Arousal: Its Genesis and Manifestation as Response Rate

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The presentation of an incentive generates a small amount of arousal that decays exponentially over time. If the time interval separating successive incentives is short enough, arousal cumulates to an equilibrium level that is predictable from decay constants derived from the presentation of isolated incentives. The accumulation of arousal accounts for the "excessive" nature of schedule-induced, or adjunctive, behaviors.

These are revolutionary times for behavior scientists. At least three major lines of research —adjunctive behaviors (Falk, 1972), species-specific constraints on learning (Hinde & Stevenson-Hinde, 1973; Seligman & Hager, 1972), and sign tracking (Hearst & Jenkins, 1974; Schwartz & Gamzu, 1977)—have developed over the last decade in response to behavioral anomalies, with proponents of each noting the inconsistency of their subdiscipline with traditional theories of learning (cf. Bolles, 1976). The present article concerns adjunctive, or scheduled-induced, behavior and attempts to provide a rational basis for those "existentially absurd" (Falk, 1972) responses. Falk (1961) was the first to demonstrate that intermittent food schedules induce excessive drinking (polydipsia). He found that rats consumed over half their body weight in water over a 3-hour period, whereas they normally consume less than 10% over a 24-hour period.

Since Falk's initial demonstration of polydipsia, a host of other schedule-induced behaviors have been identified (for review, see Falk, 1972; Staddon, 1977; Wallace & Singer, 1976). Many explanatory hypotheses, such as superstitious conditioning, have been advanced and subsequently eliminated. The most attractive rationale has been provided by Staddon and Simmelhag (1971), Segal (1972), and Falk (1972). They suggested that adjunctive behaviors, which include polydipsia, aggression, and pica, are similar to displacement behaviors; all provide pools of behavior from which crucial responses might be selected by a mechanism such as the law of effect or, over longer periods, by natural selection. Yet, the large amount of time and energy involved in adjunctive behaviors remain a puzzle.

It is our thesis that adjunctive behaviors are normally occurring parts of an organism's repertoire, but that their rate of occurrence is excited to supernormal levels by a heightened level of arousal. The "excessive" arousal is generated by the periodic delivery of food or other incentives, each of which contributes a small amount of arousal; when incentives are closely spaced, the arousal cumulates, building to an equilibrium level that depends on the size of the arousal impulses, their rate of decay, and the time interval between them. To test this theory, we will first determine the time course of arousal following a single incentive and then demonstrate that arousal will cumulate in the predicted fashion.

Temporal Control of Behavior

A convenient measure of arousal is provided by a set of microswitches under the floor of an experimental chamber. Whenever the subjects (in the present case, pigeons) move about the chamber or merely shift their weight in one position, an activity response is scored. Killeen (1975, in press) showed that activity, measured
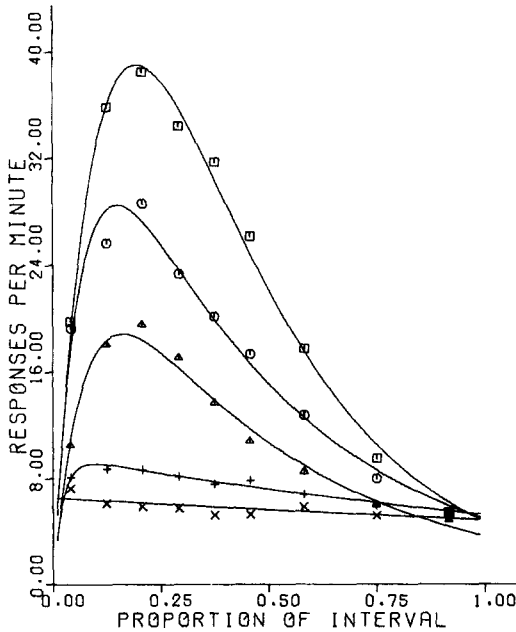
Figure 1. The rate of panel activation as a function of the time since reinforcement. (Interfood intervals range from 25 sec [top curve] to 400 sec [bottom curve]; the abscissa is normalized to range between 0 and 1. From "On the Temporal Control of Behavior" by Peter Killeen, *Psychological Review*, 1975, *82*, 89–115. Copyright 1975 by the American Psychological Association. Reprinted by permission.)

in the above fashion, was induced by periodic food schedules (see Figures 1 and 2). He modeled the time course of such activity with Equation 1, whose parameters are associated with temporal inhibition (*I*), competing behaviors (*C*), and arousal (*A*):

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

These processes are depicted in Figure 3, where the top solid line represents the level of arousal operationalized as the rate of emission of behaviors that would be expected in the absence of inhibition and competition. The right dashed curve represents rate of responding when it suffers competition from ensuing behaviors, such as key pecking or hopper inspection. It is depicted as an exponentially decaying curve with a time-constant *C*. The left dashed curve represents the decay of temporal inhibition—postprandial behaviors and quiescence elicited by the offset of the previous incentive or the onset of a conditioned stimulus (CS) that indicates the immediate

unavailability of other incentives. It is depected as an exponentially decaying curve, with a time-constant *I*. When this inhibitory process is subtracted from the right dashed curve, the line at the bottom results, whose function rule is Equation 1.

