THE DEVELOPMENT OF FIXED-RATIO PERFORMANCE UNDER THE INFLUENCE OF RIBONUCLEIC ACID[1,2]

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The transition from fixed-ratio 1 performance (every response reinforced) to fixed-ratio 30 performance (every thirtieth response reinforced) was studied in nine pigeons. These were divided into three treatment groups given daily oral doses of saline, or 250 mg/kg/day or 500 mg/kg/day of yeast ribonucleic acid. Detailed computer-assisted analyses of how fixed-ratio behavior develops revealed the following typical sequence. After the transition, the first few ratios typically were emitted without long interresponse times within the ratio. Steady responding then ceased, and numerous long interresponse times occurred, with no systematic relationship to ordinal position within the ratio. Gradually, a new pattern evolved, characterized by a consistently long post-reinforcement time, a border region of the next few interresponse times within which the mean interresponse time monotonically decreased, and short interresponse times within the last 80% of the ratio. Long interresponse times were eliminated from this last section of the ratio without regard to proximity to reinforcement. Various analytical procedures suggested that the final pattern can be conceived, in part, as the shaping of a reliable response topography. The group of three pigeons given 250 mg/kg/day of yeast ribonucleic acid responded at higher rates than the saline and 500 mg/kg/day groups. The latter group, in contrast to the saline and lower dose groups, which continued to increase their rates, reached a rate asymptote very early.

Morse (1966, p. 77) astutely observed that: "A simple schedule is one that is simple to specify and program rather than one that has a simple relation to behavior." Such a statement forcefully applies to the fixed-ratio (FR) reinforcement schedule. Despite the fact that both Skinner (1938) and Ferster and Skinner (1957) devoted large sections to it, that it has been the focus of many papers on operant behavior, that it is often employed as a baseline for studies of other variables, such as drugs, and that frequently it is seen to act in natural environments, it still presents puzzles of interpretation. For example, it is not yet wholly clear which aspects of the conventional FR schedule determine the typically observed FR pattern—a period of no responding directly after reinforcement followed by a period of relatively high response rate until the ratio requirement is fulfilled.

Two basic views about the sources of FR performance currently predominate. One sees it as a chained performnace (e.g., Ferster and Skinner, 1957), defined as, "a sequence in which each response functions as a discriminative (or eliciting) stimulus or produces a discriminative (or eliciting) stimulus" (Kelleher, 1966, p. 163). The other view sees it as the emission of a unit; that is, the entire ratio functions as a single response. Skinner (1938) defined this alternative. In practice, it is difficult to specify experimental manipulations or characteristics of performance that clearly distinguish between these alternatives (Kelleher, 1966).

One source of support for the unit view comes from Zeiler (1970). He made reinforcement dependent on whether pigeons completed a ratio within a designated maximum length of time, or, conversely, whether they exceeded a specified minimum. Both contingencies exerted control, affecting the length

of the post-reinforcement period before responding resumed as well as the subsequent rate of responding within the ratio. Kelleher, Fry, and Cook (1964), however, demonstrated that separate control could be exerted over the post-reinforcement period by using its duration alone as the element of a contingency.

Similar issues pervade interpretations of the behavior maintained by other reinforcement schedules. As an example, the pattern of responding through the interval characteristic of fixed-interval (FI) performance has been interpreted primarily as a function of delay of reinforcement (*e.g.*, Dews, 1962), and, more recently, analyzed as a two-state (non-responding and responding) process (Schneider, 1969).

A substantial part of the present discrepancies in interpretation of schedule-controlled behavior can be ascribed to the constraints of technology. The answers to many current problems require a microanalysis of behavior, which, in turn, demands an ability to acquire and store large quantities of data with precise temporal resolution and with serial order preserved, and to manipulate these data quickly and easily. Such an ability is provided by the digital computer. Another source of discrepancies is our incomplete knowledge of how the behavior evolves to its final form. The present study was an attempt to clarify the variables that act on FR performance by closely examining the transition from continuous reinforcement (FR 1) to FR 30. A detailed examination of how FR performance develops should help illuminate the sources of control, separate currently posited alternatives, and perhaps provide new ones.

An ancillary purpose of this experiment was to determine whether the chronic administration of yeast ribonucleic acid (RNA) would affect the course of the transition. RNA has been reported to produce behavioral effects, especially during acquisition (*e.g.*, Cook and Davidson, 1968), and a further examination of its properties seemed warranted, particularly during transition performance.

METHOD

Subjects

Nine male White Carneaux pigeons, obtained as castrated cocks from the Palmetto Pigeon Plant, ranged in age from 1.5 to 3 yr at the start of training. The pigeons were housed in a rack of individual bird cages in a temperature-controlled animal room with a 13:11 light-dark cycle, and maintained at 80% of free-feeding weights by post-session feeding in the home cage.

Apparatus

A large sound-insulated metal chamber with sound-deadened wooden partitions housed three standard stainless steel operant conditioning chambers (Foringer) in separate closed compartments. The chambers measured 14 in. long by 11 in. wide by 11.5 in. high (35 by 28 by 29 cm). The front, right, and rear walls were of stainless steel, the left wall and top, of Plexiglas. Each chamber was equipped with a 4-w houselight, a 2500-Hz tone device (Sonalert) for response-contingent auditory feedback, a speaker for white noise and a relay-operated, hopper-type feeder (Lehigh Valley Electronics). The 2 by 2.5 in. (5 by 6.3 cm) feeder aperture was centered 4.25 in. (11 cm) above the floor. The operandum was a wall-mounted translucent plastic key and microswitch assembly (Lehigh Valley Electronics), requiring 18 g (0.177 N) of static force to operate, with a rear-mounted yellow stimulus light (Sylvania 28ESB). The 1-in. (2.5-cm) diameter circular opening for the response key was centered 9 in. (22.5 cm) above the floor. A one-way viewing device in the outer door of each chamber permitted observation of each subject. All devices were interfaced to a classic LINC computer (Clark and Molnar, 1965) by solid-state logic and power modules (System Modules, Digital Equipment Corporation) and a plugboard system (MacPanel Corporation). Further details of the system may be found in Gott (1969) and Weiss (*in press*).

Procedure

Subjects were magazine-trained in the experimental chambers. Their behavior was shaped by manual feeder operation until they oriented toward the operandum. They were then left unattended with the FR 1 schedule in effect, so that each response on the key that closed the microswitch operated the feeder. Four subjects (869, 768, 924, 1528) spontaneously began responding in the first session. Other subjects were provided with a "punchboard" training device (Ferster and Skinner, 1957, p. 32) in the home cages after the first session. They were also given varying amounts

of shaping of the key-peck response in the experimental chambers. All subjects were pecking the key by Session 4. Fifteen further daily sessions of 40 reinforcements each on FR 1 were then given each pigeon. Each reinforcement, during this and later phases of the study, consisted of access to mixed grain for 3 sec. This sequence was followed by a nine-week period of inactivity during which the experimental apparatus and operating program on the LINC were modified.

Subjects were randomly divided, before training, into three treatment groups and given daily oral doses of yeast RNA hydrolysate ("Yeast Nucleic Acid," P. L. Biochemicals, Milwaukee, Wisconsin). Treatment Group A (Birds 1576, 911, 942) received 500 mg/kg as a 200 mg/cc NaOH-neutralized RNA solution. Group B (Birds 1699, 764, 1528) received 250 mg/kg. Group C (Birds 869, 868, 768) received 9 cc/kg of isotonic saline, to equal the saline content of the higher RNA dose.

The experiment began with the first daily RNA administration, nine weeks after the last FR 1 session. On the eleventh day of drug administration, daily sessions of 40 reinforcements each on FR 1 were resumed. On Day 21 of drug administration, the schedule was changed from FR 1 to FR 30 after the twentieth reinforcement, so that 30 key pecks were required for reinforcement.

