sec access to mixed grain every 60 sec; this schedule was independent of any behavior on their part. They were exposed to the following conditions in the order listed. Sessions were conducted daily, with two administrations of each drug, one on Wednesday and one on Friday. Control data are from the Tuesdays preceding drug administrations and from the days preceding the two prefeeding sessions.

Prefeeding. Each pigeon was given 60 grams of grain 1 hour prior to its normal session time. This amount equalled 12% of their experimental weight. After the first prefeeding session, the animals returned to their 80% weight, and additional control sessions were conducted before the second prefeeding session.

Caffeine. Each pigeon was given 10 mg of caffeine (approximately 20 mg/kg) 1 hour prior to its normal session time. Route of administration was oral.

Acepromazine maleate. Each pigeon was given 12 mg/kg of the common animal tranquilizer acepromazine maleate (Anatran) 1 hour prior to its normal session time. Route of administration was oral.

Scopolamine. Each pigeon was given .5 mg/kg of scopolamine 15 minutes prior to its normal session time. The scopolamine was injected intraperitoneally.

Results and Discussion

The effects of the experimental manipulations on response rates were generally in the expected directions. Prefeeding greatly decreased rate, while caffeine increased rate. Both the tranquilizer Anatran and scopolamine brought about slight decreases in rate (see Table 3). Inspection of Figure 8 confirms these effects. There also appears to be some change in the shapes of the curves, which may be analyzed by inspection of the parameters.

Prefeeding the animals, which brought about a fourfold decrease in rate, left the shape of the curve unchanged from control conditions: While A decreased from 74 to 19, C and I remained unchanged. This invariance is important, for it suggests that decreases in motivation due to satiation, as

TABLE 3

RESPONSE RATE AND PARAMETERS OF EQUATION 1 FOR EXPERIMENT 4

Condition	Responses per minute	A	C	I
Control	48.0	73.9	1.61	.10
Prefeeding	12.9	19.0	1.61	.10
Caffeine	51.3	149.0	.74	.21
Acepromazine maleate	40.5	50.7	2.81	.06
Scopolamine	45.8	62.1	2.63	.10

might occur within the course of an experimental session, will have a linear effect on performance at all points within the interval. Furthermore, differential effects of drugs on C and I cannot be explained as a simple appetite effect, for a substantial prefeeding generates no such effects.

The large dose of caffeine brought about only a small increase in rate of panel activation. Inspection of Table 3 and Figure 8 shows, however, that there were large effects
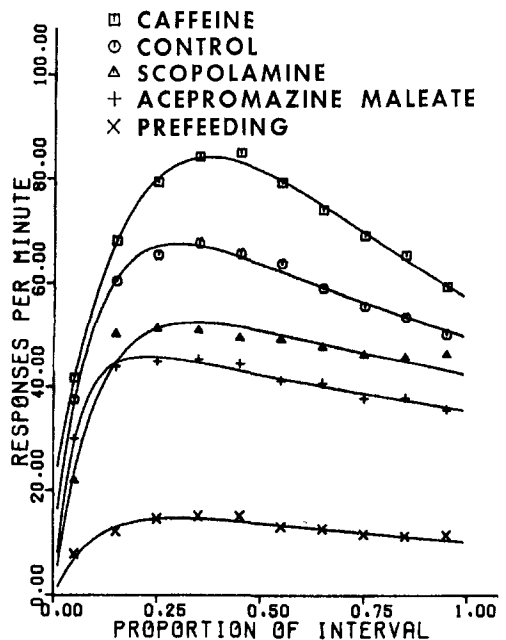

FIGURE 8. Rate of panel activation in Experiment 4b. (For clarity of presentation, the top curve, caffeine, has been displaced upward by 20 responses per minute, and the second curve, control, has been displaced upward by 10 responses per minute.)

on behavior that are not reflected in an average rate measure. The asymptotic rate, A, doubled, while the rate of approach to asymptote decreased. The activity then subsided at a faster rate than under the other conditions of this experiment, with C decreasing to less than half of the control value.

The changes under caffeine may be interpreted as an intensification both of general activity and of the terminal behaviors which compete with general activity toward the end of the interval. The slower rate of approach to asymptote might be interpreted as an intensification of "initial" behaviors which compete with interim behaviors at the beginning of the interval. But there were no obvious initial behaviors apparent during casual observations of the pigeons under various conditions of these experiments. The resonant frequency under caffeine, $1/\sqrt{CI} = 2.52$, was close to that of the control condition, 2.49.

The effects of acepromazine maleate were opposite to those of caffeine. Asymptote decreased, rate of approach to asymptote increased, and rate of recovery decreased. Resonant frequency remained close to the control value, at 2.53.

The effects of scopolamine were curious. There was a slight decrease both in average response rate and in asymptote. The rate of approach to asymptote remained at the control value, while the rate of recovery decreased. This asymmetric change in the parameters caused the resonant frequency to decrease to 1.95.

Scopolamine is known to cause a decrease in habituation to novel stimuli and a failure to inhibit incorrect responses in learning situations (cf. Carlton, 1969). The increase in C reflects a failure to inhibit general activity at a time when terminal behaviors might be more appropriate. The lack of effect on I indicates that scopolamine has no effect on the excitation of general activity but only on the excitation of specific terminal behaviors which compete with general activity.

The behavioral changes brought about in this experiment are consistent with current intuitions concerning the nature of the experimental manipulations, and thus they reinforce both those intuitions and the use of the model for their quantitative assessment. The dissociation of changes in C and I effected by scopolamine may reflect different neurochemical bases for induced (interim) and operant (terminal) behaviors (cf. Margules & Margules, 1973). The invariances that were found—the constancy of the parameters under prefeeding and the constancy of the resonant frequency under all but the scopolamine conditions—challenge the various interpretations of the model. These issues will be examined later in the General Discussion.

ADJUNCTIVE BEHAVIORS

Experiment 5a

In training animals to perform for vaudeville shows, Keller and Marion Breland (1961) noted that the form of trained operant behaviors would often drift toward that of more species-typical instinctive behaviors and that instinctive behaviors would intrude into operant chains. A prototypical example may be found in sideshows today when one commands a chicken to "play a piano" by inserting a quarter into its "modified Skinner box." The performance is frequently interrupted by vigorous scratching of the floor of the box, much as if the animal were scratching for seeds in loose dirt. This behavior was analyzed in the following experiment.

Method. Four bantam chickens hens were procured for the experiment. The chickens were reduced to 85% of their free-feeding weight and then were magazine trained using the same mixed grain that was employed for pigeons. The chickens were exposed to a 60-sec feeding schedule with no DRO contingency. Instances of scratching were recorded by depressing a thumbswitch, which incremented the data bins every .1 sec.

Results. All chickens spent a substantial amount of time scratching the floor and front wall of the chamber. Many of the scratches were directed at the hopper aperture. Figure 9 shows the average number of seconds spent scratching as a function of the time since the last feeding. The curve for panel activation was quite similar and is not shown here.

The unconditioned scratching response of chickens shows a patterning throughout the interfood interval not unlike that of the general activity of pigeons. Scratching increased
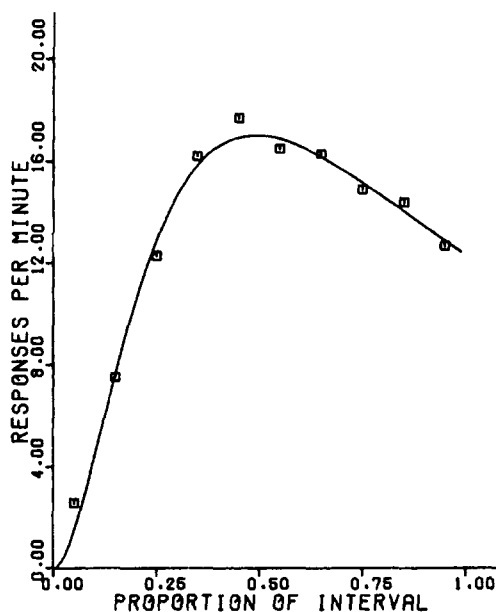
FIGURE 9. Rate of scratching (seconds per minute) induced by reinforcement in Experiment 5a. (The curve was derived from Equation 10.)

data points and accounted for 97.7% of their variance (see Figure 10).

