BEHAVIORAL ADAPTATION TO FIXED-INTERVAL AND FIXED-TIME FOOD DELIVERY IN GOLDEN HAMSTERS[1]

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Food-deprived golden hamsters in a large enclosure received food every 30 sec contingent on lever pressing, or free while their behavior was continuously recorded in terms of an exhaustive classification of motor patterns. As with other species in other situations, behavior became organized into two main classes. One (terminal behaviors) increased in probability throughout interfood intervals; the other (interim behaviors) peaked earlier in interfood intervals. Which class an activity belonged to was independent of whether food was contingent on lever pressing. When food was omitted on some of the intervals (thwarting), the terminal activities began sooner in the next interval, and different interim activities changed in different ways. The interim activities did not appear to be schedule-induced in the usual sense. Rather, the hamsters left the area of the feeder when food was not due and engaged in activities they would normally perform in the experimental environment.

Key words: fixed-interval schedule, fixed-time schedule, schedule-induced behavior, interim activities, terminal activities, lever press, hamsters

When animals have food at regular intervals, behavior becomes organized around the times of food delivery. Certain activities appear soon after food delivery while others appear just before food is scheduled. When a response is required for food (fixed-interval schedule, FI) this organization is evident in the scalloping or break-and-run on cumulative records, but it also appears with free food at regular intervals (fixed-time schedule, FT, or Pavlovian temporal conditioning). The period when food is not due and activities other than the operant, if any, are being performed has come to be known as the interim period, and that just before food delivery as the terminal period (Staddon and Simmelhag, 1971; reviews by Falk, 1971, and Staddon, *in press*).

The reliable appearance of activities other than an explicitly reinforced response at periods remote from reinforcement has been claimed to illustrate fundamental mechanisms of behavioral adaptation (*e.g.*, Staddon and Simmelhag, 1971). However, behavior on periodic schedules has been studied in only a few species and situations. Except in the studies of Staddon and Simmelhag (1971) and Staddon and Ayres (1975), in most cases only one interim activity has been recorded, and subjects have been in a confined space with stimulus support for only one of numerous conceivable interim activities, *e.g.*, water for schedule-induced polydipsia or a target for schedule-induced aggression. It is difficult to conclude from such experiments what properties interim activities *per se* may have. That is, given all the activities an animal can perform, which will appear in the interim period and which in the terminal period and why?

The generality of descriptions of interim and terminal behavior can also be limited by the choice of behavioral units. The choice of behavioral units is especially important when results are discussed in terms of adaptation and evolutionary significance (*e.g.*, Staddon and Simmelhag, 1971). Describing behavior in terms of its orientation to a particular enclosure feature (*e.g.*, "facing a window wall", Staddon and Simmelhag, 1971) may limit findings to a particular kind of enclosure, or at least make comparison with data from other environments difficult. Moreover, the kind and number of units recorded may influence the

type of temporal organization that may be observed.

In the present experiment, the behavior of golden hamsters receiving FI or FT food in a relatively large enclosure was recorded in terms of a number of mutually exclusive, exhaustive categories of motor movements or action patterns (APs, Shettleworth, 1975). The sources of control of these activities and their relations have been studied independently (e.g., Shettleworth, 1975). Hamsters were habituated to the experimental environment and then exposed to one of three conditions of food delivery. In Condition 1, where they lever pressed on FI schedules, and in Condition 2, the parallel FT condition, the interfood interval was gradually lengthened from 5 to 30 sec. In Condition 3, the final, FT 30-sec, schedule was in effect throughout, the more usual situation in such studies. The influence of the lever-pressing contingency on what behavior is exhibited in the terminal period (Moore, 1973) could be evaluated in the present situation by comparing Conditions 1 and 2. Comparing behavior under Conditions 2 and 3 would reveal any effects of changes in food density over sessions on temporal organization and overall levels of the APs, particularly with respect to possible "excessiveness" (Falk, 1971) of interim activities.

In the first two conditions, when behavior on the final schedule appeared stable, the effects of several manipulations on the behavioral organization that had emerged were assessed. Presumptive causal factors for two of the interim behaviors, grooming and picking up sawdust, were altered by spraying the animals in Condition 1 with water and changing the sawdust on the floor. These operations are analogous to those McFarland (1970) used with pigeons to determine whether the relation between two activities was competition or disinhibition.

The subjects in Conditions 1 and 2 were also "thwarted" by having food omitted on some intervals. When food is withheld or replaced by another stimulus on fixed-interval schedules, the subsequent response rate is higher than after food is given (Staddon, 1974). The analogous operation is known as thwarting in discussions of displacement activities (e.g., McFarland, 1966). The effects of food omission, in the context of continued food deliveries, on interim behavior was expected to reveal the relationship between the interim and terminal behavior, because interim or adjunctive behavior is similar in some ways to displacement activities (Falk, 1971), and thwarting increases the likelihood of displacement activities (McFarland, 1966).

METHOD

Subjects

Twelve experimentally naive, laboratory-raised golden hamsters (Mesocricetus auratus), six of each sex, were four to five months old when observations started. They weighed 94 to 120 g on free food and water, and were maintained at 85% of their free-feeding weights by being given 1 to 6 g of Purina laboratory chow daily and some sunflower seeds, greens, and fruit on the day each week when they were not run. The colony room was on a 13:11 L:D cycle with lights off at 10:00 a.m. Other details of housing and maintenance were as described by Shettleworth (1975).

Apparatus

Observations were made in an open field 61.0 cm square and 45.7 cm high and with plywood sides and back and a clear Plexiglas front. About 2 cm of sawdust (Ab Sorb Dri, Maple Leaf Mills, Toronto) covered the floor. A 7.5-W white-light bulb was centered at the top of the back wall. A 5.1-cm speaker was centered on the left wall 7.6 cm from the top. Also centered at the bottom of this wall were two metal panels 1 cm apart and 15.2 cm high. The feeder panel was 9.4 cm wide and contained a cup-like depression (diameter 5.5 cm; 3.0 cm deep) 8.3 cm from the floor. A dipper that scooped up food pellets from a trough could be presented through a hole in the bottom of the depression. The lever panel was 11.3 cm wide and held a Gerbrands rat lever, activated by about 23 g, 6.0 cm from the floor. An exhaust fan provided masking noise (about 73 dB re 2 N/m²; General Radio Corporation Sound Level Meter Type 1561A, 20 kHz scale). The open field rested on a 30.5-cm high platform in a sound-insulated chamber, lighted by the light in the open field. An observer dressed in dark clothing sat about 70 cm from the front of the open field in front of a black curtain.

All behavior other than lever pressing was recorded on a keyboard wired to electromechanical programming equipment in another room in such a way that the number of 1-sec intervals in which each key was depressed was counted. An Esterline-Angus 20-pen event recorder running at 7.6 cm per minute recorded the sequence and duration of key depressions, lever presses, and food presentations.

Procedure

Experimental sessions were conducted during the dark phase of the animals' light cycle. Each one started with the animal stepping out of the container in which it had been carried to the open field at a standard corner. Recording began as soon as the observer could sit down and ended when 1200 1-sec intervals had been counted. At the end of the session, faeces and urine-soaked sawdust were removed and the sawdust smoothed out.

Throughout each session, a subject's behavior was recorded continuously in the categories described in Table 1, and four others that occurred too rarely to be analyzed. The motor patterns falling into the various categories are readily recognized, as indicated by the high correlations between scores of independent observers using them (Shettleworth, 1975). A single observer was employed here.

For the first five sessions under all conditions, behavior was observed in the absence of food or tones. Data from the first session were discarded, as there are generally large changes between the first and subsequent sessions in the open field (Shettleworth, 1975). Beginning on Day 6, the three experimental conditions were as described below. They were presented successively, with two subjects of each sex in each.

Condition 1: FI 5-sec—FI 30-sec (62 sessions). On Days 6 and 7, subjects were magazine trained and lever pressing was shaped. Then, they were put on a series of FI schedules: FI 5-sec (four sessions); FI 10-sec (three sessions); FI 20-sec (two sessions); and finally FI 30-sec for the remainder of the experiment. A 4-sec 800-Hz tone preceded presentation of one 45-mg Noyes pellet. It added 2 dB re 20 N/m² to the ambient masking noise. Initially, each pellet was available for 12 sec, but during magazine training and shaping this was decreased to the 4 sec used in the rest of the study.