If there are additional sources of inhibition or competition—if, for instance, the measured behavior is a terminal operant (Staddon, 1977; Staddon & Simmelhag, 1971)—additional exponential processes with their parameters must be introduced. This system results in a generalized gamma function (McGill & Gibbon, 1965) of which Equation 1 is a simple instance.

If we interpret the dashed lines in Figure 3 as independent random variables, a simplification is possible. Assume that all of the time constants are identical and that the organism is quiescent until *N* inhibitory processes have terminated, after which it engages in the measured behavior for one more "count." This model yields a simple gamma process (McGill, 1963), with parameters λ (count rate), *N* (count threshold), and *A'* (area under the
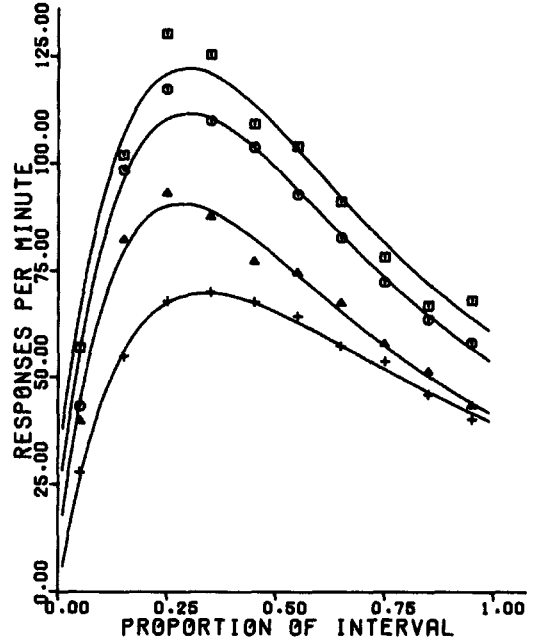

Figure 2. The rate of panel activation as a function of the time since reinforcement for interfood intervals of 5, 10, 15, and 30 sec. (The top three curves have been displaced upward by 30, 20, and 10 responses per minute. Data are from Killeen, 1975.)

curve). In order to obtain a scale factor comparable to A, the asymptotic response rate, we need merely divide by λ and obtain a normalized gamma density:

$$R = A \, (\lambda t)^N e^{-\lambda t}/N! \qquad (2)$$

The assumption of identical time constants is inappropriate for data such as those shown in Figures 1 and 2. But Equation 2 is robust over that assumption, and when fitted to such data, the parameters imply approximately the correct number of exponential processes $(N \cong 2)$ and a time constant $(1/\lambda)$ approximately equal to the average of C and I. Figure 4 shows the average behavior of three pigeons on each of three fixed-interval schedules (data from Hanson & Killeen, Note 1). The dashed lines are drawn from Equation 1 and from a Gaussian function (cf. Killeen, 1975, in press); the solid lines are from Equation 2. The fits are about equally good. The advantage of Equation 2 is that it may be applied both to interim behaviors such as general activity and to terminal behaviors such as key pecking. For the data in Figure 4, the same values of λ will accommodate both activity and pecking at each interfood interval.