Schedule-induced aggression follows a time course similar to general activity (control data from Experiment 1a for these two pigeons appears as a dashed line in Figure 10), both behaviors sustaining representation as the sum of two exponential functions. Just as general activity is suppressed by the proximity to reinforcement, so too is aggression. There was, however, a self-perpetuating aspect to the aggressive behavior, with animals often becoming "locked into" a battle, and in some cases missing food. This perseveration is evident in Figure 10, where aggression during the last 15 sec of the interval is seen to occur at a rate higher than predicted by the model. A less reactive target, such as a contact-sensitive mirror (Cohen & Looney, 1973) might provide a better preparation when the transactional aspects of behavior must be minimized.

Both schedule-induced and extinction-induced aggression are manifestations of normally occurring behaviors whose probability has been greatly increased by a free-food schedule. While such scheduling is maintained, the temporal pattern of aggression is

to a maximum about halfway through the interval and decreased thereafter. Equation 1 accounted for 95% of the variance in the data, while Equation 10, which is represented in Figure 9, accounted for 98.6%.

Experiment 5b

Another set of behaviors induced by intermittant feeding has been labeled "schedule-induced aggression" (Azrin, Hutchinson, & Hake, 1966; Flory, 1969a). This type of adjunctive behavior was studied in the following experiment.

Method. Hungry pigeons were placed in the chamber, each with an undeprived target pigeon. The experimental and target pigeons were separated by a clear plastic partition 15 cm high, placed diagonally in the chamber. The experimental subjects were fed every 60 sec, independently of their behavior. Pecks directed at the target bird were recorded by depressing a thumb-switch, which incremented the data bins every .1 sec.

Results and discussion. During the last five sessions, one pigeon spent 9 sec out of every minute attacking the target pigeon, while the other spent 5½ sec per minute in attack. Equation 1 was fit to the first seven
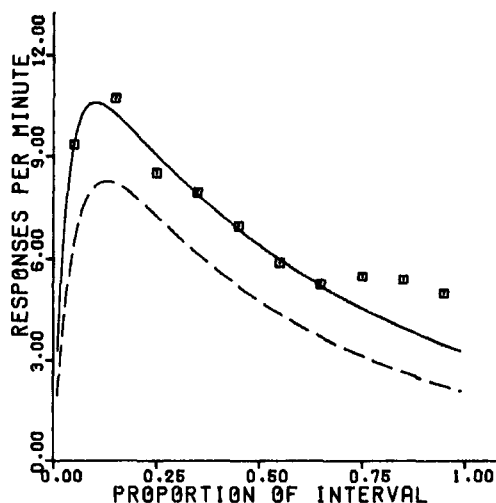

FIGURE 10. Rate of attack (seconds per minute) induced by reinforcement in Experiment 5b. (Also shown is the rate of panel activation for these two pigeons in Experiment 1a, dashed line; scale reduced by .75. The curves were derived from Equation 1.)
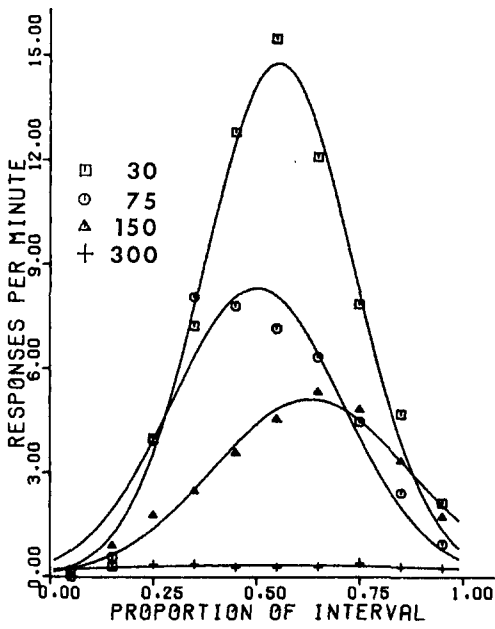
FIGURE 11. Rate of lever pressing for water in Experiment 5c. (The curves were derived from Equation 11.)

largely modulated by the proximity to reinforcement and, when present, discriminitive stimuli signaling that proximity (Cole & Litchfield, 1969; Flory, 1969b). In extinction these cues are absent, and both interim and terminal behaviors will blend and exhaust themselves, possibly according to a simple exponential decay function (cf. Azrin et al., 1966; Clark, 1959, 1964).

Experiment 5c

When a rat is exposed to periodic feeding schedules it will consume large quantities of water in the interval between feedings (Falk, 1972). Although similar patterns of excessive drinking have been noted in the rhesus monkey (Schuster & Woods, 1966) and pigeon (Shanab & Peterson, 1969) the intake of a rat is most copious, approaching half of the animal's body weight in a 3-hour session. Explanations in terms of adventitious reinforcement and mediational functions have been ruled out (Falk, 1969). To determine whether the time course of schedule-induced polydipsia corresponds to that of the interim and terminal behaviors investigated in the previous experiments, rats were

exposed to various feedings schedules with water available contingent on a lever press. In a later phase of the experiment, a wooden block was suspended in the cage, and rate of gnawing was measured.

Method. Four naive albino rats, approximately 100 days old, were exposed to feeding schedules of 30-, 75-, 150-, and 300-sec according to a Latin square design. Each depression of a lever delivered .08 ml of water to a reservoir near the food cup; food was not delivered until 5 sec had elapsed without a lever press. After 15 sessions at each of the four feeding intervals, the lever was removed and a small block of pine wood was suspended from a microswitch above the ceiling. Manipulation of the wood sent a train of 10 Hz pulses to the counters for the duration of the activity. With the wood available, the food pellets were delivered every 75 sec, but not within 5 sec of any contact with the wood. After 12 sessions the water was reintroduced, and another 10 sessions were conducted.

Results and discussion. Schedule-induced polydipsia was observed; under all but the longest interfood intervals, the rats consumed several times over their normal daily intake of water. One of the four rats showed regularly increasing response rates up until the moment of reinforcement, despite the DRO contingency employed to minimize superstitious behavior (cf. Segal, 1969). Its data are deleted from further analyses. The behavior of the other three rats is well represented by the averages shown in Figure 11. Overall rate of lever pressing for water was greatest for short intervals and decreased as the interval was lengthened (see

TABLE 4

EXPERIMENTAL CONDITIONS, AVERAGE RESPONSE RATES, AND PARAMETER VALUES FOR EQUATION 11 IN EXPERIMENT 5c

Condition	Response rate	H	S	M
Feeding condition				
30 sec	9.5	14.8	.26	.56
75 sec	6.1	8.3	.29	.50
150 sec	4.3	5.1	.33	.63
300 sec	.3	.3	.75	.51
Drinking (wood present)	3.3	7.1	.27	.56
Gnawing (water absent)	2.2	4.2	.30	.59
Gnawing (water present)	.5	1.1	.23	.50

Note. Response rates are measured as lever presses per minute or seconds gnawing per minute.