Table 1

Action Pattern Titles and Descriptions

Action Pattern	Description
Walk/sniff	Walking around or standing still and sniffing with at least three feet touching the floor.
Pouch/chew	Pushing food pellets into cheek pouches and/or depouching them and/or chewing the food.
Panel rear	Standing on hind legs with at least one forepaw touching the feeder and/or lever panels.
Wall rear	Standing on hind legs with at least one forepaw touching a wall, excluding the feeder and lever panels.
Open rear	Standing on hind legs with both forepaws off the floor and walls.
Pick up sawdust	Sitting and holding a piece of sawdust with the forepaws; may include biting and pouching or depouching it.
Wash face	Rubbing forepaw(s) over any part of the head. Includes interspersed licking of forepaws.
Groom belly and sides	Scratching with forepaws at and/or biting at belly, sides or legs.
Scratch with hind leg	Scratching any part of the body with a hind foot. Includes interspersed licking of the scratching foot.
Dig	Scraping with the forepaws directed in front of the face at the floor or walls.
Hind-kick	Pushing backward at the floor with the hind feet.
Gnaw	Biting any surface.
Scrabble	Scraping with forepaws against a wall while standing erect. Sometimes moving along wall, hopping up and down while doing this. Distinguished from digging at the wall by the fact that each stroke is directed to the side, the head is oriented up rather than toward the wall, and the hamster usually stretches up to its full extent.

The Ab Sorb Dri on the floor of the apparatus was replaced by sawdust of different color and texture on Days 41 to 44. On Days 50 to 52, each subject was covered with a fine mist of water from a house-plant sprayer just before a session began (Spraying). On Days 55 to 58, food was withheld on every second block of four intervals (Thwarting). In each thwarting session, the first four intervals began with the usual tone-food presentations, the next four with tone-only presentations, *etc.* Days 59 to 62 consisted of both spraying and thwarting.
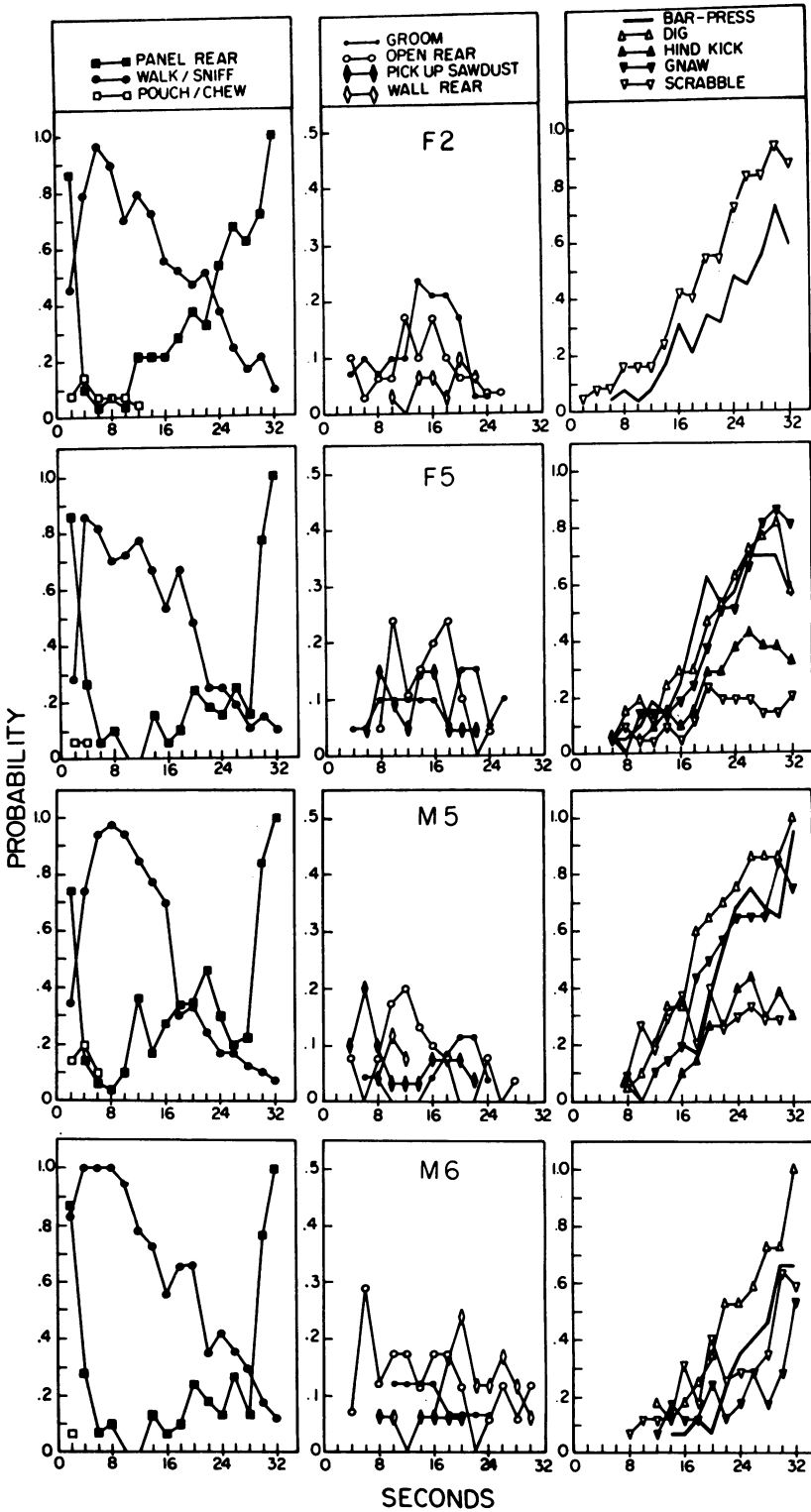
Condition 2: FT 5-sec—FT 30-sec (44 ses-

Fig. 1a. Probability of a given AP or lever pressing in 2-sec units derived from all interfood intervals shorter than 34 sec on Day 40 for each animal in Condition 1. Values of p = 0 are not shown.

sions). Days 6 and 7 consisted of magazine training. Beginning on Day 8, food was delivered on a series of FT schedules corresponding to the FI schedules of Condition 1. On Days 41 to 44, thwarting was imposed.

Condition 3: FT 30-sec (30 sessions). Beginning on Day 6, food was delivered on FT 30-sec as in the other conditions.

RESULTS

Temporal Pattern

In all three conditions, the animals collected most of the available pellets beginning soon after the final schedule went into effect. They generally collected a pellet every 30 to 34 sec, dividing sessions into 30 or more interfood intervals. These have been collapsed in Figures 1a-c to show the probability of each action pattern (AP) and lever pressing in each 2-sec interval since the last food pellet on Day 40 for Conditions 1 and 2, and Day 30 for Condition 3. Long interpellet intervals that resulted from the animal missing one or more of the 4-sec pellet presentations are omitted from the data in Figure 1 and similar figures throughout the paper.

All the APs assumed reliable temporal patterns that were similar under all three conditions. Panel rearing was the most probable AP within 2 sec after a pellet was collected. Since panel rearing was necessary in order to collect, it had to occur at the end of the interval. To some extent, this also applies to its occurrence at the beginning of intervals, because the animals tended to linger briefly, rearing before the panel after collecting the pellet. Consumption of the food pellet, when it occurred, immediately followed collection, but pellets were usually just hoarded in the cheek pouches.

After a pellet was collected, an animal usually walked briskly around the perimeter of the open field, often ending up in a corner opposite the feeder. This is reflected in Figure 1 in the rapid increase in the probability of walk/sniffing within the first 8 sec of the interval. This AP then gradually decreased to a low probability at the end of the interval.

Open rearing, wall rearing, picking up sawdust, and grooming (face washing, scratching and grooming belly and sides treated as one category) occurred most in the middle of the interval, often without well-defined peaks. The

absolute probabilities of these four activities and their levels relative to each other varied from animal to animal. They were all somewhat less likely in Condition 2 than in the other conditions.