Trace of Incentives

This discussion of models for the temporal control of behavior is preliminary to an experimental analysis of one parameter of those models, that is, A. That parameter captures the notion of vigor, response strength, and arousal. Equations 1 and 2 partial out inhibitory processes; we may therefore take advantage of the models to test a hypothesis about the provenance of those excessive levels of arousal that seem to be an earmark of adjunctive behaviors. First, we attempt to measure the time course of arousal induced by incentives and determine its function form. That will permit predictions of how arousal might cumulate. In Experiment 1, we employ a 24-hour interfood interval in order to minimize inhibitory factors, to eliminate competing behaviors such as anticipatory pecking and hopper inspection, and to ensure that the measured arousal level is not reinforced by traces from a previous feeding.
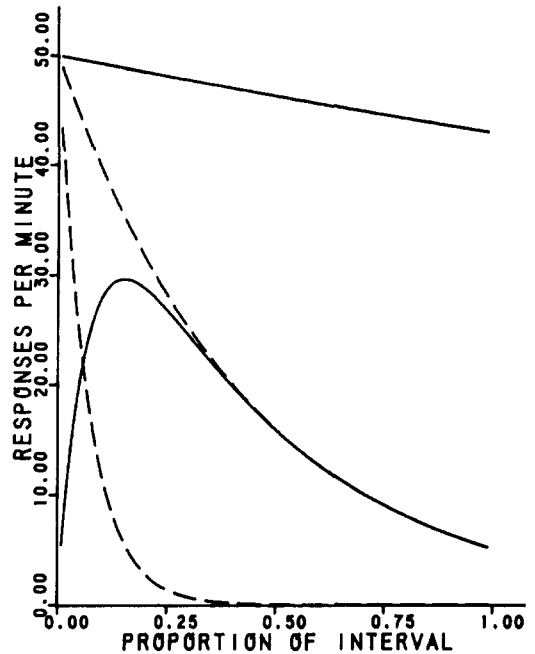

Figure 3. Hypothetical processes underlying the curves shown in Figures 1 and 2. (The top solid line represents the slowly decaying level of arousal [A]; the steepest dashed curve represents the decay of postprandial inhibitions; and the shallower dashed curve represents the onset of competing terminal behaviors. When the former is subtracted from the latter, the solid bitonic curve, representing the time course of observed behaviors, results.)

Experiment 1

Method. Experiment 1A used two common pigeons and was conducted in a standard Lehigh Valley pigeon chamber equipped with six moveable floor panels, three hinged in the front of the chamber and three hinged in the back. After hopper training, the pigeons were given 30 daily sessions, the last 16 of which were used for data analysis. Approximately 3 min after the birds were placed in the chamber, the food hopper was activated and held in place until the pigeons had eaten for 2 sec; 15 min later the chamber was darkened and the pigeons were removed. Movement that occurred after hopper activation was recorded in successive time intervals.

In order to premit extrapolation to the data shown in Figures 1 and 2, Experiments 1B and 1C employed the same chamber used by Killeen (1975). In Experiment 1B, five White Carneaux pigeons were exposed to a single timed 3-sec feeding for 25 sessions. In Experiment 1C, two White Carneaux and one homing pigeon were exposed to a single daily feeding, receiving either 2, 4, or 8 sec of access to food. Each pigeon experienced the different amounts in an irregular sequence, with approximately 20 sessions at each amount. In both experiments, activity was monitored for 15 min after each feeding.
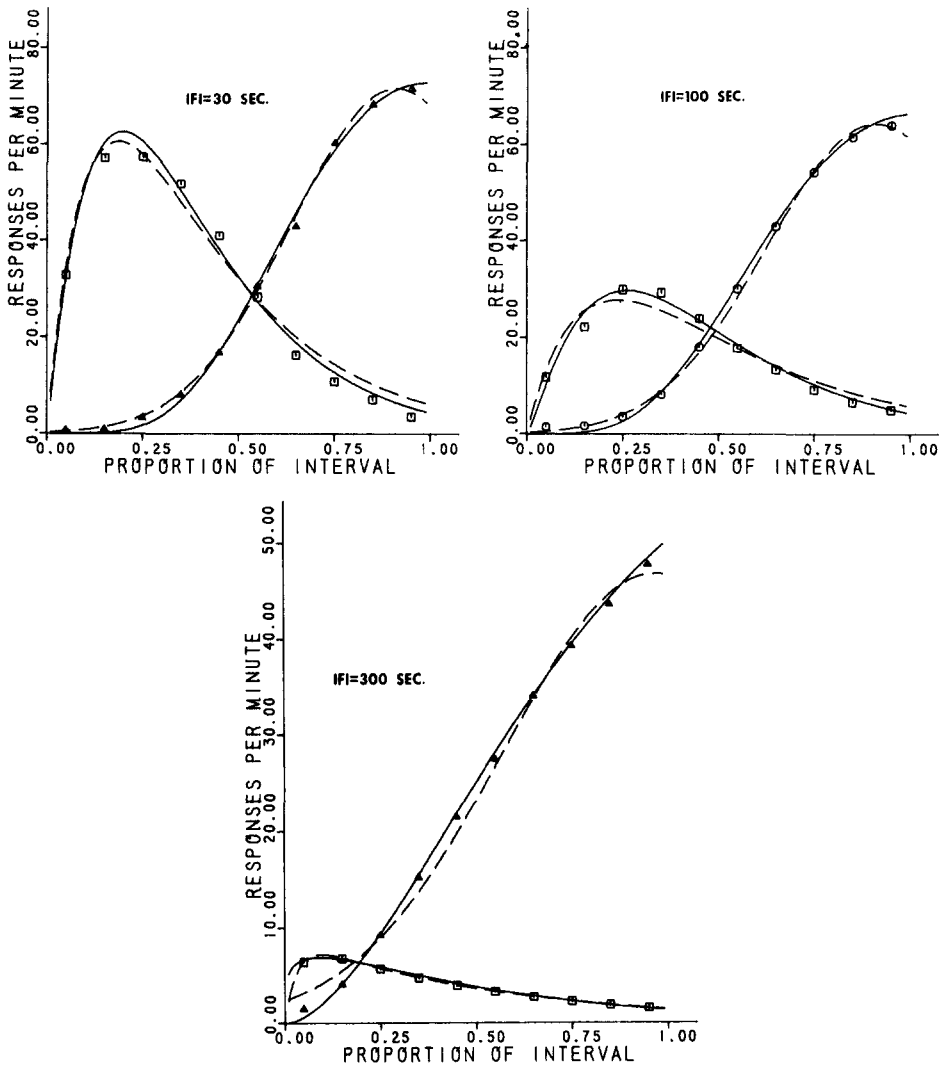
Figure 4. Distributions of activity and key pecking averaged over three pigeons. (The dashed lines are from Equation 1 [activity] or from a truncated Gaussian function [key pecking]; the solid lines are from Equation 2. Data are from Hanson and Killeen, Note 1. IFI = interfood interval.)