Table 4). Lever pressing was maximal mid-
way through the interval, with the variance
around .55 showing no systematic relation to
the interpellet interval. The curves through
the data points of Figure 11 are normal
(Equation 11); values of the parameters
are listed in Table 4.

When the pine block was introduced, a
considerable amount of gnawing took place.
Its time course was similar to that of sched-
ule-induced polydipsia. When the water was
reintroduced, gnawing decreased substan-
tially, with the maximum rate occurring
earlier in the interval. Rate of drinking in
the presence of the wood was depressed, with
the maximum rate occurring later in the
interval.

Schedule-induced polydipsia is often char-
acterized as a "postpellet phenomenon."
The present experiments belie that descrip-
tion and show that, while there is some post-
pellet drinking, the maximum rate of drink-
ing occurs halfway through the interpellet
interval. When a block of pine wood is
available to the rats, they divert some of the
time that would have been occupied drinking
water to manipulation and chewing of the
wood, with wood gnawing tending to occur
slightly earlier in the interval than water
drinking.

Both schedule-induced polydipsia and
gnawing are reasonably well described by
normal curves which account for approxi-
mately 94% of the data variance. As rate
of reinforcement increased, the maximum of
the curves (H) increased, the standard de-
viation ($S/\sqrt{2}$) decreased, and the midpoint
(M) remained unchanged.

This was the first time Equation 11 was
invoked to describe data. As the number of
steps in a series latency mechanism increases,
the resultant probability density function ap-
proaches the normal. This follows from the
central limit theorem. By the same taken,
the normal distribution is the limiting form
of many different types of mechanisms which
might be hypothesized to underlie the ob-
tained distributions. While the obtained
data might have modeled with four- and
five-step general gamma processes, there
would be little point to the exercise, for so

many parameters would dilute conviction in
any interpretation of that model.

Why is the normal distribution, rather
than a two- or three-step general gamma dis-
tribution, appropriate for these data? I sus-
pect the answer lies in the specificity of the
measured response. Where it is quite gen-
eral, as was the case for the experiments re-
ported in the first part of this review, early
steps in the gamma process are likely to be
captured as measured responses. While
subsequent responses may be chained to those
early responses and appear normally dis-
tributed, it is the earliest behaviors, with the
shortest time constants, that contribute most
heavily to the final shape of the distribution.

As the set of measured behaviors becomes
more specific, we should expect a sharpening
of the distribution. If the behaviors occur
early in the interval, they should be unalloyed
two- or three-step gamma processes. If
they occur late in the interval, with many in-
tervening steps in the chain, they should be
best described as normal distributions. In
the remainder of this article we examine
specific responses occurring late in the in-
terval and determine the shape of the dis-
tribution which best describes them.

APPLICATION OF THE MODEL TO OPERANT AND RESPONDENT BEHAVIORS

It was noted that one of the four rats in
the previous experiment behaved atypically,
ingesting water at an increasing rate through
the interval. Other investigators have noticed
that "schedule-induced" drinking may shift

TABLE 5

FIXED-INTERVAL AND PARAMETER VALUES FOR
EQUATION 11 FOR DATA FROM
VARIOUS SOURCES

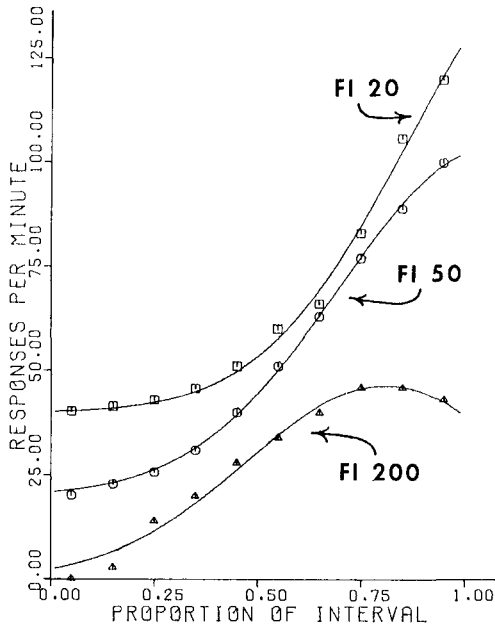| Source	Fixed interval (sec)	H	S	M
Hawkes and Shimp (1975)	5	180.0	.566	.83
Catania and Reynolds (1968)	30	106.0	.488	1.21
	50	· 83.3	.488	1.06
	200	46.5	.488	.81
Experiment 2a	60	89.4	.406	.92
Dukich and Lee (1973)	60	55.0	.347	1.05
	120	55.0	.428	1.24

FIGURE 12. Rate of key pecking by pigeons on various fixed-interval schedules. (The top curve, fixed interval 20 sec, is displaced upward by 40 responses per minute, while the middle curve, fixed interval 50 sec, is displaced upward by 20 responses per minute. From Catania & Reynolds, 1968.)

of time through the interval, for fixed intervals of 30, 50, and 200 sec. The curves through the points are normal with parameters given in Table 5. Shown in Figure 13 are data from Hawkes and Shimp (1975) for pigeons responding on an fixed-interval 5-sec schedule. Although these data were collected by different investigators and were generated on a very short fixed-interval schedule, the same normal function which fit Catania and Reynolds's (1968) data is also appropriate for Hawkes and Shimp. The performance of rats on fixed-interval schedules is similar to that of pigeons. Figure 14 shows data collected by Dukich and Lee (1973) studying the responding of rats on fixed intervals of 60 and 120 sec. The parameters are listed in Table 5.

In all cases, behavior is well represented by the left tail of a normal curve, which accounts for 99.5% of the data variance. The present analysis suggests that the form of the typical fixed-interval scallop—the smoothly accelerating curve drawn by a cumulative recorder—is a cumulative normal function. We now turn our attention to the parameters which describe that function.

toward the end of the interval and take on the "characteristic form of a fixed-interval scallop." Segal (1972) has suggested that this shift may be characteristic of the genesis of many operant performances—"induction" of some response as an interim behavior, a consequent increase in the probability of contiguity with an ensuing reinforcer, and eventual entrapment as a reinforced, operant response. This shift in the controlling contingencies should be reflected in a shift in the mode and shape of the response distribution. In the previous section we described the distribution of induced behaviors with a normal curve. What is the nature of the distribution of the operant behaviors: What is the mathematical form of a "typical fixed-interval scallop"? In the following paragraphs we select from the literature data on which to base an answer.

In a monograph published in 1968, Catania and Reynolds reported an extensive study of responding by pigeons on variable-interval and fixed-interval schedules. Figure 12 shows the rate of responding as a function
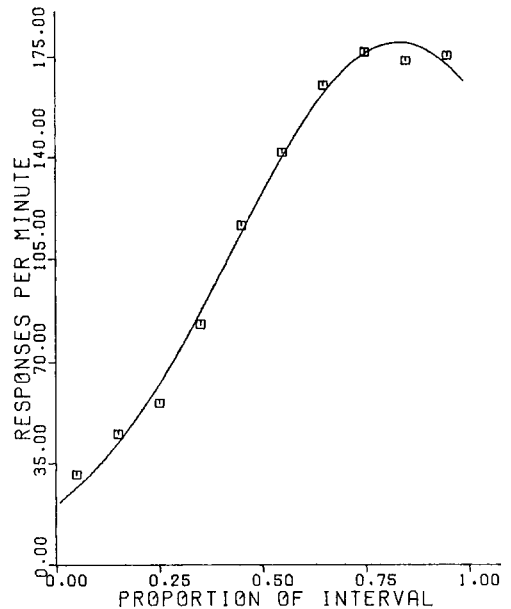

FIGURE 13. Key-pecking rate on an fixed-interval 5-sec schedule. (From Hawkes & Shimp, 1975.)