Digging and hind kicking, gnawing, and scrabbling rarely occurred within the first third of the interval, but then increased to maxima at the end of the interval. Digging and gnawing were generally the most probable of these four activities, reflecting the fact that the animals dug and gnawed at the lever in Condition 1 and around ·the hole where pellets appeared in the FT conditions. One animal in Condition 1 (F2, Figure 1a) pressed the bar mainly by scrabbling in contact with it; the level of scrabbling in Conditions 2 and 3 varied from essentially nothing (J1, Figure 1b) to levels similar to that of digging and gnawing (H7, Figure 1c). However, regardless of their relative or absolute levels, whenever these APs appeared in terminal performance, they always increased in probability through the interval, in contrast to walk/sniffing and the APs represented in the middle column of panels in Figure 1.

Digging, gnawing, and scrabbling could all function to press the lever. In Condition 1, which of these was predominantly used in lever pressing changed during the course of the experiment. On Day 12, 68 to 94% of bar depressions were accompanied by digging. By Day 40, this had decreased to 29 to 49%, with gnawing and scrabbling accounting for a concomitantly increased proportion of lever presses.

Figure 1 suggests that the transition from those activities predominating at the beginning and middle of interfood intervals to those predominant at the end was gradual. In fact, however, under all conditions it appeared to be quite abrupt and complete. In Condition 1, this transition was marked by the first bar press. During asymptotic performance, the onset of bar pressing was somewhat variable within a session, but once an animal began pressing in a given interval, APs other than dig, gnaw, hind kick, scrabble, and panel-rear rarely occurred before the next collection. This is evident from Figure 2, which represents the probability of a given AP in 4-sec intervals relative to the first bar press for each animal on Day 40. An animal would gnaw, dig, or scrabble at the feeder and lever
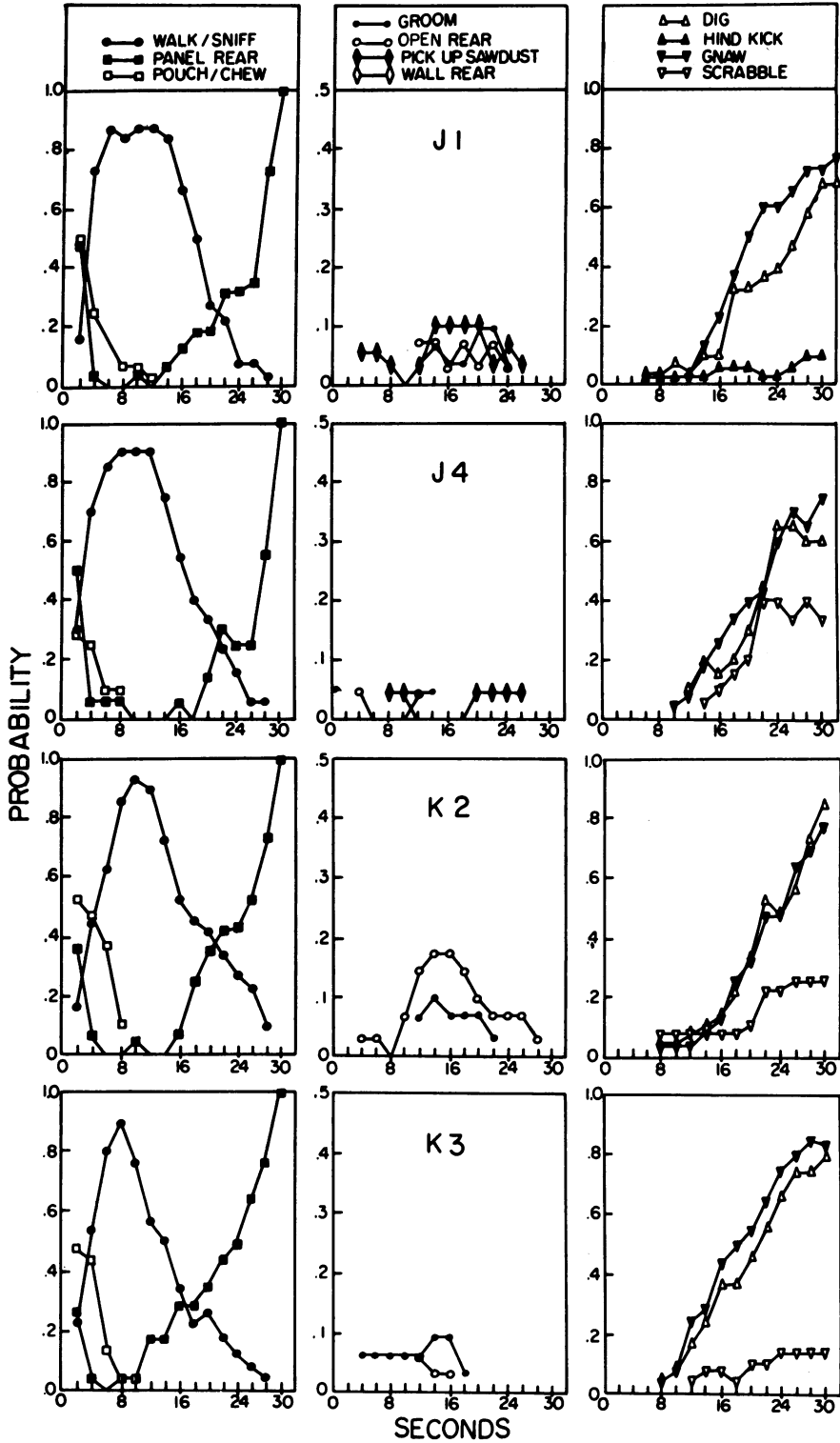
Fig. 1b. Probability of a given AP in 2-sec units of interfood intervals on Day 40 for each subject in Condition 2. Values of p = 0 not shown.
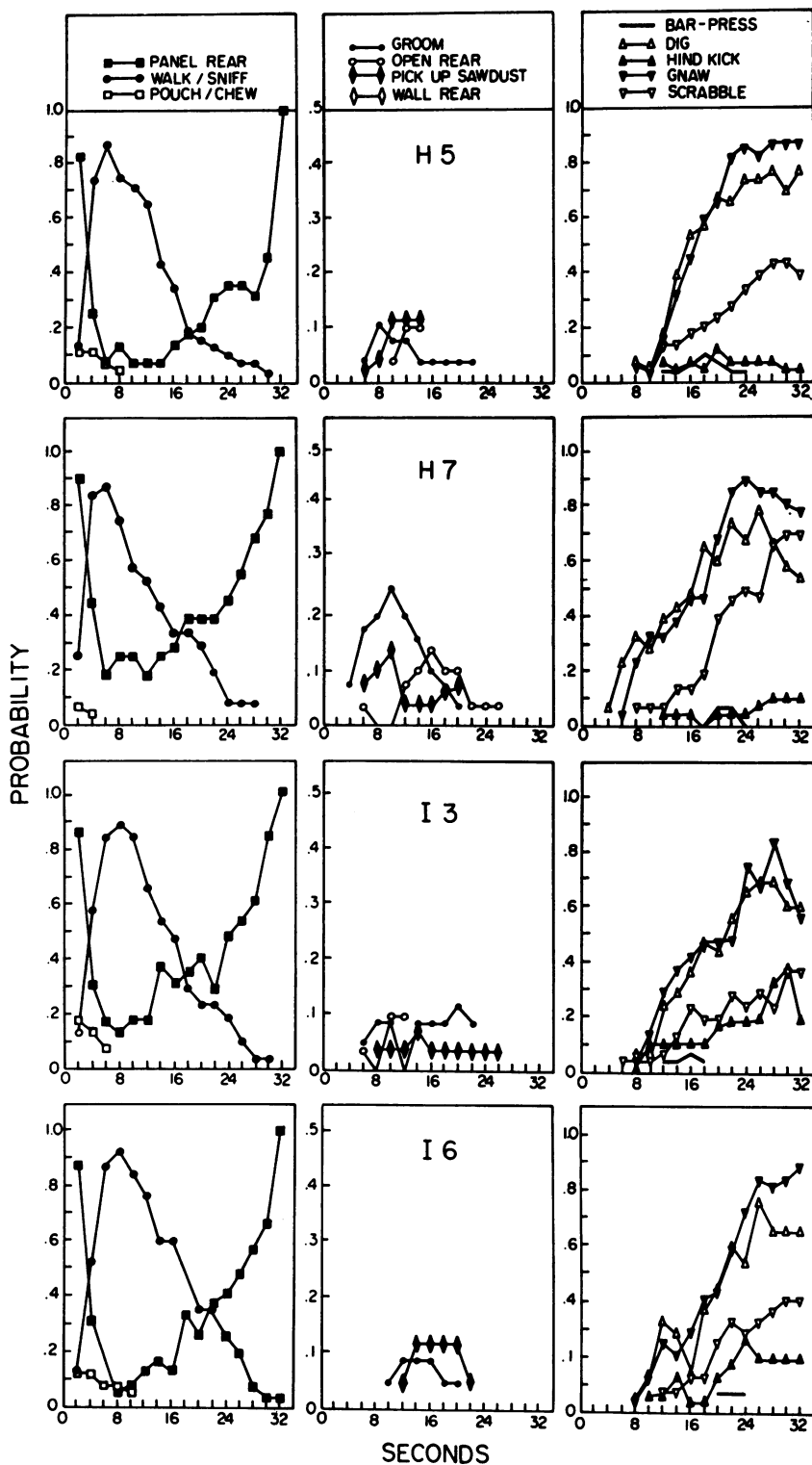
Fig. 1c. Probability of each AP in 2-sec units of interfood intervals for each subject on the last day of Condition 3. Values of p = 0 not shown.
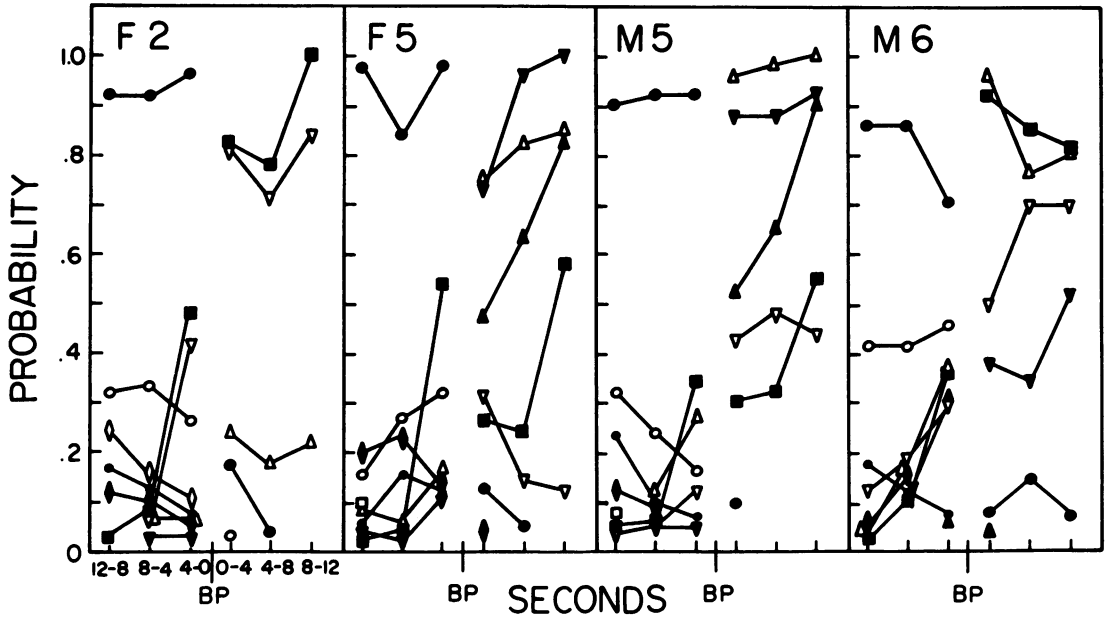
Fig. 2. The probability of each AP in 4-sec intervals before and after the first bar press for each animal on Day 40 of Condition 1. Cases where p = 0 are not represented. Legend same as for Figure 1.