Results and discussion. Figure 5 shows the rate of activation of the floor panels as a function of the time since feeding in all three experiments. The data for each experiment are averaged over subjects. In Experiment 1C, the level of activity following a feeding increased with amount of food, but there was no orderly trend in the shape of the functions (Hanson, 1978). The data for different amounts were therefore averaged together.

The effects of a single brief feeding were similar in all three experiments: Activity level increased slightly after a feeding and then

decreased slowly over time. The rate at which activity decreased was well described by an exponential function (solid lines in Figure 5) of the form

$$R = A_1 e^{-t/\alpha}, \tag{3}$$

where R is the predicted rate in responses per minute, A_1 is the intercept of the function at $t = 0$, t is the time in seconds since the feeding, α is the time constant, and e is the base of the natural logarithms. The parameters of the exponential functions are listed in Table 1. In all cases, the time constants are relatively

large, indicating that arousal decays slowly. The index 5α predicts the time necessary for the functions to decrease to 1% of their initial value; it ranges around 30 min.

Cumulation of Arousal

If feedings are delivered more frequently than every 30 min and if arousal cumulates, we would expect to see a higher level of activity with each successive feeding. The quantity A_n, denoting the arousal on the nth feeding, will have decayed by the factor $e^{-T/\alpha}$ (where T is the interval between successive feedings) when the next impulse of arousal, A_1, is added on trial $n + 1$:

$$A_{n+1} = A_n e^{-T/\alpha} + A_1. \qquad (4)$$

Telescoping this difference equation, we get the following:

$$A_2 = A_1(e^{-T/\alpha} + 1) \qquad (5)$$

and

$$A_3 = A_1[(e^{-T/\alpha})^2 + e^{-T/\alpha} + 1]; \qquad (6)$$

by induction, we then get

$$A_n = A_1 \sum_{j=1}^{n} (e^{-T/\alpha})^{j-1}, \quad 0 < T < \infty. \qquad (7)$$
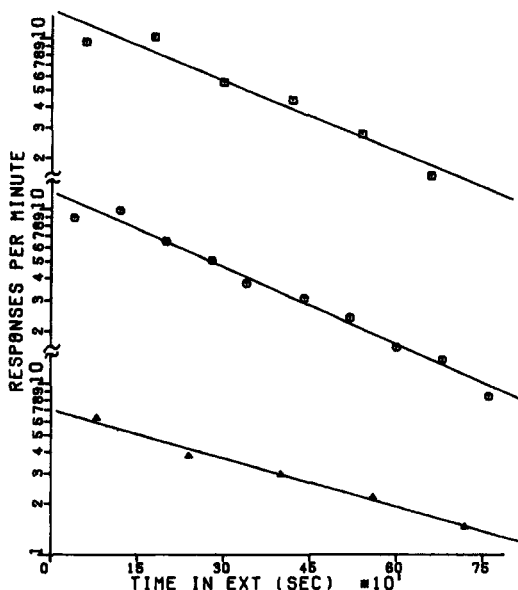

Figure 5. Rates of activity after single feedings. (Straight lines in these coordinates indicate an exponential decay of arousal; parameters are given in Table 1. EXT = extinction.)