Three subjects were studied simultaneously, under individual control, by the computer. Interresponse times (IRTs) were stored on magnetic tape with a resolution of 40 msec. Each subject was given a daily session until 40 reinforcements. An initial timeout of 10 min preceded each run.

RESULTS

Certain characteristics of responding following the change from FR 1 to FR 30 were similar for all birds except one (No. 1699). Initially, the responding was rapid and connected, with few long IRTs. After one or more reinforcements, depending on the subject, responding became more sporadic. The duration and frequency of unusually long IRTs increased in successive ratios, appearing in all ordinal positions through the ratio. Gradually, thereafter, the incidence of long IRTs declined throughout the ratio, the duration of the period after reinforcement before respond-

ing resumed, usually called the postreinforcement pause, became consistently longer than any of the IRTs within the ratio, and a relatively stable performance developed. To avoid the implication that the lengthened interval after reinforcement represents an interruption in responding equivalent to interruptions in other sections of the ratio, we will call it the post-reinforcement time (PRT).

Cumulative records. A conventional perspective on these behavioral characteristics is provided by computer-plotted facsimiles of the cumulative records. Many birds exhibited the features described by Ferster and Skinner (1957, p. 42) in their stylized plot of transition from CRF to a short FR. For example, Figure 1, for Bird 1576, shows that the first ratio was executed rapidly (region A). Disruption characterized by long periods without responding occurred early in ratio 2 (region B). The next group of six ratios, at C, represents a period of highly variable local rates superimposed on a slight deceleration, which corresponds to the secondary inflection of Ferster and Skinner's stylized transition. The sudden reduction of long IRTs in region D produced a group of ratios with features corresponding to final performance. The plot next on the left is for the following session (Day 1), and shows responding continuing at a rapid rate with much less variability.

The general features of the stylized transition were seen in most of the other subjects as well, although the point at which each feature appeared varied with the subject. Only one bird showed no extended interruptions of responding after the transition.

Individual IRTs following the change to FR 30. Plots of successive IRTs within the ratio offer a different perspective than the cumulative records. Figure 2, for Bird 1576, illustrates the abrupt onset of unstable performance in the second ratio on FR 30. Long IRTs occurred in various positions in later ratios, with no consistency in placement visible at this time. The beginning and the end of the ratio could not be distinguished by the incidence of long IRTs. Plots of individual IRTs also show the gradual recovery of cohesive responding and the evolution of the FR response pattern. They emphasize the changes over time in IRT variability throughout the ratio.

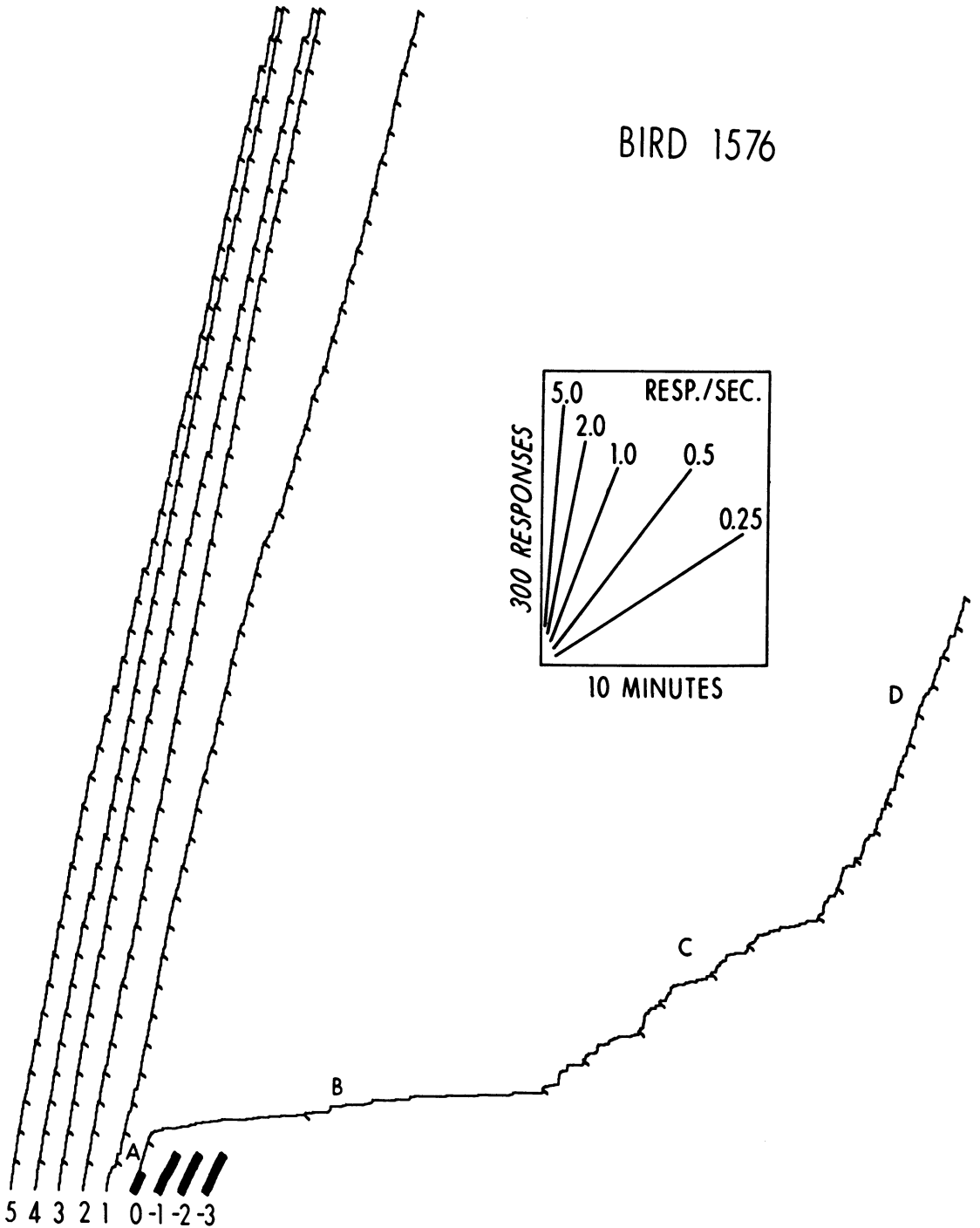Figure 3, for Bird 924, illustrates the con-