panels and at the lever itself for a few seconds before a lever press, but these three APs plus hind kicking (which was interspersed with digging when it occurred but did not itself press the bar) and panel rearing were much less frequent before the first lever press. However, walk/sniffing occurred very frequently before the first lever press and grooming, wall rearing, open rearing, and picking up sawdust occurred almost exclusively during this same period.

In summary, the APs formed three distinct aggregations on the basis of their temporal patterns (1) the consummatory aggregation (pouching and chewing the food pellet), (2) the interim aggregation (grooming, wall rearing, picking up sawdust, and walk/sniffing), and (3) the appetitive or terminal aggregation (digging and hind kicking, scrabbling, gnawing, and panel rearing). These aggregations were the same with FI or FT schedules. In Condition 1, the first bar press marked a nearly complete transition between interim and terminal activities.

Overall Levels

When food was introduced, the animals began to spend a great deal of time at the feeder, panel rearing, digging, and sometimes gnawing, at the expense of walk/sniffing and other

APs. As they adapted to the food schedule they tended to spend more time walking around the open field and doing other things between food deliveries. This was true both when food density first increased to a high level and then decreased over sessions (Conditions 1 and 2) and when the final density was imposed almost immediately (Condition 3). Figures 3a, b, and c show the number of food pellets collected and the overall levels of the various APs under each condition in blocks of sessions throughout the experiment. The APs are grouped and represented as in Figure 1. When food was introduced after the block of four baseline sessions, in every case panel rearing increased while walk/sniffing decreased (top row of panels). In later sessions, walk/sniffing recovered toward its baseline level while panel rearing declined. Changes in digging (second row of panels) paralleled those in panel rearing in Condition 1, partly reflecting the fact that at first the animals pressed the lever mainly by digging. Digging increased more gradually over sessions in Condition 2. In Condition 3, it abruptly increased to near its maximum in the first block of trials with food and was fairly stable thereafter.

Gnawing and scrabbling, the other terminal activities shown in the second row of panels, changed in various ways. In Condition 1, gnaw-
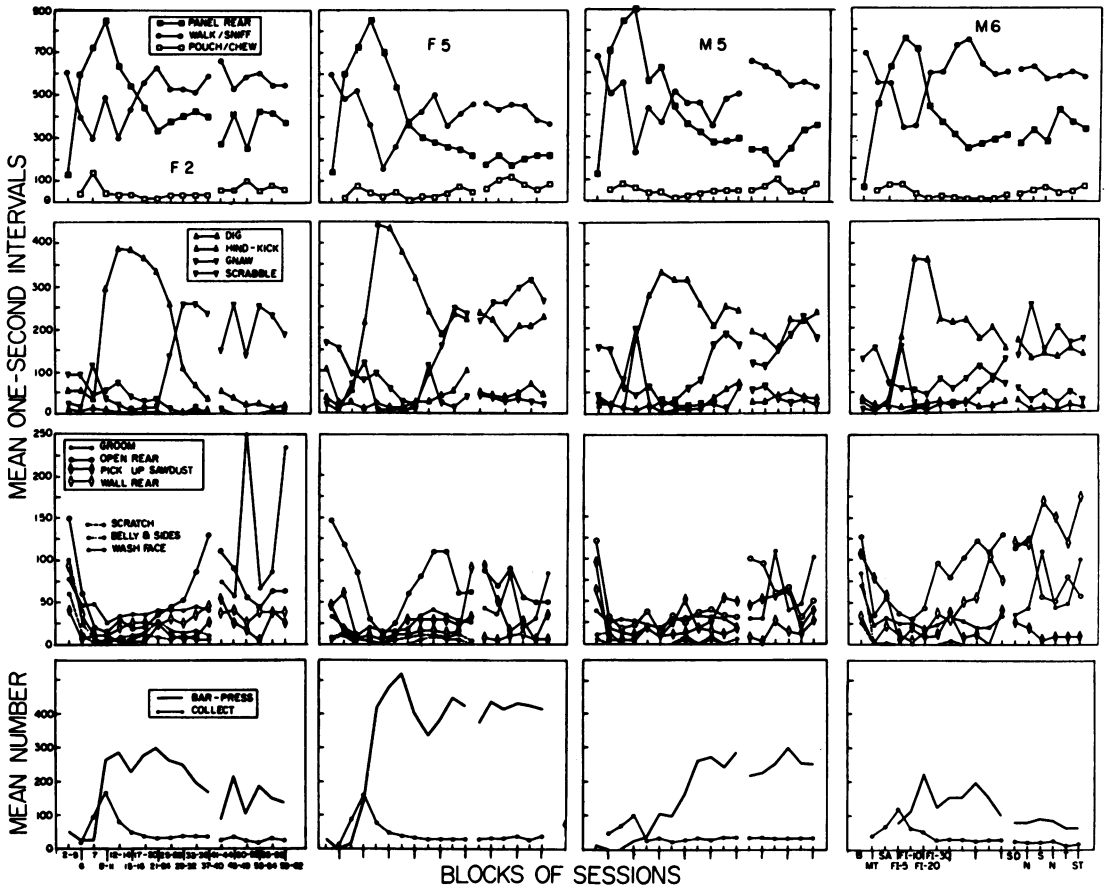
Fig. 3a. Mean number of 1-sec intervals in which each AP occurred, and lever presses and food collections for blocks of sessions for each subject in Condition 1. Experimental conditions are indicated: B—Baseline; MT—Magazine Training; SA—Successive Approximations (shaping); S—Spraying; N—Normal, *i.e.*, baseline, conditions; SD—changing sawdust; T—Thwarting; ST—Spraying and Thwarting. In the third row of panels, the three types of grooming are displayed separately for the first 40 sessions as indicated in the legend and grouped as Groom for the rest of the experiment.