Table 1
Parameters of the Functions Shown in Figure 5

Experiment	A_1 (in responses/min)	α (in sec)
1A	14.5	315
1B	12.5	300
1C	7.0	463
Average of 1B and 1C	9.7	380

The sum of this geometric series takes the more convenient form:

$$A_n = A_1 \frac{1 - e^{-nT/\alpha}}{1 - e^{-T/\alpha}}. \qquad (8)$$

However, Equation 8 models only the peak values of arousal and does not take into account the decay that occurs between successive feedings. To obtain the average arousal on any one trial, we must multiply by $e^{-t/\alpha}$ and integrate over the interval $(0, T)$:

$$\bar{A}_n = \frac{1}{T} \int_0^T \frac{A_1(1 - e^{-nT/\alpha})e^{-t/\alpha}}{1 - e^{-T/\alpha}} \, dt. \qquad (9)$$

This yields the following:

$$\bar{A}_n = \frac{A_1 \alpha}{T}(1 - e^{-nT/\alpha}). \qquad (10)$$

Equation 10 may also be derived from weaker stochastic assumptions, that is, assumptions that allow a random interfood interval (T) and random unit arousal amplitudes (A_1; see Appendix). Figure 6 demonstrates how arousal cumulates for a time constant of 360 sec and interfood intervals of 30 sec and 120 sec. The envelopes are derived from Equation 8 and depict the increase in arousal from one interval to the next.

Given time constants for the decay of arousal for a single feeding and a model for the cumulation of arousal over successive feedings, we may now address the question of whether the exponential–integral curves generated by Equation 10 account for the time course of activity when organisms are shifted to periodic feeding schedules. However, before this question can be answered, the effects of accumulating inhibitions must be taken into account. The temporal patterning of response rates results from the interaction between the level
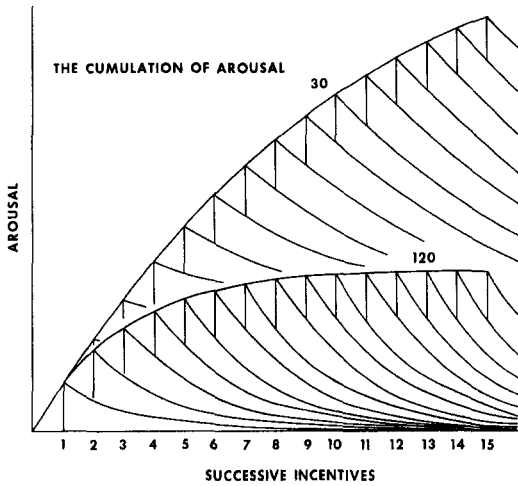
THE CUMULATION OF AROUSAL

AROUSAL

SUCCESSIVE INCENTIVES

Figure 6. The manner in which arousal might cumulate, given the parameters from Figure 5 and interincentive intervals of 30 sec and 120 sec. (The envelope is from Equation 8.)

of arousal (A) and competing behaviors that arise under periodic feeding schedules (whose time courses are indexed by I and C). Consequently, the growth of response rates cannot be predicted from the cumulation of the arousal function until these inhibitory processes are included. The simplest assumption is that inhibition grows in the same fashion as excitation and combines algebraically with it to determine average response rates; that is, arousal is reduced at any moment after the feeding by the inhibitory quantity $e^{-t/\omega}$. This new construction should account for response rates occurring on trial $n + 1$, given the initial arousal level (A_1) and its rate of decay (α):

$$R_{n+1} = A_n(e^{-t/\alpha} - e^{-t/\omega}) + A_1. \quad (11)$$

Solving this equation results in a form similar to Equation 10 but includes the parameter ω, the time constant for aggregate inhibitory processes, to be estimated from the data:

$$\bar{R}_n = \frac{A_1\alpha}{T} \left[1 - (e^{-T/\alpha} - e^{-T/\omega})^n\right]. \quad (12)$$

Experiment 2 provides a test of the above models.

Experiment 2

Method. The experimental chamber was the one used in Experiments 1B and 1C. In Experiment 2A, the subjects of Experiment 1C were shifted to a 3-sec

feeding every 50 sec. In Experiment 2B, two White Carneaux pigeons were shifted from a 300-sec interfood interval to a 30-sec interval. In both experiments, activity level was recorded for each successive feeding.

Results and discussion. Figure 7 shows activity rates from the first session of successive feedings when the interfood interval was 30 sec (Experiment 2B) or 50 sec (Experiment 2A). The unconnected symbols represent the obtained data; the dashed lines were generated from the solution of Equation 12 using the average values of A_1 and α obtained in Experiments 1A, 1B, and 1C. Note that in both cases, the solution to Equation 12 provides a good description of the data.