In Figure 15 I have plotted the product of M and T as a function of T. M may be taken as a psychological judgment of the duration of the interval, and multiplication by T returns it to a nonnormalized form. The data from Experiment 2a and from Catania and Reynolds (1968) fall along a straight line with a slope of .8. The data from Hawkes and Shimp (1975) fall below that line.[2] On the strength of the former data, we suggest that the psychophysical scale of duration for pigeons is a power function with an exponent of .8. Catania (1970) came to the same conclusion from an analysis of behavior on other reinforcement schedules, as did DeCasper and Zeiler (1974). The fractional slope of the function indicates that pigeons typically overestimate short intervals and underestimate long ones. This tendency is reflected in the truncation of the behavior during a period of accelerating responding on short fixed-interval schedules, and during a period of decelerating responding on longer schedules. For the present

---

[2] The differences which exist, such as the larger value of S, the smaller value of M, and the larger intercept at $t = 0$, may be due in part to the use of a 2.5 sec time-out after reinforcement.

FIGURE 15. Top line: The theoretical maximum number of responses induced by food as a function of the interfood interval. (Data are from Catania & Reynolds, circles; from Experiment 2a, squares; and from Hawkes & Shimp, triangles. The slope of the line is .6.) Bottom line: The relation between interfood interval and midpoint of the normal curve (M). (The data from Catania & Reynolds, circles, and from Experiment 2a, squares, fall along a straight line with a slope of .8, while the data from Hawkes & Shimp, triangles, fall below that line.)
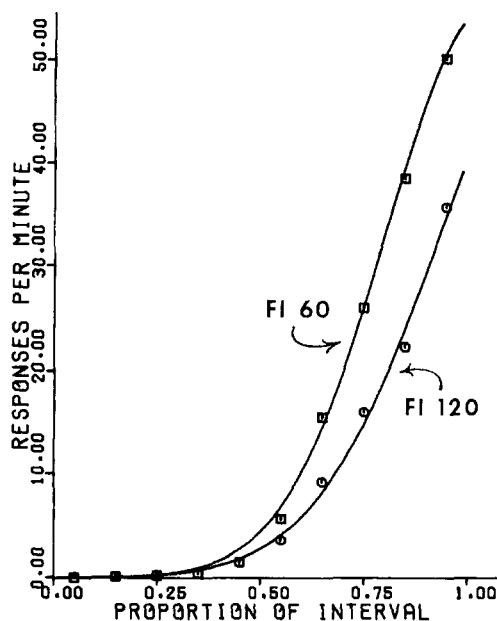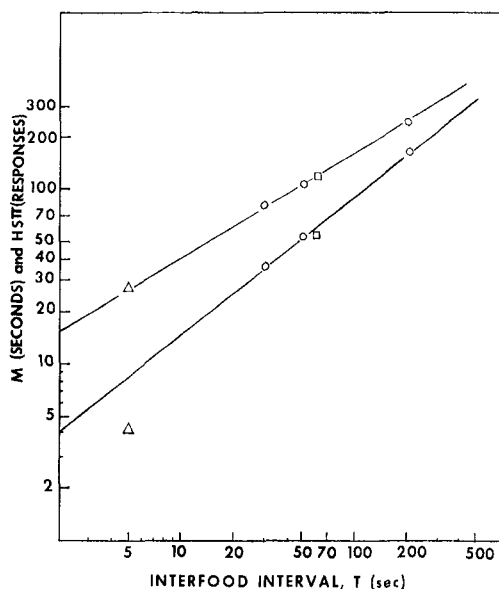

FIGURE 14. Rate of lever pressing by rats on a fixed-interval 60-sec schedule (squares) and a fixed-interval 120-sec schedule (circles). (From Dukich & Lee, 1973.)

data, estimation is most accurate at a fixed-interval value of about one minute, where reinforcement interrupts pigeons at their maximal rate.

The parameters for the rats are not shown in Figure 15. Their behavior was markedly different from that of pigeons—the maximum rate, H, remained the same for FI 60 and FI 120, while M increased, rather than decreased with T. Since these data are from the control conditions of but one study, they should not be weighed too heavily. If they are replicated, these qualitative differences may implicate an important distinction drawn by Seligman (1970) between "prepared" responses such as pecking, induced by and closely bound to reinforcement, and "unprepared" responses, such as lever pressing, that are more loosely coupled to reinforcement.

The existential status of the right, descending limbs of the truncated normal curves is

uncertain. When reinforcement is only occasionally withheld on fixed-interval schedules, rate does not usually drop off as quickly as would be predicted by the present formulation (cf. Staddon & Innis, 1969; Zimmerman, 1971). A higher ordered exponential equation would provide the necessary "asymmetrical normal curve" shape. Unfortunately the necessary data have not been collected to evaluate such a model. When reinforcement is withheld on a more regular basis (e.g., Catania, 1970; Myerson, 1972), response rate does drop off in a symmetric, normal fashion. Equation 11 therefore seems appropriate for well-learned behaviors such as fixed-interval responding and discriminated extinction. Other models, such as a simple exponential decay function, may apply to nondiscriminated extinction (Clark, 1959, 1964; Furumoto, 1967).

To calculate the maximum number of responses evoked by a reinforcer, one integrates the normal curve from $-\infty$ to $+\infty$ and finds it to be, quite simply, $HS\pi$. In Figure 15 I have plotted $HS\pi$ as a function of T. The equation

$$HS\pi = kT^{.6}, \qquad [12]$$

whose locus appears as a solid line, represents well Catania and Reynolds' (1968) data (circles), Experiment 2a data (square), and Hawkes and Shimps' (1975) data (triangle). It should also be mentioned that the unnormalized value of S is approximately proportional to T, and H is a power function of T with an exponent of $-.4$. It is not yet clear which of these relations will turn out to be fundamental, and which derivative.

To predict the average obtained response rate on fixed-interval schedules, one must multiply $HS\pi$ by the area under the curve between $t = 0$ and $t = 1$ and then divide by T. Figure 15 shows us, however, that the normal curve was centered around 1 only for fixed intervals of approximately 60 sec: For shorter schedules, the animals overestimated the time, thereby truncating the normal curve before maximum rate was attained. As the interval grows smaller, less and less of the maximum possible rate is attained. This attenuation might be termed "inhibition by reinforcement" (cf. Gormezano & Moore, 1969; Hovland, 1936). The mechanism of

such "inhibition" is simply the nonlinear psychophysical scale of duration demonstrated in Figure 15.

The present model throws additional light on some regularities in behavior noted by Nevin (1974). Nevin measured response rates on two alternating variable-interval schedules in the presence of explicit competing responses (a fixed-interval schedule on a second key). Over a range of different reinforcement probabilities for the variable interval schedules, he found

$$R_1 = q \, R_2{}^s, \qquad [13]$$

rate on one schedule was a power function of rate on the other. Rates on the variable-interval schedules were greatest at the beginning of the fixed interval and decreased as the interval progressed and as fixed-interval responding became predominant. Their time course looked much like that of interim behaviors (Figure 1); the analogy has some face validity and will be examined.