Fig. 1. Computer-plotted facsimiles of cumulative records for sessions before and after the day of schedule change to FR 30 (Bird 1576). Successive sessions appear from right to left, with the day of change indicated as Session 0. Each continuous tracing represents one complete session with a maximum of 40 ratios.
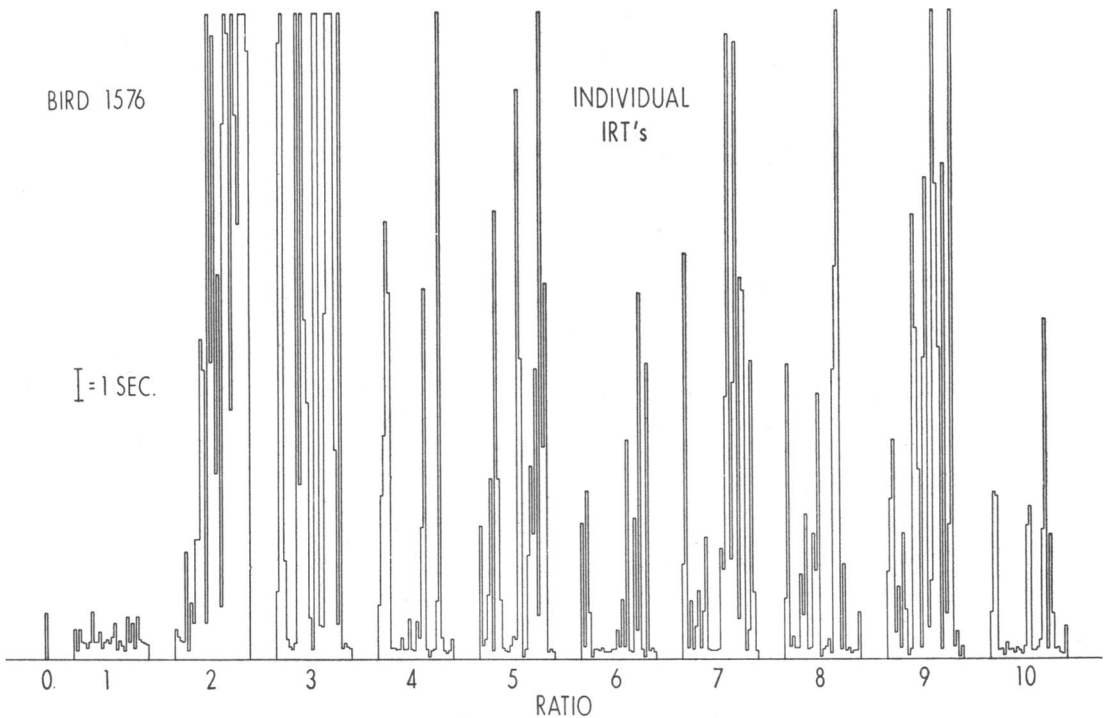
Fig. 2. Plots of individual IRTs following the change to FR 30 (Bird 1576). Each figure shows the last ratio on FR 1 at the left and then the first 10 ratios on FR 30. Each ratio is plotted with the first IRT (the PRT) at the left and the reinforced IRT at the right. Each bar represents one IRT. The time scale for IRT duration is indicated on the figure.

sistency that may be achieved in just two or three sessions. Ratios 61 to 65 show the uniformity achieved by the start of Session 2 after the switch to FR 30. Ratios 96 to 100 for Bird 924 display the FR pattern attained by the end of Session 3, which closely resembled the final pattern. The PRT was prominent, and variability low among the succeeding IRTs. Although further subtle changes continued to occur, the essential features of FR responding developed in this bird within 100 ratios.

Mean ordinal IRTs with standard errors: variability across sessions. Averages based on total session performance can also help clarify certain features of developing FR performance. Figure 4 presents session mean IRTs, based on complete sessions of 40 ratios, and the associated Standard Errors of the Means (SEM) for Bird 924.

Data are grouped by ordinal position in these plots, with ordinal positions represented in succession. Ordinal position 30 lies at the extreme left, and ordinal position 2 at the right; the PRT (ordinal position 1) is not shown. The first eight sessions on FR 30 are

depicted in each group of bars, with Session 1 at the left (the elevated end) and Session 8 at the right.

Figure 4 illustrates the major features seen for most subjects. Note first the large degree of correspondence between the two measures. Both the Mean Ordinal IRTs and the SEM generally were largest in Session 1. Each ordinal position showed a sharp decline between Sessions 1 and 2, and a gradual decline (an IRT gradient across sessions) for several sessions thereafter. A second gradient developed over the ratio after Session 1. This gradient runs from right to left in the low-order positions (at the right) in both measures, and persisted despite the gradual reduction in magnitude at all ordinal positions (except the first) through the ratio.

The transition to FR 30 performance as reflected in IRT distributions. Still another perspective is afforded by IRT distributions for the sessions following the change to FR 30. The next group of illustrations shows these distributions with a temporal resolution of 40 msec.
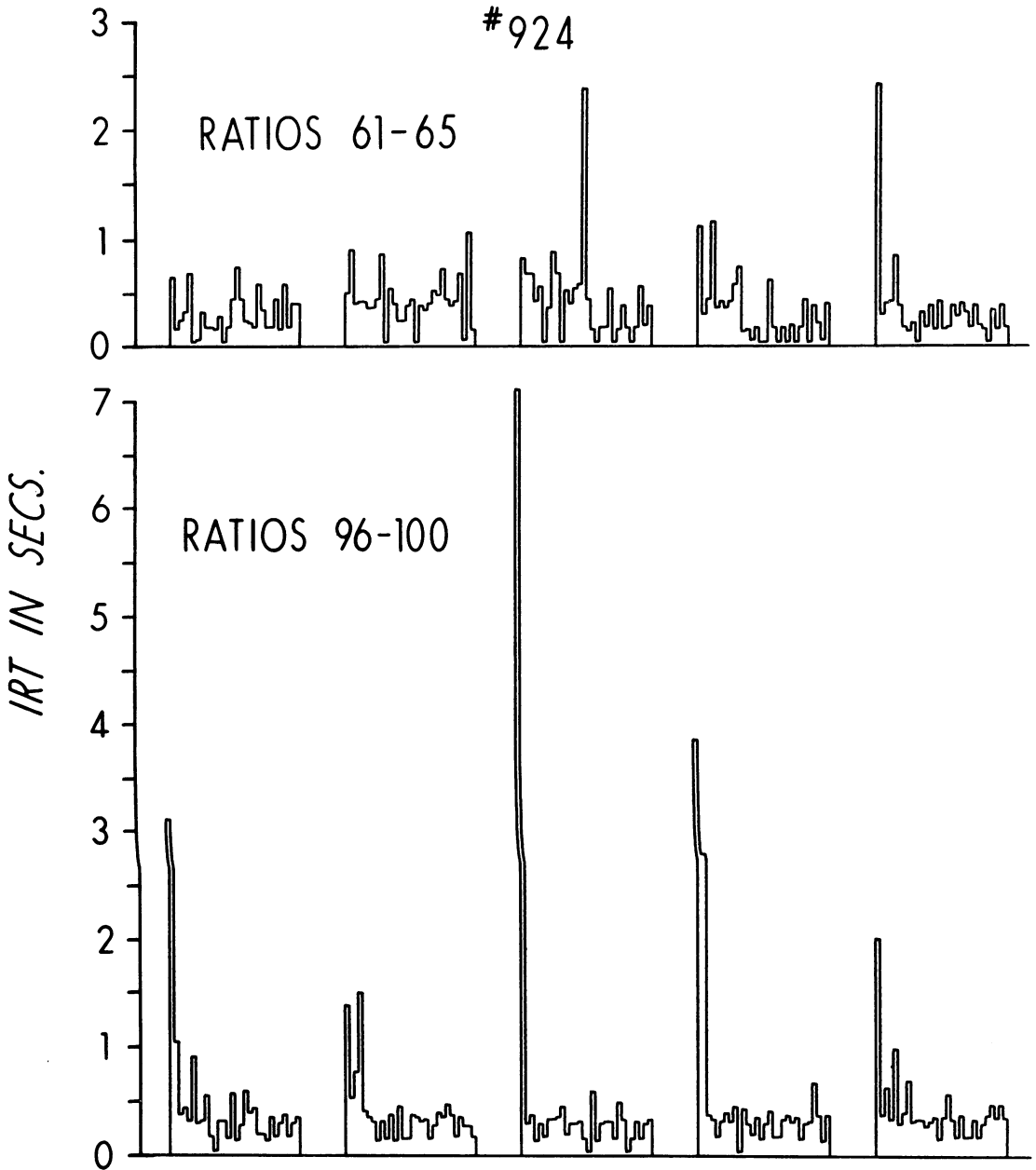
Fig. 3. Transition to FR 30 shown by plots of individual IRTs (Bird 924). See Legend for Figure 2. This figure shows two groups of five ratios selected from the beginning and end, respectively, of the session two days after the change to FR 30. Note the stable within-ratio responding and the prominence of the PRT.

The major component of the stabilized response topography in most birds was the well-defined pecking motion directed at the response key. During the transition after the change to FR 30, this was not always the predominant type of response, however. In those early sessions other topographies often appeared.