Subsequent sessions do not start with the low response rate of the first; apparently, the experimental chamber becomes a conditioned elicitor of activity, for there is a progressive increase in the starting level of activity from one session to the next. This conservation of arousal via situational conditioning permits a cumulation of arousal from session to session as well as from interval to interval. Such conditioning also occurred in the one trial per day experiments, but since primary arousal was always small, the conditioned arousal was minimal.

Asymptotic Arousal

Given the constants A_1 and α, asymptotic levels of arousal may be predicted. As the number of intervals increases, Equation 10 reduces to Equation 13:

$$\lim_{n \to \infty} \bar{A}_n = A_1\alpha/T, \quad (13)$$

or simply to

$$A = kR, \quad (14)$$

where A is the asymptotic average arousal, k is the product of A_1 and α, and R is the rate of incitement, $1/T$.

In Figure 8, we display the values of A obtained by Killeen (1975) for the data shown in Figures 1 and 2. We may attempt to predict those values from the results shown in Figure 5 and Table 1. Taking as k in Equation 14 the product of the obtained A_1 and α found in Experiments 1B and 1C (see bottom of Table 1), we predict a proportionality between A

and rate of incitement, with a slope of 61 responses per incentive. In the logarithmic coordinates of Figure 8, this translates to a unit diagonal with an intercept of 61, the solid line in Figure 8. The regression equation has an intercept of 53. Given the existing variability among subjects, this prediction is quite good and not significantly different than the obtained regression line. We emphasize that the solid line in Figure 8 is not a regression, not an extrapolation, and not a post hoc "accounting for"; it is a parameter-free pre-

diction from one experimental paradigm to another quite-different paradigm. The prediction was based on the measurement of fundamental constructs (A_1 and α) and their instantiation in a model for the cumulation of arousal.

Furumoto (Note 2) replicated the data shown in Figures 1 and 2 with both domestic and feral pigeons. We have fitted Equation 1 to her average data and display the As in Figure 9. Although we do not know A_1 (and therefore k) for her experiment, our model
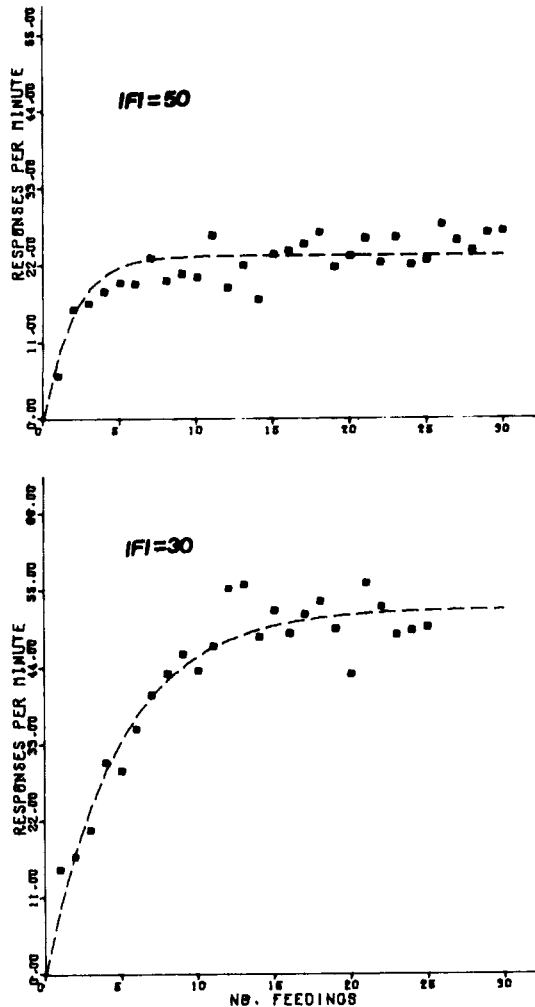