ing decreased at first and recovered to varying degrees later; in Condition 2, it increased gradually along with digging; in Condition 3, it changed in varying ways from baseline but was at a fairly stable high level after food was introduced. Scrabbling decreased when food was introduced in Conditions 1 and 3 and increased again much later. In Condition 2, there was no very consistent change in scrabbling.

The interim APs besides walk/sniffing—*i.e.*, grooming, picking up sawdust, open rearing, and wall rearing, shown in the third row of panels in Figure 3—always decreased abruptly when food was introduced and recovered more or less later. Lilke walk/sniffing, these APs generally did not recover their baseline levels.

Altered Sawdust, Spraying

Neither of these manipulations in Condition 1 had the expected effect of changing interim activities within interfood intervals. Changing the sawdust did not affect picking up sawdust or any other AP, though it lowered bar pressing in some animals (Figure 3a, block SD). Spraying the animals with water, both alone and in conjunction with thwarting, did increase grooming (Figure 3a, third row, blocks S and ST). However, most of this increase occurred early in spraying sessions, when the animals simply groomed themselves to the exclusion of pressing the bar and other activities.
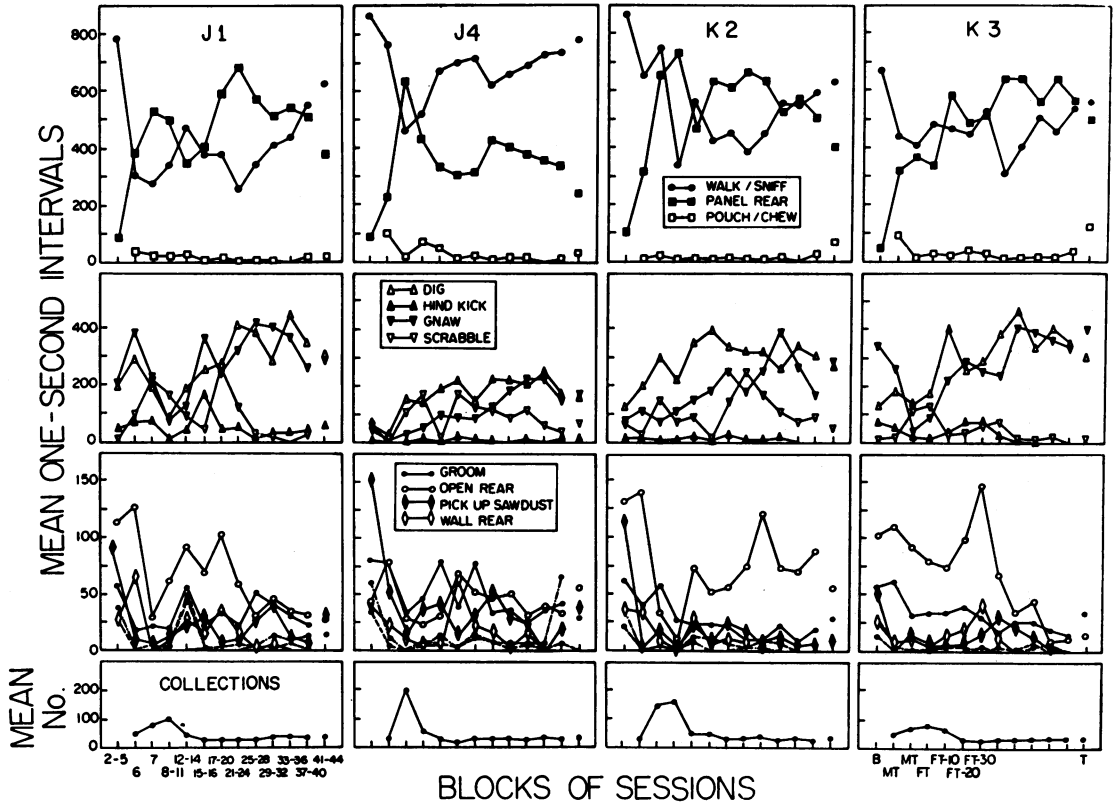
Fig. 3b. Mean number of 1-sec intervals in which each AP occurred and mean food collections for blocks of sessions for each subject in Condition 2. Experimental conditions are also indicated: B—Baseline; MT—Magazine Training; T—Thwarting. In the third row of panels, the three types of grooming are displayed separately as in Figure 3a for the first 40 sessions.

Thwarting

When the animals in Conditions 1 and 2 were thwarted by having food omitted on every second block of four terminals, they all increased the number of intervals in which they failed to pause in lever pressing or another activity when the tone sounded. Generally, however, when a pellet was due they reared at the feeder opening and put their noses to the hole where food usually appeared. In sessions with thwarting, such attempts to collect in the absence of a pellet marked the start of "thwarted intervals", just as successful pellet collections began "regular intervals".

Figures 4a and b represent performance of one subject in each condition for the last two sessions of thwarting, analyzed separately for regular and thwarted intervals in the same way as the baseline data in Figure 1. The other subjects performed similarly except for one in Condition 1 (M6), which collected too few

times for its data to be analyzed. The results with spraying and thwarting together in Condition 1 were essentially the same as those for thwarting alone.

An omission effect is evident in Figure 4: panel rearing and other appetitive APs began sooner in thwarted than regular intervals. In Condition 1, the omission effect was also evident in lever pressing: on the last day of baseline the mean pause after collecting a pellet was 17 to 21 sec; on the last day of thwarting, and spraying plus thwarting respectively, each animal's mean pause in regular intervals was similar to its baseline value, but 4 to 9 sec shorter in thwarted intervals.