Many subjects displayed two response variants. One was "biting", or grasping with the beak the metal edge of the key opening in the front wall of the box. The second was a rapid
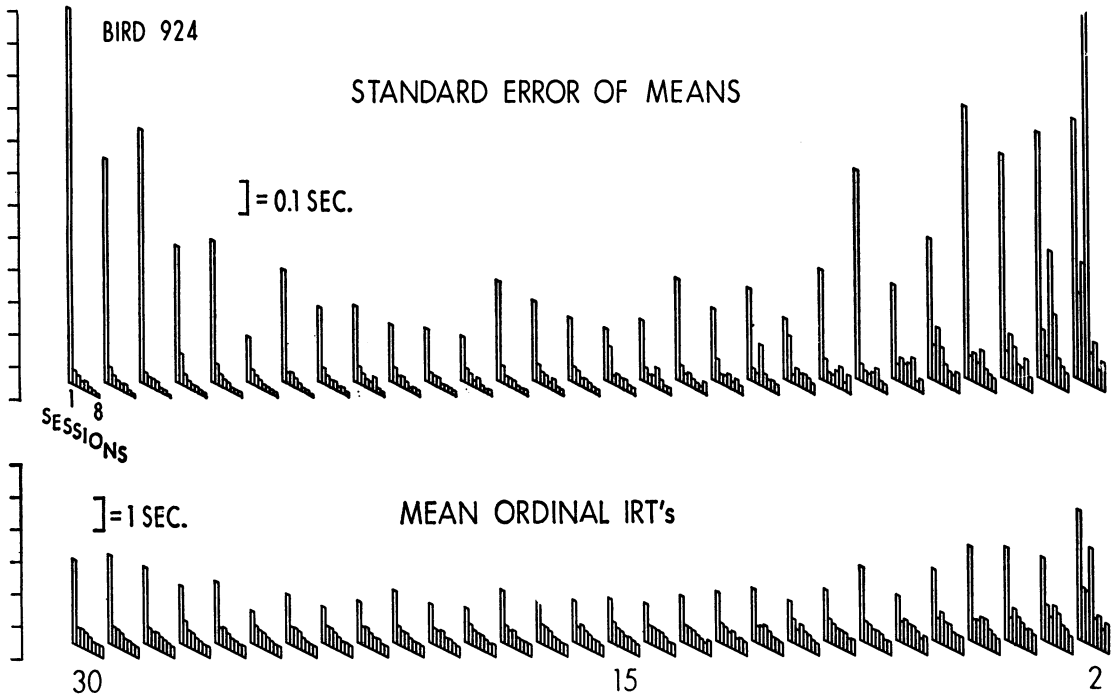
Fig. 4. Mean ordinal IRTs (bottom) and standard error of mean (top) for Bird 924. The session mean IRT value at each ordinal position is plotted for the first eight sessions following the change to FR 30. Each bar in the lower half represents the mean of 40 IRTs and each bar in the upper half represents the corresponding standard error of the mean. These measures are grouped by ordinal position with IRT 2 (following the PRT) at the right and the reinforced IRT (IRT 30) at the left. Each group of eight bars represents successive daily values with Session 1 at the left rear and Session 8 at the right front. Note that the scale for the standard error is 10 times that for the mean values.

"nibbling" motion, in which the conventional rhythmic alternation of thrusting toward and withdrawing from the key was not seen. Instead, the head was held close to the key, where it made slight rapid bobbing motions accompanied by opening and closing of the beak against the key. The two phenomena of nibbling and biting were, singly or jointly, observed in most birds. Both types of response are termed "nibbles" in this paper.

Birds with a high incidence of nibbles also displayed a high incidence of relatively short IRTs. Bird 1699 maintained this topography throughout the transition period and beyond. Figure 5 illustrates its IRT distribution in Session 8. A single large peak is present at 120 msec. This mode corresponds to a response rate of somewhat more than eight responses per second. The calculated within-ratio rate (ignoring only PRTs) was 5.1 responses per second, a lower but nonetheless very high value.

What might be called the traditional, clean-

cut, pecking response is illutrated in Figure 6, which presents the distribution for Bird 1528 in Session 8. The major group of IRTs in this distribution is centered at 320 msec, corresponding to a rate of just over three responses per second. Within the predominant group lay 82% of all IRTs in the session, as reflected by the calculated within-ratio rate of 2.9 responses per second. Note, incidentally, that a small nibble mode was present at 80 msec, containing 3% of the IRTs.

A third major response component probably was the result of intermittent failure of the beak to contact the key during a pecking motion. For most subjects in early sessions, and for a few subjects after many sessions, effective pecks on the key often were followed by one or more pecking motions which failed to strike the key. Typically, these motions ended in striking the box wall, but sometimes they ended short of any physical contact, yielding the appearance of a "feint" toward the key. The significance of these motions in the over-
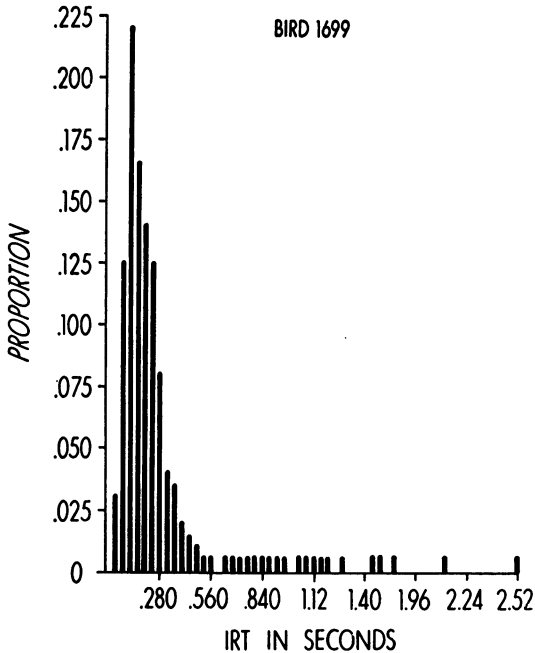
Fig. 5. Normalized histogram plot of the IRT distribution based on 1200 responses for Session 8, Bird 1699. The temporal resolution is 40 msec/bin on the abscissa.

Fig. 6. Normalized histogram plot of the IRT distribution based on 1200 responses for Session 8, Bird 1528. The temporal resolution is 40 msec/bin on the abscissa.

all performance varied with the subject, and was reduced with experience in all birds.

One result of this topography of regular, rhythmic, but intermittently ineffective responding was a striking multimodal appearance in the IRT distributions, which also has been observed on variable-interval schedules (Blough, 1963; Weiss, 1970a). A clear example of this component is illustrated by the IRT distribution of Bird 911 in Session 6 (Figure 7). It displays a series of regular peaks with declining amplitudes and a common intermodal spacing of about 320 msec. Because of these properties, such distributions are called "harmonic", since the later peaks are multiples of the dominant one. The lowest (leftmost) grouping is typically the largest, and is referred to as the fundamental mode. Higher modes are designated by their ordinal positions as "first harmonic", "second harmonic", *etc.* Nearly all subjects exhibited at least a small first harmonic mode in the IRT distributions.