Figure 7.   Rate of activity during successive intervals when pigeons are first exposed to periodic feedings at 50-sec and 30-sec intervals. (The dashed lines are from Equation 12, with parameters A_1 and α taken from Table 1. ωs were 50 sec and 16 sec for the 50-sec and 30-sec intervals, respectively. IFI = interfood interval.)
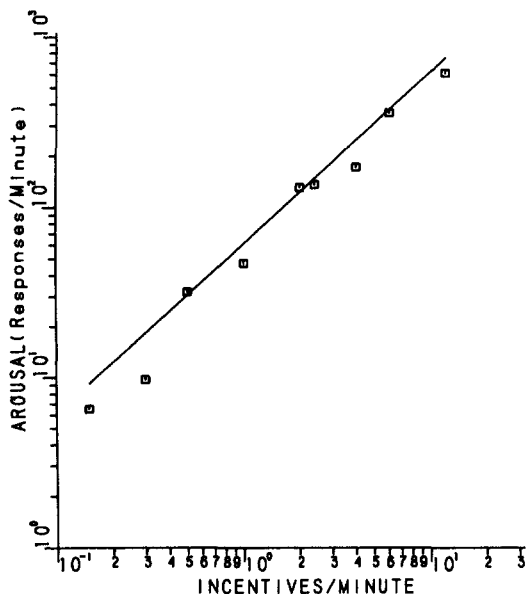
Figure 8. Theoretical level of arousal obtained by Killeen (1975). (Predictions from Equation 14 using the values of A_1 and α obtained from Table 1 are represented by the solid line.)

does predict that the relation between A and rate of incitement be linear with zero intercept. Furumoto's data support that prediction.

Other Adjunctive Behaviors

Scheduled-induced polydipsia is the prototypical adjunctive behavior: It was the first to be so labeled, it is obviously "excessive," and it has been the most thoroughly investigated of all adjunctive behaviors. Killeen (1975) recorded the time course of scheduled-induced drinking in rats exposed to various feeding schedules. We have refitted those data with Equation 2 and plotted the As in Figure 9 as plusses. They too are an approximately linear function of the rate of incitement.

The As from the activity functions shown in Figure 4 are also displayed in Figure 9. Although the small number of data points preclude a test for quadratic trend, the locus of the points appears to be slightly concave.

The prediction of linearity fails when Equation 2 is applied to instrumental behaviors. As from Figure 4, from Lowe and Harzem (1977), and from Catania and Reynolds (1968) are presented in Figure 9. The first two curves are negatively accelerated.

This bending may be due to physical ceilings on response rates (cf. Killeen, in press). But that explanation does not suffice for the instrumental behavior of rats, whose asymptotes (derived from Lowe & Harzem, 1977; Dukich & Lee, 1973; not shown in Figure 9) are relatively constant over different rates of incitement.

Greater insight into the relations shown in Figure 9 may be gained from considering the slope constant k. Our development equates this to $A_1\alpha$, the product of the intercept and slope of the unit arousal curves shown in Figure 5. The integral of those curves—the total number of responses that a single incentive will sustain—is also equal to $A_1\alpha$. The coefficient k, therefore, measures the constraint that an incentive exerts on the measured behavior, or the "preparedness" (Seligman, 1970), of organisms to respond after that incentive. The value of the coefficient depends on the units in which the response is measured, and comparisons will be most meaningful when a common unit, such as time spent responding, is employed (Baum, 1976; Premack, 1965; Rachlin & Burkhard, 1978; Staddon, in press). Even so, the coefficients for pecking are an order of magnitude greater than those for activity and polydipsia. We conclude that pecking is a highly prepared response for pigeons. Conversely, the coefficients for rat's lever pressing were close to zero, and the regression lines had large intercepts. Lever pressing, we argue, is not induced by the incentives but is brought about only by contingent reinforcement. Whereas reinforcement contingencies may merely redirect prepared responses (Barrera, 1974; Staddon & Simmelhag, 1971), they may generate de novo unprepared responses (LaJoie & Bindra, 1976). Such new behaviors may not be susceptible to induction by heightened levels of arousal.