Let us simplify Equation 1 by ignoring the inhibition of reinforcement:

$$R_i = A_i e^{-t/C_i}. \qquad [14]$$

Response rates on each of the two variable-interval schedules should approximate exponential decay functions of time through the interval. To determine the relation between response rates, we may compare rates only at the same point in time and thus collapse Equation 14 over t:

$$-C_1 \ln(R_1/A_1) = \\ t = -C_2 \ln(R_2/A_2). \qquad [15]$$

Rearrangement yields

$$R_1 = A_1 \left(\frac{R_2}{A_2}\right)^{C_2/C_1}, \qquad [16]$$

a form equivalent to Equation 13, with

$$s = C_2/C_1, \qquad [17]$$

and

$$q = A_1/A_2{}^s. \qquad [18]$$

While Nevin's (1974) Equation 13 thus follows from the present theory, independent quantitative predictions of his data are difficult, because the present analysis provides no basis for predicting the nature of changes

in C with changes in the probability of rein-
forcement for interim behaviors (i.e., vari-
able-interval schedule responding). If we
assume, however, that A is proportional to
the rate of reinforcement, we may use
Nevin's values of s in Equation 18 to pre-
dict his obtained values of q. The unknown
constant of proportionality enters Equation
18 in a nonlinear fashion, causing the pre-
diction for individual animals to be in error
by the factor $k^{(1-s)}$. Nonetheless, approx-
imate prediction is possible, and the scatter-
gram of obtained versus predicted intercepts
(Figure 16) shows it to be effective.

The relevance of the present analysis to
Nevin's data is important in light of the as-
sumptions that were made in the course of
the analysis. Key pecking on multiple vari-
able-interval schedules, maintained by contin-
gent reinforcement, was successfully treated
as an "interim" behavior. Such responding
shares with interim behaviors the same rela-
tively homogenous probability of reinforce-
ment over time, and, like interim behaviors,
suffers competition from periodically occur-
ring reinforcers. The use of Equations 1
and 10 should not, therefore, be thought to
be restricted to schedule-induced, or interim
behaviors but may be taken as a model of the
changes in any tonic, or background, be-
havior in the context of periodic occurrences
of reinforcers which elicit competing be-
havior.

Application to Respondent Behavior

While the paradigms which generated
much of the data in the present experiments
would be classified as respondent, or classical
conditioning, it is useful to look at a more
traditional instance of respondent behavior
from the perspective of the present theory.
Pavlov (1960; pp. 95, 96) reported several
experiments involving "inhibition of delay";
conditioned stimuli of 3-min duration were
presented at intervals of 12 min. The un-
conditioned stimulus was the injection of a
weak acid solution into a dog's mouth. Al-
though some of the trials involved compound
stimuli, Pavlov reported the number of drops
of saliva emitted every 30 sec during 20
control trials. I have averaged these data,
transformed them into a rate measure, and
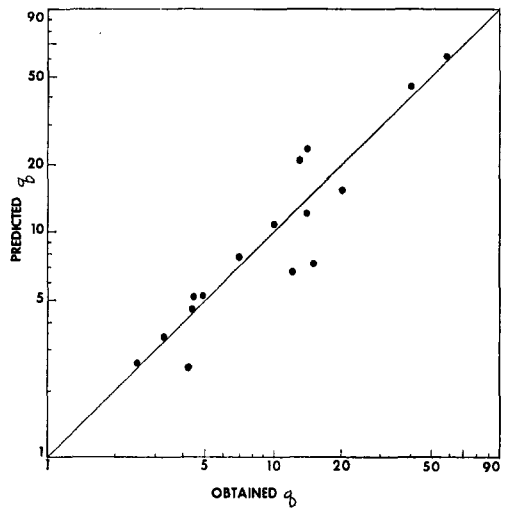graphed them in Figure 17. A normal curve

FIGURE 16. Obtained versus predicted values of
q, the intercepts of Nevin's (1974) power functions.
(The predictions followed from Equation 18, with
A assumed proportional, $k = 150$, to the reinforce-
ments per minute. The predictions are for indi-
vidual subjects from each condition, with the ex-
ception of Pigeon 60 Condition 4, for whom no
slope could be determined.)

with a mean of .95 and a standard deviation
of .43 accounts for practically all of the data
variance.

Equations 10 and 11 are also reasonable
descriptors of the behavior occurring during
much shorter conditioned stimulus-uncon-
ditioned stimulus intervals. Smith (1968)
classically conditioned the nictitating-mem-
brane response of rabbits, employing in-
tervals between 125 and 1,000 msec. Third-
order exponential functions described the
data from the three shortest intervals and
a normal curve described the data from the
longest interval. Approximately 95% of the
data variance was accounted for by those
models.[8]

GENERAL DISCUSSION

The study of the general activity of pigeons
during the interval between feedings gener-
ated regular data conducive to representation

---

[8] An additional transformation was necessary to
permit these models to fit Smith's data: 90 msec
were arbitrarily subtracted from the abcissa before
Equations 10 and 11 were fit. This latency should
be treated as an additional free parameter and
might be interpreted as an estimate of the absolute
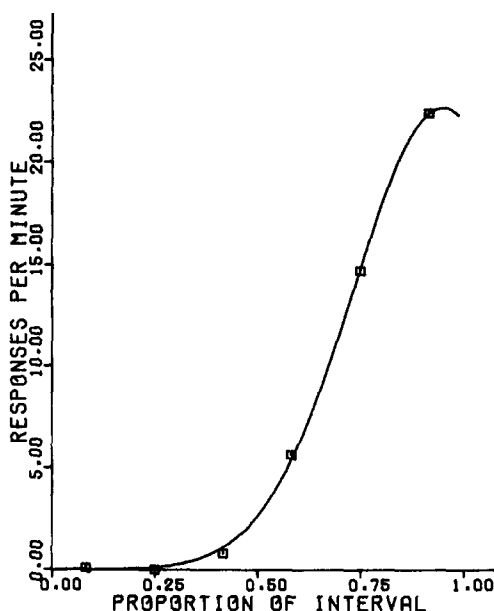refractory period.

FIGURE 17. Rate of salivation (drops per minute) as a function if time within a 3 min conditioned stimulus (data from Pavlov, 1960).

by a simple mathematical model (Equation 1). The two exponential decay functions of the model were identified as a short-term inhibitory process reflecting the remoteness of one food delivery from the next and a longer term process reflecting the rise of competing ("terminal") behaviors.

Whereas this simple model provided an adequate account of general activity, the addition of a third exponential was necessary to accommodate the interim behaviors reported by Staddon and Simmelhag (1971), and it improved the fit to some other data. This third, very fast exponential permitted the early portions of the curves to show positive acceleration and was attributed to a carry-over of consummatory responses or orienting responses into the beginning of short intervals. Although responses occurring toward the middle and end of an interval could be represented by three or four interacting exponentials, the normal function required fewer parameters and provided a superior fit to the data. The normal curve is the limiting distribution when many exponential decay functions interact.

Changes in the parameters of the model showed a gratifying concordance with changes

in independent variables. The theoretical maximum, A, was proportional to the feeding rate, while H was a power function of the feeding rate. The time constants of the component exponential processes showed regular changes with changes in rate of feeding and a consistent (inverse) relationship with each other. The parameters of the normal curve were either relatively invariant or changed smoothly with changes in the interfood interval.

Equations 1 and 10 may be interpreted as the impulse response curves of second and third order control systems. In this construction, response rate is presumed proportional to the deviation of the system from homeostasis. This deviation is brought about by an impulse—in the present case, food delivery. It may be assumed either that the measured response drives the system back to equilibrium (a traditional servo-system with proportional negative feedback) or simply that the return occurs as an exponential function of time. The latter assumption is more congenial to the behavior in question. It is also necessary to assume either inertia in the system or an exponential delay involved in communicating the impulse to the response mechanism. The latter interpretation is adopted. (Still other control devices are modeled by second order systems, e.g., devices with proportional and integral control, but these seem further removed from the data, cf. Baylis, 1966).