Bird 768 was an unusual subject with an interesting variation on the harmonic pattern. Its Session 1 distribution is plotted in Figure 8. Unlike most birds, this subject regularly
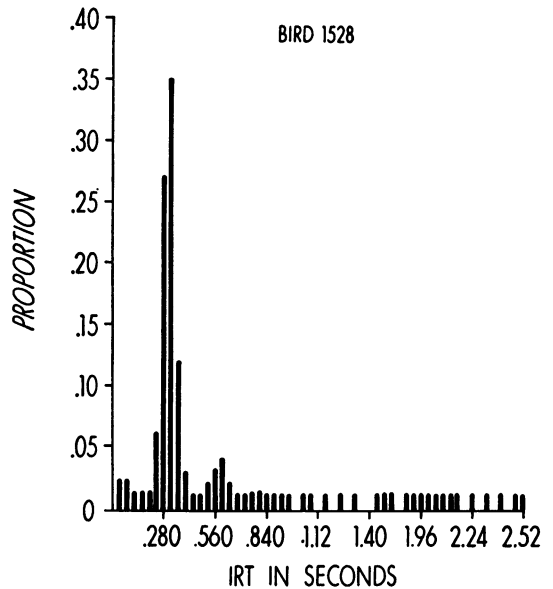
interspersed one or more incomplete pecking motions ("feints") between effective responses. Further, the time period for the feinting motion appeared to be less than that of the effective pecking response. The result is an initial displacement of three to four clock cycles in the otherwise uniform harmonic distribution. That is, although the fundamental mode is located at 400 msec, the spacing be-
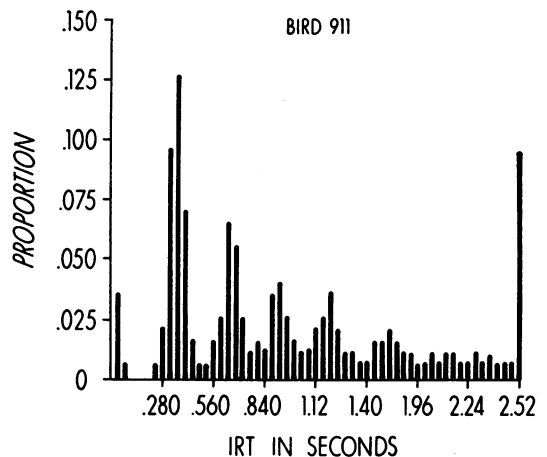

Fig. 7. Normalized histogram plot of the IRT distribution based on 1200 responses for Session 6, Bird 911. The temporal resolution is 40 msec/bin on the abscissa.
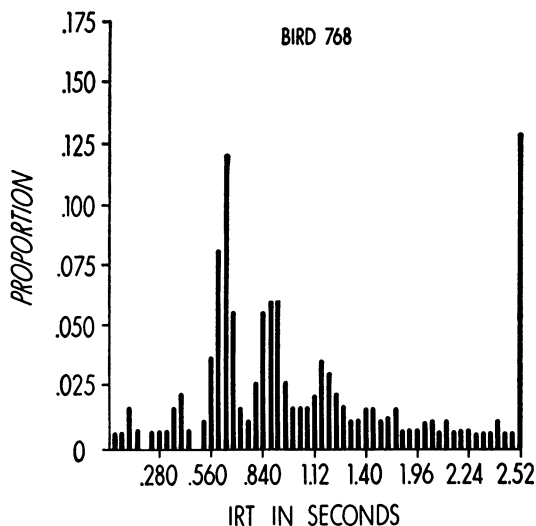
Fig. 8. Normalized histogram plot of the IRT distribution based on 1200 responses for Session 1, Bird 768. The temporal resolution is 40 msec/bin on the abscissa.

tween successive harmonic modes is only 240 msec, reflecting, we believe, the presence of interspersed, abbreviated pecking motions.

A suprising conclusion may be drawn from the small size of the cluster at the primary position of 400 msec for this bird. Only 5% of all IRTs are represented there, while the next mode at 640 msec accounts for 29% of all IRTs, and further IRTs appear in the subsequent modes at regular spacings of 240 msec. If we interpret the primary mode as straightforward pecks at the key, then most of this bird's pecking motions must have been ineffective, since 95% of all IRTs lay outside the primary mode.

Each subject presented a characteristic profile in the IRT histograms, and each session's performance reflected in varying degrees the several common characteristics described above. The distribution profile for a subject was not static but changed gradually and systematically as the performance evolved over time. The harmonic component of responding occurred in most of these nine subjects. "Nibbling" or "biting" at the key was also common, and even constituted the predominant response mode for some subjects. These interpretations of the IRT distributions are based on direct observations of the subjects.

Incidence of long IRTs (outliers). A prominent feature of the transition from FR 1 to FR 30 was the elimination of relatively long IRTs
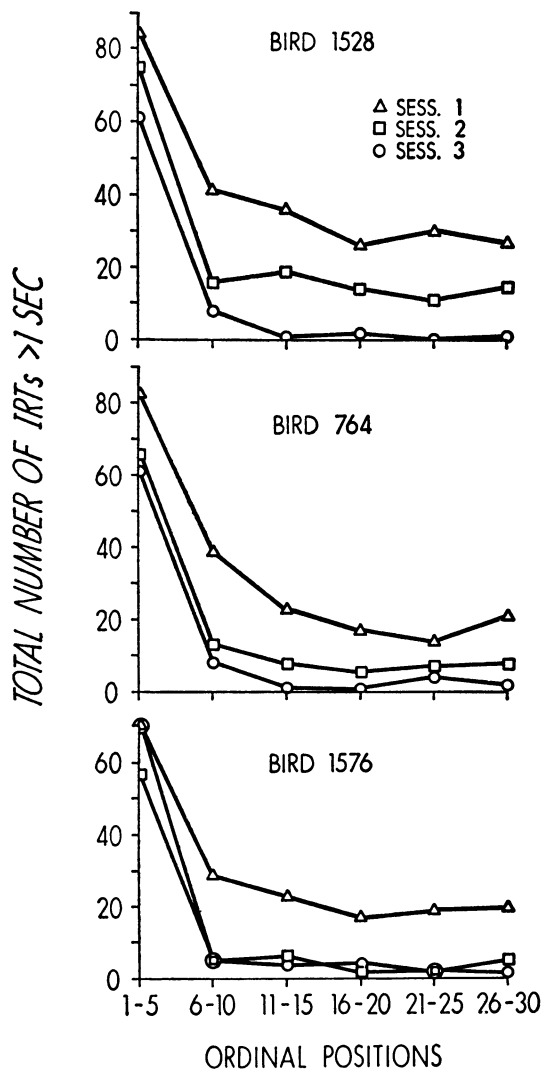
Fig. 9. Incidence of IRTs > 1 sec (outliers) as a function of ordinal position for Birds 1528, 764, and 1576. The incidence of outliers over the session is shown as total number in successive groups of five ordinal IRTs. Sessions 1 to 3 are shown for each subject.

within the ratio. Although their incidence, even in the early transition sessions, was relatively low, they contributed disproportionately to measures such as rate of responding, variance, *etc.* As can be seen in Figures 5 through 8, an arbitrary but sensible criterion for a "long" IRT is a duration of 1 sec or more. We have termed such IRTs "outliers" (Weiss and Gott, 1972) and find that they serve a useful function in describing certain aspects of the transition process.

Figure 9 plots the incidence of outliers for

three birds over the first three sessions on FR 30. The highest incidence occurred during the first session. Incidence fell during the next two sessions.

The most important information in the figure, however, is the distribution through the ratio. Ordinal positions 1 through 5, which include the PRT, show the typically high incidence of outliers in the early section of the ratio. Only a slight gradient is apparent over the last two-thirds of the ratio and virtually none is evident in the last half.

Patterning of terminal responses aligned at reinforcement. A study of transition performance must consider how the event of reinforcement shapes the development of the characteristic final response pattern. One way to approach this question is through close attention to the responses leading to reinforcement, in this instance, the terminal ratio performance. To illustrate this facet of the transition, plots of terminal responses aligned at reinforcement were prepared for each session. Referring to Figure 10, each ratio in the session is represented by a line of printed symbols, and each symbol (X) represents the occurrence of a response in time leading up to reinforcement. Each line is positioned so that the last (reinforced) response from each ratio falls in the column at the rightmost side of the plot. This arrangement permits a capsule illustration of temporal patterning in the terminal portion of all ratios over the session.