Food omission also affected the temporal patterns of interim activities, most obviously walk/sniffing (Figure 4, left panels). The probability of walk/sniffing peaked earlier following food omission. It also declined disproportionately soon, so there was actually less walk/sniffing following thwarting. Thwarting also
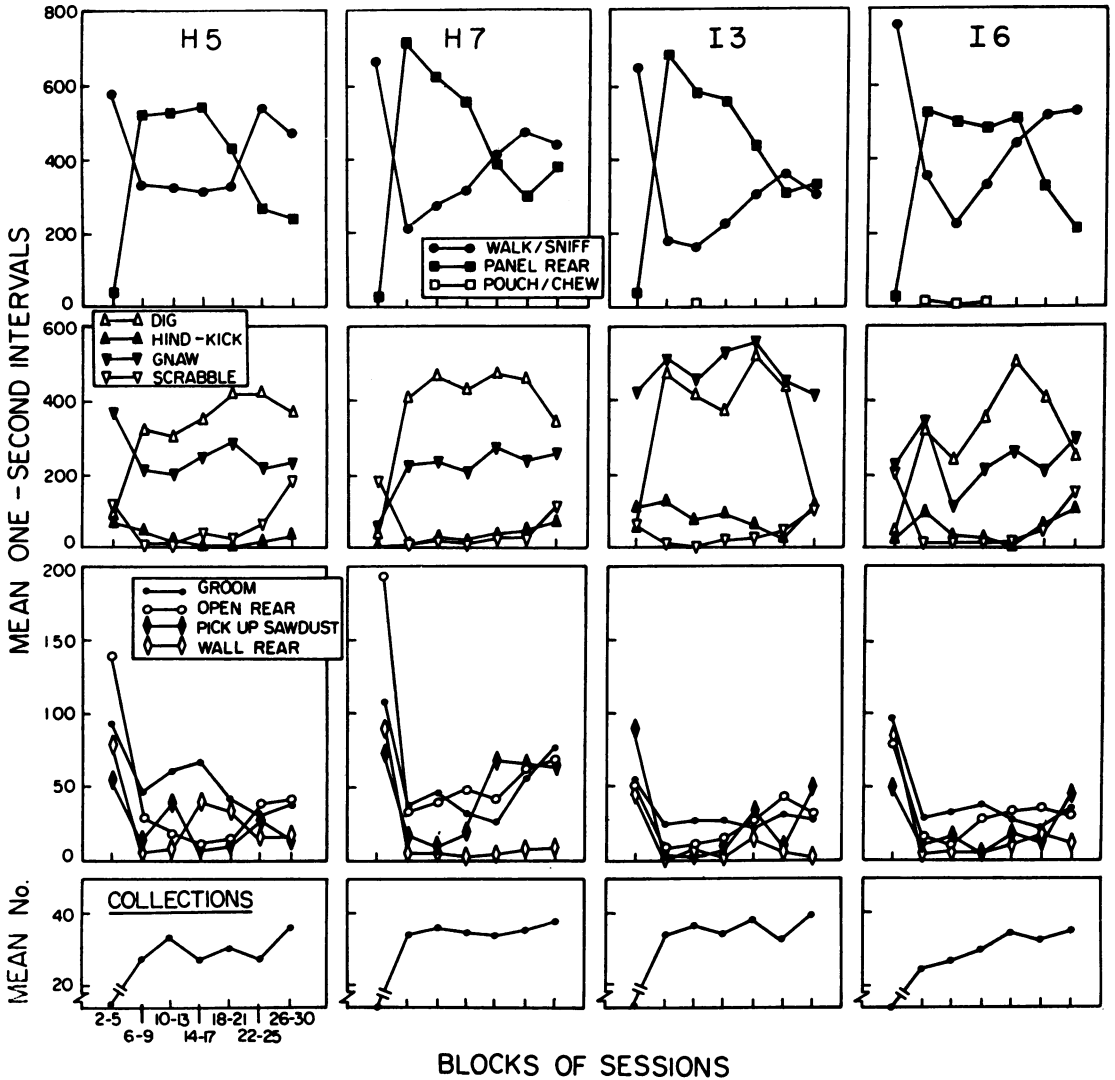
Fig. 3c. Mean number of 1-sec intervals in which each AP occurred and mean food collections for blocks of sessions for each subject in Condition 3.

affected the temporal pattern of grooming, but it did not affect that of open rearing, wall rearing, or picking up sawdust. To make the temporal organization of these relatively infrequent interim APs more apparent, interfood intervals for the last three sessions of baseline, thwarting, and spraying plus thwarting, were divided into quartiles, and the proportion of all 2-sec intervals with a given interim AP that fell into each quartile was calculated. (Only grooming and open rearing were analyzed in Condition 2 because the other two APs were so infrequent). During baseline, and during regular intervals in thwarting sessions,

the second and third quartiles generally had the greatest proportion of 2-sec intervals with open rearing, wall rearing, picking up sawdust, and grooming. The pattern was similar in thwarted intervals, except in the case of grooming. In every case, the proportion of grooming in the first quartile of the interval increased after food omission. In most cases this became the part of the interval with the highest proportion of grooming.

DISCUSSION

The behavior of the hamsters in the present experiment was similar in many ways to
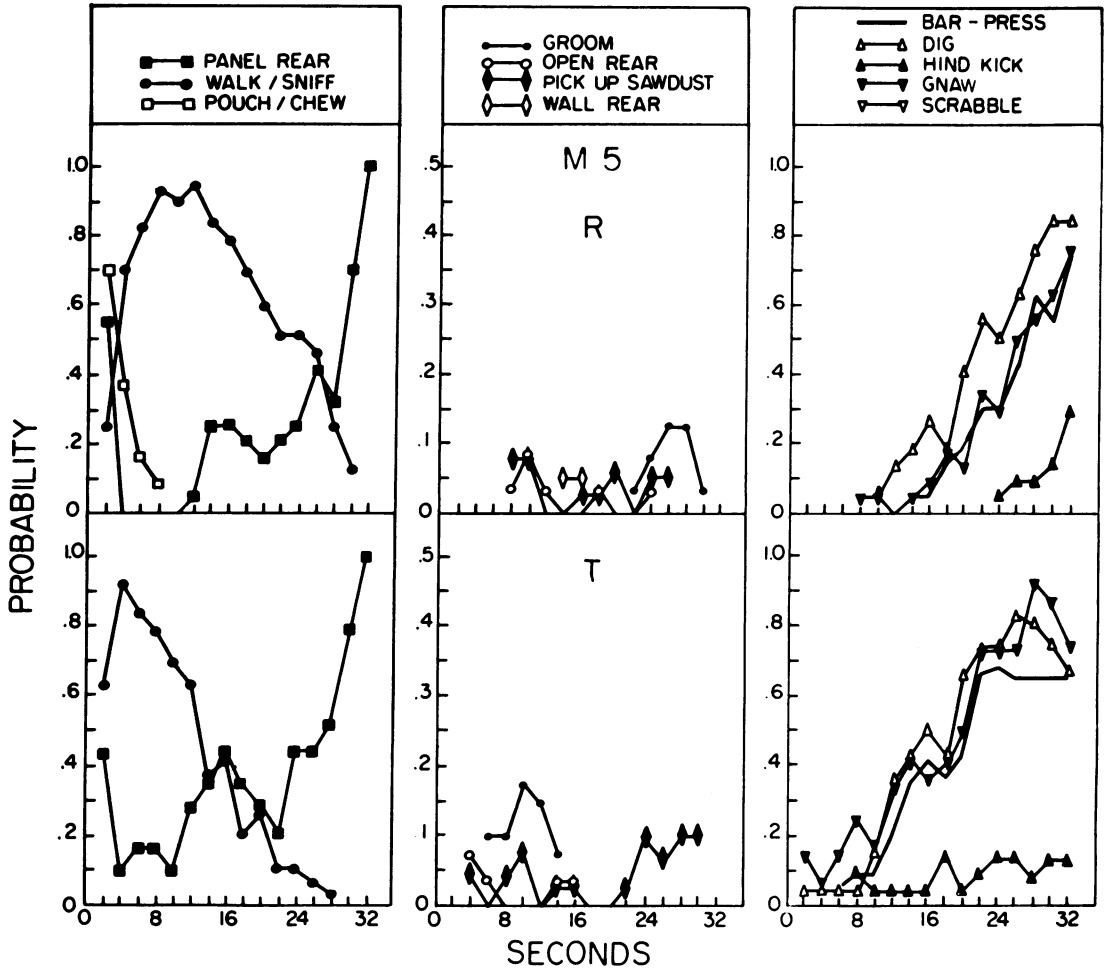
Fig. 4a. Probability of a given AP or lever pressing in each 2 sec of 30- to 34-sec intervals on the last two days of thwarting (Days 57 and 58) for one subject in Condition 1. R—Regular intervals, those beginning with tone and food; T—Thwarted intervals, those beginning with tone only.

that of rats and pigeons observed on periodic food schedules in different sorts of environments with different behavioral classification schemes. Activities became organized around the times of food delivery into three aggregations: consummatory, interim, and terminal. The times at which specific activities were performed relative to food were the same whether food was free or obtained by lever pressing (Falk, 1971; Killeen, 1975; Staddon, *in press;* Staddon and Simmelhag, 1971). And after food omission, lever pressing and the terminal activities began sooner than otherwise, and some interim activities peaked sooner (Killeen, 1975; Staddon, 1974).