The mapping of induced behaviors onto control systems, via Equations 1 and 10, brings into focus some behavioral regularities and provides indices for other behavioral changes. The damping ratio ($\zeta = \sqrt{C/I}/2$) governs the speed with which the system returns to equilibrium. This index changed in the appropriate manner in Experiment 2 and across Experiments 1a and 1b. The constancy of the normalized resonant frequency (ω) provided a picture of organisms finely tuned to the temporal regularities in their environment. At the same time, however, the dependence of this basic system parameter on the input frequency ruled out both a simple reflexive interpretation of the data and the general usefulness of simple linear control systems, which predicate a reflexive system having input-invariant param-

eters! Further experiments should be conducted before a cybernetic interpretation is discarded. But one of the most severe impediments to this construction is its interpretation of a low response rate before food delivery as a return to equilibrium. If that feeding were omitted, response rate would soon increase to record highs, a phenomenon beyond the purview of simple control theory. Although such a rebound might be accommodated by control systems with predictive elements, the complexity of those models is not justifiable with the present limited data base.

An unramified stochastic process, such as was presented earlier, fares little better than control theory as an interpretation of the fundamental equations. The constancy of the number of inferred parallel processes in Experiments 1a and 1b was encouraging. It is possible that simple modification of the organism's environment, such as a change in chamber size, will have direct effects on the index. It is possible that the steps in the chain will be correlated with the perception of and reaction to environmental stimuli and thus tie the present model into stimulus-sampling theories of behavior acquisition (Estes, 1959; Kintsch, 1970).

But there are problems with the simple stochastic interpretation. The number of hypothetical processes was constant in no other parts of these experiments, and the changes that occurred under drugs were unenlightening. Especially damaging is the constancy of the product of C and I over large changes in feeding rate and insult by various drugs. This powerful invariance in the data would go unnoticed for there is no index in series latency mechanics which involves the product of C and I. Finally, the construal of individual responses from homogenous sets of behavior, such as pacing or drinking, as independent outcomes of parallel processes seems unsympathetic to the data.

General activity comprises many behaviors which hang together as unitary phenomena. The stochastic model may be modified to preserve this molar structure of the data. Assume the gamma distribution represents a "behavioral state" of the organism during which time a particular activity, such as

polydipsic drinking, occurs at a uniform rate. It is called a "behavioral" state to avoid connotations of a "drive" state, such as "thirst." Let us assume the presence of another state, represented by a gamma distribution with the same values of A and I but a different value of C (C'). Correlated with this state are other behaviors, such as running in a wheel, which are suppressed ("displaced") by the behaviors of the first state. The probability of being in the second state at a given point in time (and therefore the average rate at that time) will be equal to the difference of the two equations:

$$R = A(e^{-t/C} - e^{-t/C'}). \qquad [19]$$

This behavioral state development seems most in accord with observed behaviors. Furthermore, it explains quantitative properties of data collected by Staddon and Ayres (in press) and analysed by them and by Staddon (in press) in a state theoretic manner. Their analysis, which motivated the above development, showed that the duration of one activity (e.g., running) was negatively correlated with the time of offset of a previous activity (e.g., drinking). They took the significant negative correlations, along with data from experiments in which one of the activities was prevented, as evidence *against* a simple chaining interpretation (i.e., drinking leads to running) and *for* central timing of each of the states. Inspection of Equation 19 shows that the total amount of time in a state will indeed be negatively correlated with variations in the time constant governing entry into that state (C'). The machinery of generalized gamma processes may thus be retained, but the emphasis upon the termination of a state is now shifted to the behavior occurring during a state. The "latent period" is revealed by the measured responses, which are taken to signify the outcome of competition among parallel behavioral states.

There are implications to the present research that go beyond the provision of an adequate model for the time course of behavior and the leverage on related problems which that provides. Four historically distinct phenomena—general activity, schedule-induced behaviors, operants, and respondents

—have been encompassed by a single mathematical formulation. While there are qualitative distinctions among these various behaviors, they have a common foundation in Equations 1, 10, and 11. If future research shows that multiple behaviors within an interval share some parameters (e.g., A, corrected for response units) and exert predictable effects on the parameters of other behaviors (as the introduction of an operant in Experiment 2a increased the value of C), the theoretical usefulness of those distinctions will fade.

What then will remain as important discriminanda among behaviors? Operants are said to be emitted while respondents are elicited. But "emission" cannot be taken to imply lack of prior causal stimuli (Staddon, 1973); all operants must be "elicited" by stimuli of some sort. If an external discriminative stimulus is not provided, time will serve. And time serves operants and respondents similarly, for we have seen that the same mathematical function of time describes both types of behavior.

Respondents are said to extinguish more quickly than operants and to suffer greater decrement under conditions of partial reinforcement. But that distinction is confounded by the historic difference between the response systems studied within the operant and respondent paradigms. When similar systems are studied, similar partial-reinforcement effects may be found (e.g., Williams & Williams, 1969). In the experiments modeled in this article, many key pecks and many drops of saliva occurred during the intervals between feedings. Which was on a thinner schedule of partial reinforcement is moot. The same equation describes the time course of each and provides theoretical asymptotes for each. Only when the scale factors for various behaviors receive relative calibration (e.g., by the measurement of concomitant changes under manipulations of drugs, deprivation, or amount of reinforcement) can meaningful comparisons be made. And only then can the apparent differences in resistance to extinction in discrete-trial experiments be fully understood.

Some behaviors are more malleable than others; typical respondents are not so readily

shaped with differential reinforcement and might therefore justify distinction from operants. But the Brelands (1966) have alerted us to the limitations on our ability to shape operant behaviors. Moore (1973) suggests that the topography of operants is closely related to forms of behavior induced by "reinforcement"; contingencies merely change the location of induced behaviors. Hearst and Jenkins (1975) provide a possible mechanism for that spatial control in their analysis of "sign-tracking" (cf. Neuringer & Neuringer, 1974; Schneirla, 1959). Certainly more research is necessary, but the presently available data suggest that sign-tracking, schedule-induced arousal, and the present model of temporal control may provide the basic "laws" for a theory of behavior more powerful than any founded on the law of effect.

The asymptotic level of general activity, schedule-induced behaviors, and operants increases with increases in the frequency of reinforcement. This systematic change is taken as evidence for an intervening state of "arousal." The construct has much in common with the "anitcipation–invigoration mechanism" of Cofer and Appley (1967), the "emotion" of Segal (1972), the "central-motive state" of Bindra (1972), and the "arousal" of Wayner (1970), Valenstein, Cox, and Kakolewski (1970), Glickman (1973), and Fentress (1973). It is taken here to be a general and nonspecific activator of behaviors, functioning essentially as the gain-control of an amplifier. An essential problem for this and all similar theories is that of specifying which behaviors will be amplified—what functions as the channel selector of the organism?

While temporal cues govern the transition between behavioral states, situational cues determine the nature of the state selected. Within a range dictated by its ecological niche, the history and immediate environment of the organism become important factors in determining the types of behavior that will be induced. The plasticity of the induced behaviors and the amount and kind of stimulus support necessary to release them from an aroused organism remain important and largely unexplored topics for research.