Each such plot may be condensed to yield another figure called the Terminal Response Convergence, which is prepared, as shown in Figure 11, by summing all responses in each 40-msec time interval leading up to reinforcement. It has the appearance, and some of the characteristics, of an Expectation Density plot (Huggins, 1957; Poggio and Viernstein, 1964; Weiss and Laties, 1965). It reveals the exis-
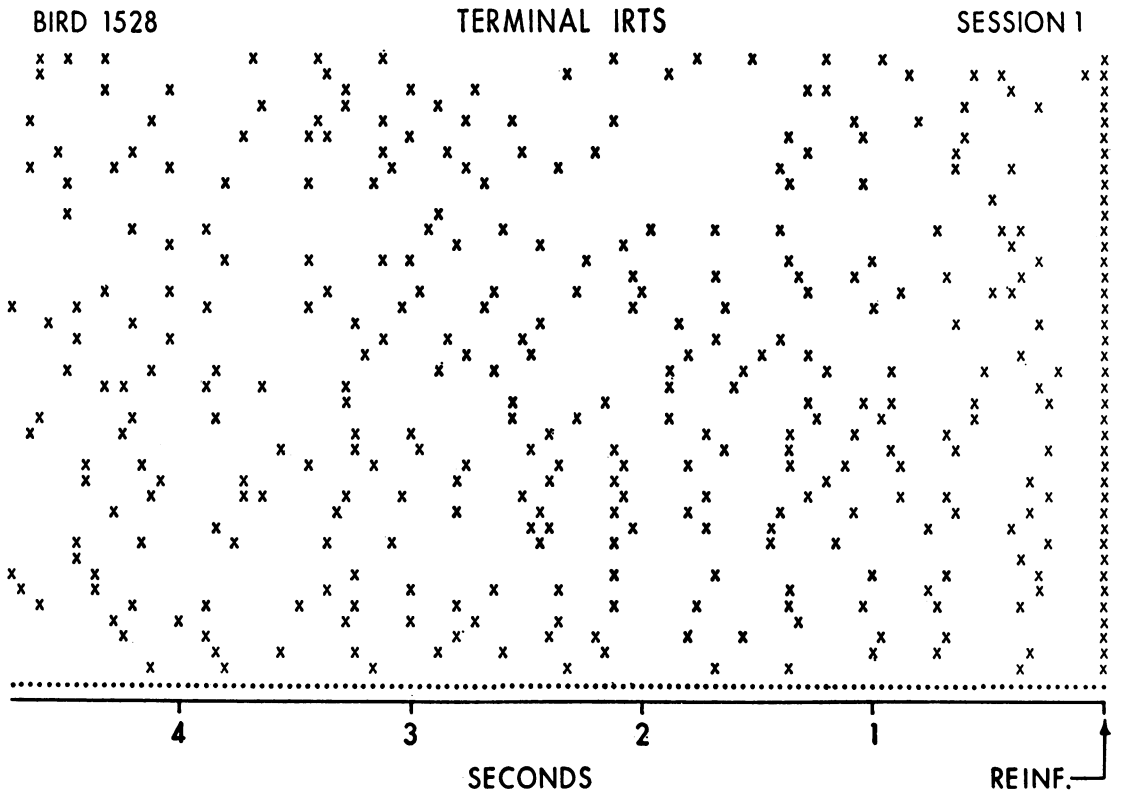
Fig. 10. Terminal response alignment for Bird 1528 in Session 1. The plot of terminal responses aligned on reinforcement is a computer-prepared temporal map of responding prior to reinforcement. Each of the 40 rows represents successive ratios in one session from top to bottom. The reinforced IRT of each ratio is represented by an "X" in the column at the far right. Responses before reinforcement in time are designated by Xs at appropriate positions to the left. The temporal resolution is 40 msec/bin.

Fig. 11. Terminal response convergence for Bird 1528 in Session 1. This is a derivative plot obtained by summing all Xs in each time bin of the plot of terminal response aligned on reinforcement (Figure 10). The development of temporal patterning in the responding is shown in these plots by the appearance of regularly spaced peaks. The greater the regularity in response patterning, the more prominent and numerous are the peaks.
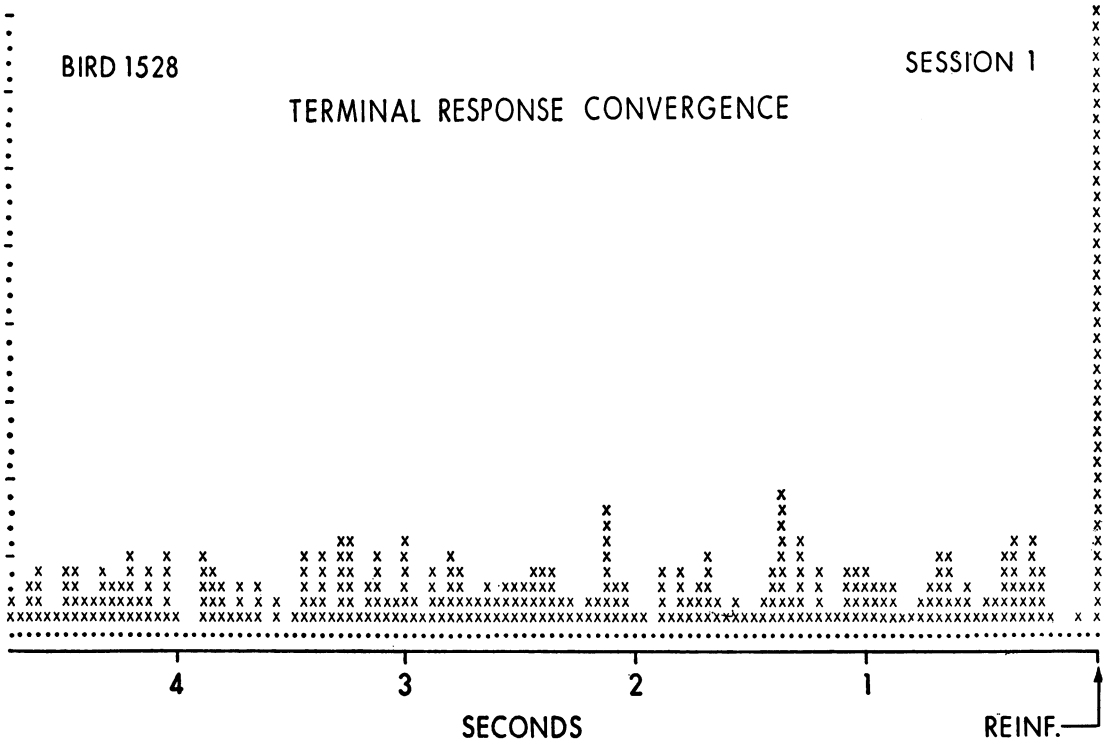
tence of patterning by the prominence of regular peaks.

Bird 1528 rapidly progressed toward stable performance on FR 30. The Session 1 terminal response plot (Figure 10) presents a haphazard appearance, reflecting the contributions of the varied modes in the IRT distribution. Twenty six of the reinforced IRTs (65%) fell between 240 and 440 msec, inclusively, corresponding to the primary grouping of the IRT distribution, which contained 52% of all IRTs in the session. Although about 6% of all IRTs lay in the nibble mode of the distribution, only a single nibble response was reinforced (2.5% of the reinforced IRTs). This occurred in ratio 2, at the upper right in the figure. Other 80- and 120-msec IRTs were scattered throughout the figure. In general, the population of reinforced IRTs seems to be a reasonable representation of the parent IRT population.

The plot shows a within-session effect, namely, a trend toward shorter values of reinforced IRTs in the middle third of the session.

Also, the density of points near the end of the ratio, (and hence, the terminal rate) is greater in the second half of the session.

The corresponding summary plot (Figure 11) shows subdued peaks in the plot extending backward in time from the reinforced IRTs at the extreme right. The first three broad peaks are centered at -320, -680 and -1000 msec, respectively, reflecting the coincidence of IRTs from the primary mode with its center at 320 msec.