Conclusions

We have demonstrated that the small elevation in arousal impelled by small amounts of food may cumulate, leading to an exponential-integral growth in activity with each feeding and, at asymptote, leading to a proportional relation between rate of feeding and arousal level. Whereas there are many ways to generate a heightened level of arousal (large amounts
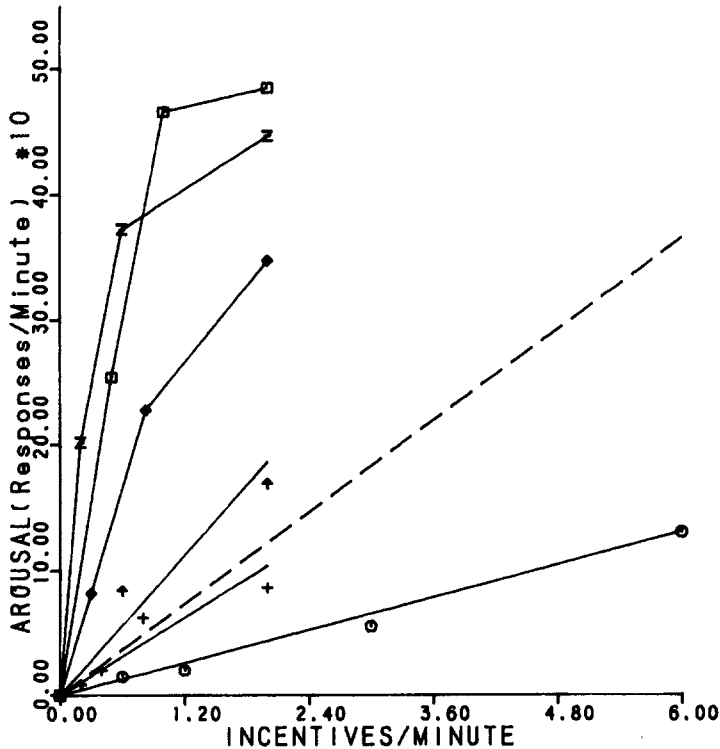
Figure 9. Asymptotic levels of arousal from various experiments. (The dashed line represents the prediction from Equation 14 for the data shown in Figure 8. Furumoto's, Note 2, data are represented by circles; the polydipsia data by plusses; Hanson and Killeen's, Note 1, activity by umbrellas and key pecking by the letter *Z*; Lowe and Harzem's, 1977, data by squares; and Catania and Reynolds's 1968, data by diamonds.)

of food, electric shock, species-specific threats, etc.), either such stimuli concomitantly decrease arousal through satiation, or the vigorous responses that are elicited seem appropriate to the salience of the stimuli. It is only when animals are titillated with small periodic incentives that the ensuing "adjunctive" behaviors have time to unfold and are deemed inordinate and anomalous.

Not all behaviors are equally instigated by heightened levels of arousal. This difference between behaviors may be captured by the slope constant *k*, a "coefficient of constraint." Coefficients were lowest for rat's lever pressing and highest for pigeon's key pecking. When measured in commensurable units, such as time engaged in activity, this coefficient may provide a metric for response preparedness.

Reference Notes

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2. Furumoto, L. *Temporal control of activity in White Carneaux and feral pigeons.* Unpublished manuscript, 1977.

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Appendix

Alternate derivation of the fundamental equations

We demonstrate that Equation 10 may be derived from weaker stochastic assumptions, ones that are more commensurate with typical foraging conditions (Pyke, Pulliam, & Charnov, 1977).

Suppose that both feeding duration and time of feeding are random, thus producing random unit arousal amplitudes occurring in time according to a Poisson process. Suppose also that the initial arrival amplitudes are independent and have some common distribution. We have already shown that the amplitude of the arousal impulses at arrival decay exponentially with time constant α.

If $S_1, S_2, \ldots$ are the feeding times and $A_1, A_2, \ldots$ are the amplitudes of the arousal impulses, then

$$A(t) = \sum_{k=1}^{N(t)} A_k e^{-(t-S_k)/\alpha} t > S_k \quad (A1)$$

represents the total arousal amplitude at time t after $N(t)$ feedings. The first moment of this density is of interest and will be most conveniently found by computing its characteristic function, that is,

$$\phi'_A(u) = E[e^{iuA(t)}]. \quad (A2)$$

This function is shown (Ross, 1970) to be the following:

$$\phi'_A(u) = \sum_{k=0}^{\infty} e^{-\lambda t} \frac{(\lambda t)^k}{k!} \left[\frac{1}{t} \int_0^t \phi_A(ue^{-y/\alpha}) dy \right]^k,$$
$$(A3)$$

which reduces to

$$\exp\left\{ -\lambda \int_0^t [1 - \phi_A(ue^{-y/\alpha})] dy \right\}. \quad (A4)$$

The first moment of the arousal cumulation density is simply the first derivative of the characteristic function evaluated at 0:

$$E[A(t)] = \frac{d\phi_A(u)}{idu} \bigg|_{u=0} \quad (A5)$$

$$= \lambda \int_0^t \frac{d\phi_A(0)}{idu} e^{-y/\alpha} dy, \quad (A6)$$

where $u = 0$ and ϕ_A is the characteristic function of A_1, then,

$$E[A(t)] = \lambda E(A_1)\alpha(1 - e^{-t/\alpha}). \quad (A7)$$

Let $t = N*E(T)$, the number of feedings times the expected interfood interval, and $\lambda = E(R)$, the mean rate of feeding.

Equation A7 then becomes equivalent to Equation 10:

$$E(R)E(A_1)\alpha(1 - e^{-E(T)*N/\alpha}). \quad (A8)$$

For large N, it reduces to a linear relation between feeding rate and expected asymptotic arousal:

$$E(A_\infty) = E(R)E(A_1)\alpha. \quad (A9)$$