An important question remains: What in

the present theory distinguishes "normal," "operant," or "terminal" behaviors from "interim," "adjunctive," or "displacement" behaviors? Two aspects of the incentive-motivator will account for the distinction: (a) The incentive is available only at the end of the interval; behavior appropriate to it will therefore be elicited toward the end of the interval, and only then; and (b) Adequate contact with the incentive will satiate the organism, thereby turning off the arousal.[4]

Elements of the present theory have been suggested before (cf. Bindra, 1972, Staddon, 1972, on temporal versus situational control; Moore, 1973, on Pavlovian mechanisms in operant behavior; Fentress, 1973, on the nonspecificity of the central motive state of arousal). They may seem too simple and incomplete to account for the data under purview; but consider: The theory suggests that a state of elevated arousal is generated by events traditionally referred to as reinforcers. The arousal increases the vigor of all responses elicited by situational stimuli, both interoceptive and exteroceptive, acting in concert with temporal stimuli. The elicitation of behavior is quite general, with those behaviors favored by the organism's phylogenetic or ontogenetic history and present drive condition being predominant. Since many of these behaviors do not abate the organism's arousal, they may continue at "excessive" levels. But as time wears on, behaviors appropriate to the appeted stimulus will increase in frequency according to equations such as 10 and 11. All of the "fine control" of behavior attributed to law of effect strengthening may be reducible to the time-contingent elicitation of approach to stimuli that are correlated with reinforcement.

The present theory repudiates the traditional distinctions between classes of behavior and questions the future usefulness of the law of effect. That law was historically necessary, for it established "reinforcement" as a firm temporal reference point from which to view the immediately preceding "terminal" behaviors. With the present model of temporal control, we may trace the course of all behaviors that are referenced to signals of forthcoming incentives, such as feedings. "Reinforcement" and its retroflex action may be dispatched.

REFERENCES

Amsel, A. Frustrative nonreward in partial reinforcement and discrimination learning: Some recent history and a theoretical extension. *Psychological Review*, 1962, *69*, 306–328.

Amsel, A. Behavioral habituation, counterconditioning, and a general theory of persistance. In A. H. Black & W. F. Prokasy (Eds.), *Classical conditioning II: Current theory and research.* New York: Appleton-Century-Crofts, 1972.

Amsel, A., & Work, M. S. The role of learned factors in "spontaneous" activity. *Journal of Comparative and Physiological Psychology*, 1961, *55*, 527–532.

Azrin, N. H., Hutchinson, R. R., & Hake, D. F. Extinction-induced aggression. *Journal of the Experimental Analysis of Behavior*, 1966, *9*, 191–204.

Baylis, L. E. *Living control systems.* San Francisco: Freeman, 1966.

Bindra, D. Neuropsychological interpretation of general activity and instrumental behavior. *Psychological Review*, 1968, *75*, 1–22.

Bindra, D. The interrelated mechanisms of reinforcement and motivation, and the nature of their influence on response. In W. J. Arnold & D. Levine (Eds.), *Nebraska Symposium on Motivation* (Vol. 18). Lincoln: University of Nebraska Press. 1970.

Bindra, D. A unified account of classical conditioning and operant training. In A. H. Black & W. F. Prokasy (Eds.), *Classical conditioning II: Current research and theory.* New York: Appleton-Century-Crofts, 1972.

Bindra, D., & Palfai, T. Nature of positive and negative incentive-motivational effects in general activity. *Journal of Comparative and Physiological Psychology*, 1967, *63*, 288–297.

Blough, D. S. New test for tranquilizers. *Science*, 1958, *127*, 586–587.

Bolles, R. C. *Theory of motivation.* New York: Harper & Row, 1967.

Bolles, R. C. Interactions with motivation. In M. Marx (Ed.), *Learning: Interactions.* London: Macmillan, 1970. (a)

Bolles, R. C. Species-specific defense reactions and avoidance learning. *Psychological Review*, 1970, *77*, 32–48. (b)

Breland, K., & Breland, M. The misbehavior of organisms. *American Psychologist*, 1961, *16*, 681–684.

Breland, K., & Breland, M. *Animal behavior.* New York: Macmillan, 1966.

Brown, P. L., & Jenkins, H. M. Auto-shaping of the pigeon's key-peck. *Journal of the Experimental Analysis of Behavior*, 1968, *11*, 1–8.

---

[4] This feature is missing when the reinforcer is intracranial stimulation of the brain.

Campbell, B. A., & Sheffield, F. D. Relation of random activity to food deprivation. *Journal of Comparative and Physiological Psychology,* 1953, *46,* 320–322.

Capaldi, E. J. Partial reinforcement: A hypothesis of sequential effects. *Psychological Review,* 1966, *73,* 459–477.

Capaldi, E. J. An analysis of the role of reward and reward magnitude in instrumental learning. In J. H. Reynierse (Ed.), *Current issues in animal learning.* Lincoln: University of Nebraska Press, 1970.

Carlton, P. L. Brain-acetylcholine and inhibition. In J. T. Tapp (Ed.), *Reinforcement and behavior.* New York: Academic Press, 1969.

Catania, A. C. Reinforcement schedules and psychophysical judgments. In W. N. Shoenfeld (Ed.), *The theory of reinforcement schedules.* New York: Appleton-Century-Crofts, 1970.

Catania, A. C., & Reynolds, G. S. A quantitative analysis of the responding maintained by interval schedules of reinforcement. *Journal of the Experimental Analysis of Behavior,* 1968, *11,* 327–383.

Clark, F. C. Some quantitative properties of operant extinction data. *Psychological Reports,* 1959, *5,* 131–139.

Clark, F. C. Effects of repeated VI reinforcement and extinction upon operant behavior. *Psychological Reports,* 1964, *15,* 943–955.

Cofer, C. N., & Appley, M. H. *Motivation: Theory and research.* New York: Wiley, 1967.

Cohen, P. S., & Looney, T. A. Schedule-induced mirror responding in the pigeon. *Journal of the Experimental Analysis of Behavior,* 1973, *20,* 395–408.

Cole, J. M., & Litchfield, P. M. Stimulus control of schedule-induced aggression in the pigeon. *Psychonomic Science,* 1969, *17,* 152–153.

DeCasper, A. J., & Zeiler, M. D. Time limits for completing fixed ratios. III. Stimulus variables. *Journal of the Experimental Analysis of Behavior,* 1974, *22,* 285–300.

Dukich, A. D., & Lee, A. E. A comparison of measures of responding under fixed-interval schedules. *Journal of the Experimental Analysis of Behavior,* 1973, *20,* 281–290.

Estes, W. K. The statistical approach to learning theory. In S. Koch (Ed.), *Psychology: A study of a science* (Vol. 2). New York: McGraw-Hill, 1959.

Falk, J. L. Conditions producing psychogenic polydipsia in animals. *Annals of the New York Academy of Sciences,* 1969, *157,* 569–593.

Falk, J. L. The nature and determinants of adjunctive behavior. In R. M. Gilbert & J. D. Keehn (Eds.), *Schedule effects: Drugs, drinking, and aggression.* Toronto, Canada: University of Toronto Press, 1972.

Fentress, J. C. Specific and nonspecific factors in the causation of behavior. In P. P. G. Bateson & P. H. Klopfer (Eds.), *Perspectives in ethology.* London: Plenum, 1973.

Flory, R. K. Attack behavior as a function of minimum inter-food interval. *Journal of the Experimental Analysis of Behavior,* 1969, *12,* 825–828. (a)

Flory, R. K. Attack behavior in a multiple fixed-ratio schedule of reinforcement. *Psychonomic Science,* 1969, *16,* 156–157. (b)

Furumoto, L. *Studies of experimental extinction in the pigeon.* Unpublished doctoral dissertation, Harvard University, 1967.

Glickman, S. E. Responses and reinforcement. In R. Hinde & J. Stevenson-Hinde (Eds.), *Constraints on learning: Limitations and predispositions.* New York: Academic Press, 1973.

Gormezano, I., & Moore, J. W. Classical conditioning. In M. Marx (Ed.), *Learning: Processes.* London: Macmillan, 1969.