By Session 8, temporal coincidence was unmistakable in both the alignment plot (Figure 12) and in the convergence plot (Figure 13) where six regularly spaced peaks are clearly evident, with a period of about 300 msec. Such a sharpening of the peaks indicates that the key pecks were emitted in a rhythmic manner, as part of a rather homogeneous sequence of repeated movements.

Effects of RNA administration. Results from the group of birds given 250 mg/kg/day differed both from the saline group and the

Fig. 12. Terminal responses aligned on reinforcement for Bird 1528 in Session 8. See Legend for Figure 10.

Fig. 13. Terminal response convergence for Bird 1528 in Session 8. See Legend for Figure 11.
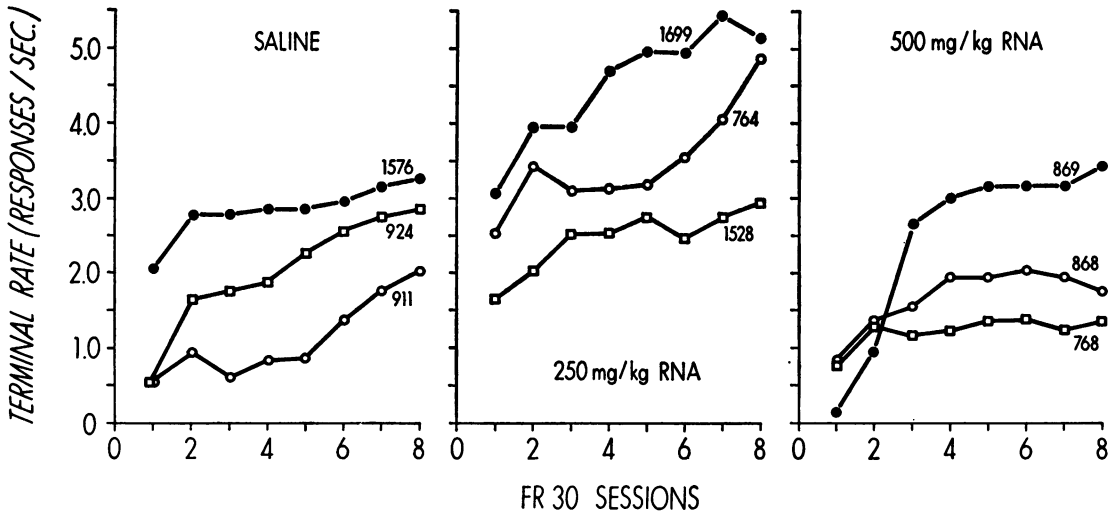
Fig. 14. Effects of yeast RNA on terminal rate (responses 21 to 30) in three groups of pigeons.

group given 500 mg/kg/day. The mean PRTs for the 250 mg/kg group remained rather stable and relatively short. Both the saline and high-dose group tended to lengthen the PRT over the first few sessions, a trend that the birds given saline later reversed.

A similar difference among groups prevailed when the terminal rate (responses 21 to 30) of the ratio was examined. Figure 14 shows that the highest rate prevailed in the 250 mg/kg group, with the groups given saline and 500 mg/kg again overlapping almost completely. Note, however, the progressive increase in rate for the saline and low RNA dose groups, and the rapidity with which the 500 mg/kg group reached an asymptote.

DISCUSSION

The conclusions that can be drawn from these data are limited, first, by our reliance on only one FR value, one form of transition (abrupt rather than gradual), and one parameter of initial training (FR 1), and, second, by the diversity among subjects. The choice of FR 30 arose, in large part, because it lay in a range often used in drug experiments (for example, Bignami and Gatti, 1969). The additional restrictions were imposed because more than one parameter value would have made it difficult to assess the contribution of RNA.

The diversity among subjects, although considerable, is less vexing because, despite it, a recognizable sequence can be discerned in the

development of FR behavior. Consider the properties of this sequence.

Characteristics of the Transition

After the change to FR 30 there was a period of initial rapid responding, lasting one to three ratios for most subjects. Thereafter, responding was interrupted for frequent and prolonged periods in all ordinal positions. Then, after one to three sessions of 40 ratios each, responding again became cohesive as the incidence of these periods within the ratio gradually declined. Concomitantly, the PRT emerged as a prominent feature of the performance. Stable responding did not recover smoothly and monotonically; brief periods of regression to the earlier pattern occurred between periods of improved performance.

Within-ratio changes (gradients). The observed decline in long IRTs over time was correlated with a similar decline in mean IRTs and in variability. For most subjects, the PRT evolved as a prominent feature at the same time that the within-ratio IRTs became more uniform. The within-ratio reduction of long IRTs occurred simultaneously and uniformly over the last half to two-thirds of the ratio; outlier incidence in mid-ratio declined concomitantly with incidence at or near reinforcement, as shown in Figure 9. We did not observe a decline in outliers that began at the terminal IRT and subsequently propagated to earlier positions in the ratio. Such a mechanism would be compatible with the "chain-

ing" explanation of how ratio behavior develops.

On the other hand, both the mean IRT plots and the incidence of outliers indicate persistent gradients over the first few ordinal positions of the ratio. Perhaps this gradient reflects a junction of two disparate influences. One of these would be the PRT, which dominates the period directly following reinforcement, and which could generalize to adjacent IRTs. The other would be the event of reinforcement, which dominates the last part of the ratio, that is characterized by rapid and cohesive responding. The gradient could then represent a border region between these two influences. Some of the outlier and mean IRT data did suggest a propagated change over sessions, with the gradient narrowing toward earlier ordinal positions in the ratio. The incidence of outliers at these positions, in some birds, continued slowly to decline long after the terminal ratio stabilized.

Interresponse times. A study of the IRT distributions combined with direct observations emphasized the diversity of form in responding. Three distinct modes were identified. These were called, respectively: nibbles (due to biting motions of the beak); pecks (the stereotyped traditional response motion); and harmonics (arising from interspersed regular pecking motions that failed to operate the key). All subjects showed combinations of these modes in their performances, but most showed characteristic tendencies toward one or another type. These distribution characteristics also shifted with experience on FR 30, more rapidly at first, and more gradually thereafter.

Response rates rose in the early sessions as the incidence of long IRTs declined. Subsequent rate increases occurred with decreases in variability. They seemed due largely to a decreased incidence of harmonic IRTs and a slight downward shift in the primary mode IRTs. The character of later performance appeared to be related to performance during the initial exposure to the schedule. When birds were ranked according to the proportion of IRTs shorter than 120 msec, a high correlation (Spearman rank correlation coefficient $= 0.98$) was found between the rankings in Sessions 1 and 8. Most subjects drifted slowly toward a predominance of rhythmic, regular pecking responses after many weeks of ex-

posure to the schedule, although many retained a definite incidence of harmonic-type responding over several months that could be increased by drugs (Weiss and Gott, 1972). Two subjects showed predominantly nibble-type responding. Others showed a small nibble component over many weeks without acquiring a predominantly nibble-type distribution, an interesting finding in view of the fact that consistent nibble responses would increase reinforcement rate.

Implications of harmonics. One consequence of the existence of harmonic responding is that most subjects were working initially on *de facto* variable-ratio schedules. The incidence of IRTs in higher modes may be multiplied by the order of the mode (*i.e.*, its harmonic position) to give an estimate of the actual total number of "responses", in terms of head thrusts, required to satisfy the schedule requirements. For example, looking again at Bird 768 in Session 1 (Figure 8), the occurrence of 29% of all IRTs in the first harmonic cluster implies the emission of $(2 \times 0.29 \times 1200)$, or 696 "responses", rather than the nominal requirement of 348. Cluster 3, the second harmonic, represents approximately 30% of all IRTs; this implies the emission of $(3 \times 0.30 \times 1200)$, or 1080 "responses" rather than only 360. These two harmonic modes alone almost double the effective ratio requirement for this bird. It should be understood that not all longer IRTs are interpreted as involving multiple emission of a basic pecking "unit motion", as it were. Clearly, many long IRTs merely represent schedule-irrelevant activities such as turning, preening, *etc.* Still, the fact that considerable numbers of IRTs lay in harmonic clusters does imply some coordinating mechanism. Furthermore, even though harmonic IRT distributions could arise without overt mediating movements, the mechanism here proposed is in accord with observations of the subjects; birds often did emit multiple thrusts toward or around the key before completing one effective response.