Immediately after collecting a food pellet, the animals lingered a few seconds at the feeder and pouched and/or chewed the food pellet if one had been delivered (the consummatory aggregation). Evidence for similar behavior can be seen in the data of Staddon and Ayres (1975). Its occurrence immediately after food delivery is to be expected.

After collecting the food, the hamsters generally walked briskly around the open field, pausing to open rear, wall rear, groom, or pick up sawdust. Walk/sniffing was the most probable interim AP, with a probability near 1.0 about a quarter of the way through food-food intervals. The curves for walk/sniffing as a function of time since food are similar to those Killeen (1975) shows for "general activity" (depressions of a panel in the floor) of pigeons on a variety of FI and FT schedules, and for
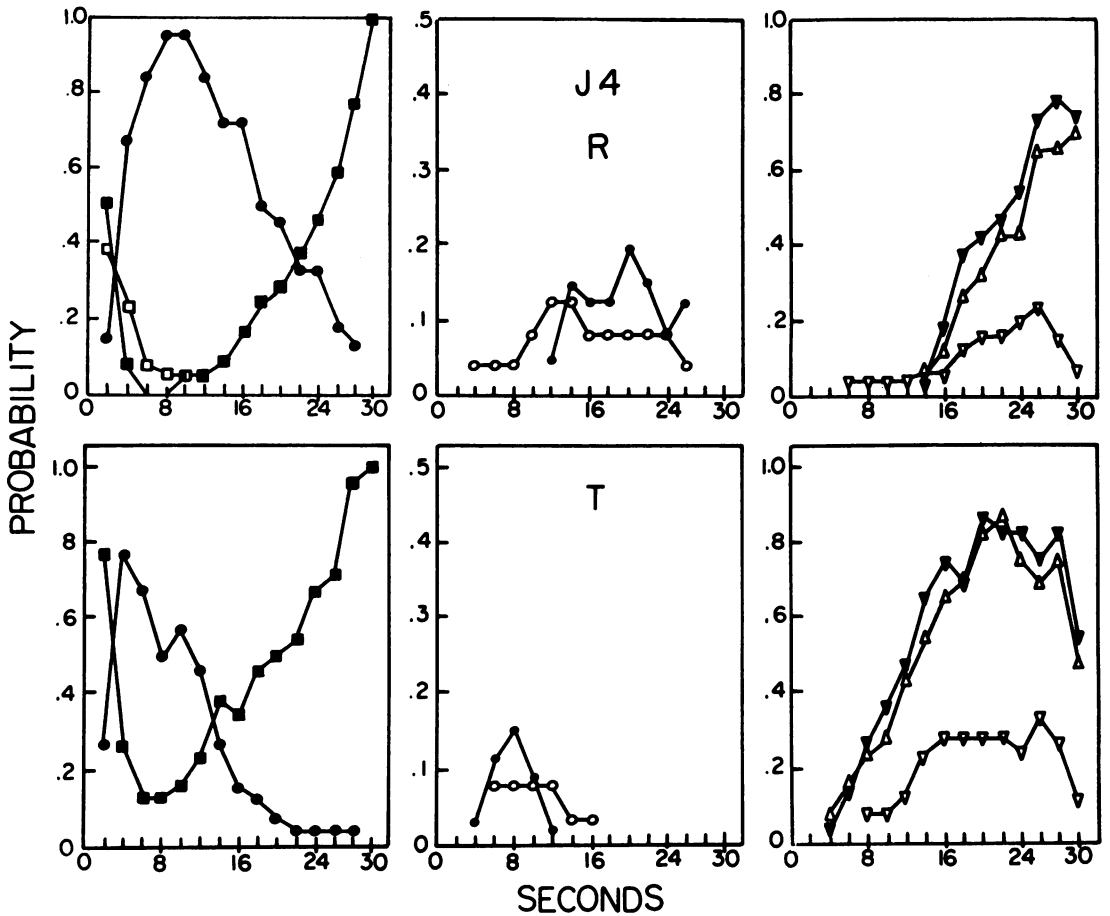
Fig. 4b. Probability of each AP in each 2 sec of the interval on the last two days of thwarting for one subject in Condition 2. R—Regular intervals, those beginning with tone and food; T—Thwarted intervals, beginning with tone only.

other behaviors in several species. Walk/ sniffing functioned similarly to schedule-induced escape, in that it took the hamsters away from the feeder when food was not due. Similarly, pigeons stand farther away from the response key during a food CS- than during a CS+ (Wasserman, Franklin, and Hearst, 1974).

When rats were observed on FT 30-sec food schedules (Staddon and Ayres, 1975), two classes of interim activities emerged: the rats drank with high probability immediately after food and then ran in a wheel or engaged in other activities, with lower probability than drinking (cf. Knutson and Schrader, 1975). Pigeons on FT and FI 12-sec schedules (Staddon and Simmelhag, 1971) did not show two classes of interim APs, perhaps because of the short intervals. Such a division of interim

activities is also not so apparent in the present data, partly because the interim activities other than walk/sniffing did not have very well defined peaks (cf. Figure 1). Furthermore, the different activities recorded by Staddon and Ayres were performed in different parts of the apparatus (e.g., at the water bottle, in the running wheel), whereas most of the APs recorded here could be performed anywhere. Therefore, they would be more likely to be intermingled. To the extent that the peaks of the other interim activities follow that for walk/sniffing, this reflects the observation that the hamsters would generally walk away from the feeder before engaging in the other interim APs, but thereafter they were interspersed with walk/ sniffing. Thus, walk/sniffing was generally the first interim AP to be performed, but it was also usually the last, recorded as the animals

trotted back to the bar and feeder area. This is apparent in the high probabilities of walk/sniffing just before the first bar press in Figure 2.

The terminal activities, those that steadily increased in probability up to the time of food delivery, consisted of rearing at the feeder and lever panel, and digging (often followed by hind kicking), gnawing, and scrabbling in contact with it. Rats also gnaw and dig at a feeder when free food is due (Davis and Hubbard, 1972; Staddon and Ayres, 1975), and gnaw at a lever they are required to press for food (Moore, 1973).

Thus, the broad outlines of the present results extend a number of findings already in the literature to a new species, situation, and system of behavioral classification. Further details of the data are particularly relevant to understanding the role of an instrumental contingency in determining terminal activities, the possible excessiveness or schedule induction of interim activities, and the causal relation between interim and terminal activities. These issues are discussed in turn.

Role of the Instrumental Contingency

In Condition 1, none of the interim APs (walk/sniffing, grooming, wall rearing, open rearing, and picking up sawdust), could result in pressing the lever except by accident, whereas all terminal APs (gnawing, digging and hind kicking, scrabbling, and panel rearing) could depress the lever when performed in the proper orientation. By itself, this difference among the APs could have been responsible for their emergence in different parts of the interval. However, when food was free in Conditions 2 and 3, the particular APs that occupied the interim and terminal periods were the same as in Condition 1. This finding supports suggestions that Pavlovian temporal conditioning plays a large role in determining the behavior animals exhibit when reinforcers are delivered at predictable times, and that response contingencies simply select from among activities that are facilitated by conditioned anticipation of the reinforcer (e.g., Bindra, 1972; Moore, 1973; Staddon and Simmelhag, 1971).