Hawkes, L., & Shimp, C. P. Reinforcement of behavioral patterns: Shaping a scallop. *Journal of the Experimental Analysis of Behavior,* 1975, *23,* 3–16.

Hearst, E., & Jenkins, H. M. *Sign-tracking: The stimulus-reinforcer relation and directed action.* Austin, Texas: Psychonomic Society, 1975.

Hovland, C. I. "Inhibition of reinforcement" and phenomena of experimental extinction. *Proceedings of the National Academy of Science, Washington,* 1936, *22,* 430–433.

Jenkins, H. M. Sequential organization in schedules of reinforcement. In W. N. Schoenfeld (Ed.), *The theory of reinforcement schedules.* New York: Appleton-Century-Crofts, 1970.

Jensen, C., & Fallon, D. Behavioral aftereffects of reinforcement and its omission as a function of reinforcement magnitude. *Journal of the Experimental Analysis of Behavior,* 1973, *19,* 459–468.

Keehn, J. D. Schedule-dependence, schedule-induction, and the law of effect. In R. M. Gilbert & J. D. Keehn (Eds.), *Schedule effects: Drugs, drinking, and aggression.* Toronto, Canada: University of Toronto Press, 1972.

Kintsch, W. *Learning, memory, and conceptual processes.* New York: Wiley, 1970.

Konorski, J. *Integrative activity of the brain: An interdisciplinary approach.* Chicago: University of Chicago Press, 1967.

Levitsky, D., & Collier, G. Schedule-induced wheel running. *Physiology and Behavior,* 1968, *3,* 571–573.

Margules, D. L., Margules, A. S. The development of operant responses by noradrenergic activation and cholinergic suppression of movements. In J. D. Maser (Ed.), *Efferent organization and the integration of behavior.* New York: Academic Press, 1973.

McFarland, D. J. *Feedback mechanisms in animal behavior.* New York: Academic Press, 1971.

McGill, W. J. Stochastic latency mechanisms. In R. D. Luce, R. R. Bush, & E. Galanter (Eds.), *Handbook of mathematical psychology* (Vol. 1). New York: Wiley, 1963.

McGill, W. J., & Gibbon, J. The general-gamma distribution and reaction times. *Journal of Mathematical Psychology,* 1965, *2,* 1–18.

Milsum, J. H. *Biological control systems analysis.* New York: McGraw-Hill, 1966.

Moore, B. R. The role of directed Pavlovian reactions in simple instrumental learning in the pigeon. In R. A. Hinde & J. Stevenson-Hinde (Eds.), *Constraints on learning: Limitations and predispositions.* New York: Academic Press, 1973.

Myerson, J. *Trace stimulus control in second-order schedules.* Unpublished doctoral dissertation, Arizona State University, 1972.

Neuringer, A., & Neuringer, M. Learning by following a food source. *Science,* 1974, *184,* 1005–1008.

Nevin, J. A. Response strength in multiple schedules. *Journal of the Experimental Analysis of Behavior,* 1974, *21,* 389–408.

Pavlov, I. P. *Conditioned reflexes* G. V. Anrep, (trans.). New York: Dover, 1960.

Schneirla, T. C. An evolutionary and developmental theory of biphasic processes underlying approach and withdrawal. In *Current theory and research on motivation.* Lincoln: University of Nebraska Press, 1959.

Schuster, C. R., & Woods, J. H. Schedule-induced polydipsia in the rhesus monkey. *Psychological Reports,* 1966, *19,* 823–828.

Scull, J. W. The Amsel frustration effect: Interpretations and research. *Psychological Bulletin,* 1973, *79,* 352–361.

Segal, E. F. Transformation of polydipsia drinking into operant drinking: A paradigm? *Psychonomic Science,* 1969, *16,* 133–135.

Segal, E. F. Induction and the provenance of operants. In R. M. Gilbert & J. R. Millenson (Eds.), *Reinforcement: Behavioral analyses.* New York: Academic Press, 1972.

Seligman, M. E. P. On the generality of the laws of learning. *Psychological Review,* 1970, *77,* 406–418.

Shanab, M. E., & Peterson, J. L. Polydipsia in the pigeon. *Psychonomic Science,* 1969, *15,* 51–52.

Sheffield, F. D. A drive-induction theory of reinforcement. In R. N. Haber (Ed.), *Current research in motivation.* New York: Holt, 1966.

Sheffield, F. D., & Campbell, B. A. The role of experience in the "spontaneous" activity of hungry rats. *Journal of Comparative and Physiological Psychology,* 1954, *47,* 97–100.

Siegel, S., & Domjan, M. Backward conditioning as an inhibitory procedure. *Learning and Motivation,* 1971, *2,* 1–11.

Skinner, B. F. Superstition in the pigeon. *Journal of Experimental Psychology,* 1948, *38,* 168–172.

Slivka, R. M., & Bitterman, M. E. Classical appetitive conditioning in the pigeon: Partial reinforcement. *Psychonomic Science,* 1966, *4,* 181–182.

Smith, M. C. CS–US interval and US intensity in classical conditioning of the rabbit's nictitating membrane response. *Journal of Comparative and Physiological Psychology,* 1968, *66,* 679–687.

Staddon, J. E. R. Temporal effects of reinforcement: A negative "frustration" effect. *Learning and Motivation,* 1970, *41,* 227–247.

Staddon, J. E. R. Temporal control and the theory of reinforcement schedules. In R. M. Gilbert & J. R. Millenson (Eds.), *Reinforcement: Behavioral analyses.* New York: Academic Press, 1972.

Staddon, J. E. R. On the notion of cause, with applications to behaviorism. *Behaviorism,* 1973, *1,* 25–63.

Staddon, J. E. R. Temporal control, attention, and memory. *Psychological Review,* 1974, *81,* 375–391.

Staddon, J. E. R. Schedule-induced behavior. In W. K. Honig & J. E. R. Staddon (Eds.), *Operant behavior* (Vol. 2). New York: Appleton-Century-Crofts, in press.

Staddon, J. E. R., & Ayres, S. L. Sequential and temporal properties of behaviors induced by a schedule of periodic food delivery. *Behavior,* in press.

Staddon, J. E. R., & Innis, N. K. Reinforcement omission on fixed-interval schedules. *Journal of the Experimental Analysis of Behavior,* 1969, *12,* 689–700.

Staddon, J. E. R., & Simmelhag, V. L. The "superstition" experiment: A re-examination of its implications for the principles of adaptive behavior. *Psychological Review,* 1971, *78,* 3–43.

Valenstein, E. S., Cox, V. C., & Kakolewski, J. W. Re-examination of the role of the hypothalamus in motivation. *Psychological Review,* 1970, *77,* 16–31.

Wayner, M. J. Motor control functions of the lateral hypothalamus and adjunctive behavior. *Physiology and Behavior,* 1970, *5,* 1319–1325.

Williams, D. R., & Williams, H. Auto-maintenance in the pigeon: Sustained pecking despite contingent non-reinforcement. *Journal of the Experimental Analysis of Behavior,* 1969, *12,* 511–520.

Zamble, E. Classical conditioning of excitement anticipatory to food reward. *Journal of Comparative and Physiological Psychology,* 1967, *63,* 526–529.

Zamble, E., & Kirkwood, R. Discriminative classical conditioning of excitement anticipatory to food reward. *Psychonomic Science,* 1969, *16,* 252–253.

Zener, K. The significance of behavior accompanying conditioned salivary secretion for theories of the conditioned response. *American Journal of Psychology,* 1937, *50,* 384–403.

Zimmerman, D. W. Rate changes after unscheduled omission and presentation of reinforcement. *Journal of the Experimental Analysis of Behavior,* 1971, *15,* 261–270.