Another interesting implication emerges about the nature of the increase in rate with practice on the schedule. For most subjects, the position of the primary group changed only slightly over time. The most significant change, after the elimination of outliers, lay in the proportion of IRTs in the various clusters. In particular, the incidence of IRTs

in the harmonic modes typically declined while the incidence in the primary mode increased. After the early decline in long IRTs that followed the period of disruption, the major factor in a further rate increase could have been a change in the topography, from one with multiple ineffective responses, to one with a high proportion of effective responses. Not surprisingly, then, one aspect of the transition to stable FR 30 performance can be viewed, in the broad sense, as a shaping of response topography. Moreover, the decline in ineffective responding, and its replacement by effective responding, appeared to take place throughout the ratio, and may partly account for the observed uniform decline of outliers without regard to ordinal position during the last two-thirds of the ratio.

The Effects of RNA Administration

In assessing the contribution of RNA, it is important to understand that dose-response functions are typically used to validate a pharmacological effect. The present study suggests a facilitative effect of RNA at 250 mg/kg daily and hints at impairment at• 500 mg/kg. Since, however, two of the birds in the 250 mg/kg group gave a high incidence of nibble responses, the differences among groups may be due as much, if not mostly, to intrinsic differences among response topographies as to differential pharmacological effects. The problem is whether it is valid to claim that the effect of the low RNA dose was to enhance the nibble component of responding, the topographical idiosyncrasy that largely produced the high terminal rates by Birds 1699 and 764 of that treatment group.

Cook and Davidson (1968) presented the most complete dose-response data available for yeast RNA. These are based on rats, undergoing training on a pole-climb avoidance task, that were given daily intraperitoneal injections ranging from 75 to 1200 mg/kg/day for 27 days. Number of trials to criterion varied inversely with dose. Siegel (1968) administered 1000 mg/kg/day intraperitoneally to pigeons, and found an increase in FI rates. These data suggest that we are not on the downward slope of the dose-response function at 500 mg/kg, although the route used by Cook and Davidson (1968) and Siegel (1968) may differ fundamentally from the oral route that we used. Cook and Davidson (1968), for example, reported a variety of side effects and histopathological changes in rats from intraperitoneal administration.

The most notable effect of the high RNA dose was a rapid flattening of the function plotting rate over sessions. This strongly suggests an effect characteristic of amphetamine, which tends to reduce response rate on FR 30 (Weiss and Gott, 1972). Such an interpretation is compatible with Siegel's (1968) finding of an increase in FI rates, another well-known effect of amphetamine in pigeons (e.g., Bignami and Gatti, 1969).

Components of FR Performance

Rate variables. The course of the transition suggests that FR performance might be envisaged as a three-component process: the PRT, the "junction zone", and the final cohesive train.

The PRT, as pointed out earlier, can be controlled independently of the subsequent IRTs within the ratio (Kelleher, Fry, and Cook, 1964). In experiments explicitly directed toward the variables that influence its duration, it has been shown that duration is a direct function of the size of the ratio (Felton and Lyon, 1966; Powell, 1968). Since ratio length is confounded with time to completion, which determines both frequency and delay of reinforcement, these factors must be evaluated in their own right. Neuringer and Schneider (1968), and Killeen (1969) have shown that PRT duration is a function of the interval between reinforcements.

What is puzzling is the fact that long PRTs lower the density of reinforcement. Given everything else known about the actions of reinforcement, such a finding is anomalous, particularly because the prominence of the PRT emerges only in the later stages of the transition, as the incidence of long IRTs falls at other ordinal positions within the ratio. Skinner (1938) proposed that the long PRT on FR schedules developed as a temporal discrimination because responses immediately after reinforcement are never reinforced. This view is supported by data from Ferster and Skinner (1957), who demonstrated that the PRT shortened when an intervening period without the opportunity to respond (a timeout) occurred after each reinforcement. A similar explanation can be applied to the low rate that follows reinforcement on fixed-inter-

val schedules. The similarities do not end there, for Schneider (1969) demonstrated, in a quantitative fashion, that FI performance in highly practiced pigeons could be conceived as a two-state process, much as FR performance often is viewed (Powell, 1970).

The similarity between FI and FR performance is also emphasized by data from Shull and Brownstein (1970). They measured the first 12 IRTs from FI performance in pigeons and found the median IRT in position 1 to vary as a function of time since the last reinforcement, but not IRTs beyond, say, position 6. These resemble Kintsch's (1965) findings from variable-interval and variable-ratio schedules, and relate to what we call the "junction zone".

As pointed out by Powell (1970), the relationship between FR size and response rate within the ratio is an inconsistent one. Powell proposed that within-ratio rate differences are determined by the incidence of "pauses" (his definition of a pause was an IRT $\geq$ 5 sec). Pause incidence, in turn, is governed by proximity to reinforcement. The present data do support an explanation partly based on the incidence of pauses, but do not support the hypothesis that incidence is related to remoteness from reinforcement, except for the junction zone.

An explanation of FR performance that plausibly accounts for these features, and accords with the present data, was framed by Dews (1962, p. 373):

"... the possibility should be considered that the high rates of responding engendered by fixed-ratio schedules (FR) may come about as follows: The higher the average rate of responding on an FR schedule the closer, temporally, the initial response and all subsequent responses in the FR are to reinforcement, and, therefore, the greater the retroactive enhancing effect of that reinforcement. This will tend to increase the rate of responding, which in turn will tend to bring the responses closer to reinforcement, which will increase the rate further. Thus, there is in effect, a positive feedback situation, in which random increases in rate will tend to be self-enhancing."

Response topography and operants. The preceding analysis follows traditional practice by classifying as responses only those actions by the pigeons that operated the key. Although such an assumption helps to simplify an immensely complex situation, it may be time to question its usefulness as typically applied.

Consider our analysis of "harmonics". Observational evidence, as well as the IRT distributions, convinces us that much vital information is lost by focusing exclusively on the conventional criterion of switch operation. Key-pecking topography has been shown by several investigators not to be under the simple, direct control by schedule contingencies implicitly assumed by many experiments. Staddon and Simmelhag (1971), for example, noted that certain birds in their "superstition" experiment emitted a high proportion of pecking motions that failed to depress the key enough to activate the scheduling circuitry. They also observed, as did Bachrach (1966), and Brown and Jenkins (1968), a high incidence of pecks aimed at the chamber wall. Dunham, Mariner, and Adams (1969) were able to demonstrate, with special instrumentation, that punishment of key pecking did not suppress the incidence of pecking motions, but mainly directed them away from the key.

Such phenomena emphasize the selective function of reinforcement contingencies, a function not wholly congruent with their role as determinants of response rate. The latter, in fact, can be viewed as an indirect index of selectivity. From this perspective, transition state experiments, particularly, require a broader compass of response dimensions than usually employed if they are to provide an adequate account of the transition process. Applied behavior analysis has been forced to deal with these questions and tried to resolve them by techniques such as multiple-response baselines (*e.g.*, Baer, Wolf, and Risley, 1968). The technology for equivalent approaches in the laboratory is available (*e.g.*, Weiss, 1970*b*; Rilling, Kramer, and Askew, 1970) and ought to be applied more vigorously.

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