Several aspects of the present data support this notion. First, not every subject performed all the terminal activities, digging, gnawing, and scrabbling, at the same levels (Figures 1 and 3). Nevertheless, whenever these APs occurred in the final sessions, they were always in the terminal and never in the interim period. For example, digging and gnawing were the most probable terminal APs in all subjects that got free food, with scrabbling low or absent. These animals generally dug and gnawed around the feeder opening as the time for food approached. When lever pressing was required for food, scrabbling was more probable than gnawing in two animals, reflecting the fact that the lever could be pressed by scrabbling as well as by gnawing. The relative overall levels and session-by-session changes in the terminal APs were also affected by the lever-pressing requirement. For example, digging increased more gradually and gnawing reached higher terminal levels in Condition 2 than in Condition 1 (Figure 3).

The gradual shift from digging at the bar to scrabbling or gnawing in Condition 1 cannot be explained by the notion that an instrumental requirement simply selects from among a class of APs that are facilitated by temporal proximity to food. Staddon and Simmelhag (1971) made similar observations: pigeons that initially had their heads in the magazine at the time of food delivery nevertheless shifted to pecking the wall above the feeder. Some principle that overrides the law of effect could be involved in both cases. Moreover, both cases seem to differ from "instinctive drift" (Breland and Breland, 1966), in that one food-anticipatory activity is replaced by another, rather than an arbitrary behavior being replaced by a food-related behavior. Apparently the law of effect influences lever pressing itself, and where digging, gnawing, and scrabbling are directed, but exactly which AP is used to press the lever may be influenced by other factors as well.

Schedule Induction of Interim APs

Most previously described interim behaviors are adjunctive or schedule induced, in that they are absent or performed only at low rates in the absence of a food schedule and develop in step with the terminal behavior once a schedule is imposed. Falk (1971) made schedule induction a defining feature of adjunctive behaviors. Falk also defines adjunctive behavior as excessive. Excessiveness is obvious in schedule-induced drinking, the prototype of interim behavior, where the amount drunk on

a periodic food schedule far exceeds that needed to maintain normal water balance. However, this criterion is less easy to apply to activities that do not normally serve a clear homeostatic function.

The interim activities in the present experiment could not reasonably be termed schedule induced or excessive in any absolute sense. Walk/sniffing and the other interim APs never exceeded and seldom even equalled their levels when the animals were hungry but not receiving food in the situation. (Figure 3.) This was true even of APs like picking up sawdust and grooming, which normally increase with exposure to the open field (Shettleworth, 1975). However, by themselves, these observations do not necessarily mean that the interim activities were not schedule-induced. Comparisons with their levels in hamsters with various kinds of experience in the apparatus for the same number of sessions are needed.

It is more of a problem for schedule induction that, rather than developing in step, the overall levels of some interim and terminal APs changed in opposite ways during the early sessions. Most strikingly, panel rearing and walk/sniffing (top panels in Figure 3) showed large and reciprocal changes whether food density first increased and then decreased (Conditions 1 and 2) or whether it was roughly constant throughout (Condition 3). The other interim activities (third row of panels in Figure 3) generally changed similarly to walk/ sniffing. In contrast, different terminal activities changed in different ways. For example, in Condition 1, digging increased and then decreased like panel rearing, but in some cases gnawing and scrabbling had patterns like interim activities. In Condition 2, digging and gnawing changed together but did not parallel panel rearing. Thus, it is virtually meaningless to speak of interim and terminal activities developing in step in the present case because the course of development of the terminal activities differed both within and between conditions, while the interim activities showed similar patterns under all conditions.

Thus, in terms of overall levels, the interim APs do not fit two of the criteria for adjunctive or schedule-induced behavior: they are not obviously "excessive" and they do not "develop in step" with the terminal APs. However, it must be noted that a different way of recording behavior might have resulted in

some of the interim activities becoming "excessive". In particular, although "walk/sniffing" is a measure of general activity, in that it was recorded while the animals were walking around, it includes everything from standing still sniffing to running. If rate of motion had been used, as in Killeen's (1975) experiments, activity in excess of baseline levels might have emerged.

Relation between Interim and Terminal Activities

The alternation between interim and terminal activities has been described as an alternation between states (Schneider, 1969; Staddon and Simmelhag, 1971). This terminology is particularly appropriate in the present case because groups of activities, rather than single activities are involved. It is most meaningful if the same groups of activities can be identified in other situations that might be expected to induce the same states. In the present case, the terminal state seems appropriately identified with anticipation of feeding and the interim state with some other state, possibly escape from the food situation or exploration of the apparatus. However, although all the terminal activities are ones identified as food-anticipatory previously (Shettleworth, 1975), the interim activities also include some that are food-anticipatory by previous criteria and others that are not. In particular, rearing would not be expected to occur in the same period as grooming and picking up sawdust.

The conclusion that the interim APs are mixed in nature is supported by the effects of thwarting in the present experiment, since the temporal patterns of the various interim APs were affected differently by this operation. The terminal activities are not homogeneous either, since they showed different types of changes over sessions.

In principle, two mechanisms could be involved in the alternation of two states or classes of activities: disinhibition and competition (McFarland, 1974). With disinhibition, the terminal period is always "in control", in that it periodically inhibits and disinhibits the interim state. With competition, the terminal state relinquishes control to the interim state and then re-acquires it. These mechanisms may be distinguished by whether altering the causal factors for an interim activity alters its temporal locus. For example, McFar-

land (1970), found that pigeons key pecking for food invariably preened during the first pause in pecking. Because time to the first pause was not affected by putting paper clips on the pigeons' wings, which increased the tendency to preen, preening was a disinhibited activity.

Both disinhibition and competition have been suggested as being responsible for interim behaviors. For example, in drawing attention to the similarities between adjunctive behavior and displacement activities, Falk (1971) implicitly suggested that interim behavior is disinhibited, since this is the mechanism for some displacement activities. Staddon and Simmelhag (1971) implied something similar in suggesting that interim behavior illustrates how animals are free to do other things at times when food is not forthcoming. In contrast, schedule-induced behavior competes with the terminal behavior because it is directly generated by the food schedule. Staddon (*in press*) makes this suggestion, and Killeen's (1975) quantitative formulation explicitly includes competition between interim and terminal behaviors.

In the present experiment, thwarting, spraying, and changing the sawdust were designed to differentiate between these mechanisms. With spraying, grooming did compete with lever pressing and the other terminal APs, but only in the trivial sense that the animals groomed continuously after being sprayed to the exclusion of all other activities. Thwarting, however, did provide some information about the normal relation among interim and terminal activities. Behavior after food omission showed that the food-paired tone did not simply control a chain of activities. Walk/sniffing, which might be expected to peak sooner because of the absence of opportunity to perform the consummatory APs, also declined disproportionately soon, so that there was actually less walk/sniffing in thwarted intervals, even though there was in a sense more time for it. In addition, the other interim activities were affected differently, with the peak of grooming appearing earlier in the thwarted intervals but that of open rearing unaffected.

Thwarting also increased the influence of the terminal state, in that the appetitive APs began sooner after thwarting than otherwise. Staddon (1974) suggested that such omission

effects occur because food on periodic schedules acquires the ability to inhibit performance of the terminal behavior, and the inhibition is less when other stimuli are given instead. In the present case, the presence or absence of food also influenced the organization of the interim activities. However, changes in the overall levels of the various APs suggest that the interim APs were primarily disinhibited. Introducing food raised some of the APs that later became terminal APs to high levels while inhibiting the APs that became interim activities. With exposure to the situation, the interim APs returned toward their former levels while the terminal APs became more confined to late in interfood intervals. The suggestion that the interim APs in the present situation are not schedule induced also supports the interpretation that they were disinhibited.

Thus, behavior in the present experiment seems to consist of an alternation of classically conditioned appetitive activities (digging, gnawing, and scrabbling at the feeder and panel rearing) with other activities normal to the situation. These could be described as "exploring the open field". They are disinhibited during the period immediately after food deliveries. However, although their form and overall levels suggest that they are not schedule induced in the usual sense, the organization of the interim behaviors was affected by periodic food. Walk/sniffing took the animals away from the feeder, where they groomed, reared, and picked up sawdust. Then they returned to the area of the feeder. In this sense, the temporal and spatial organization of the interim activities was induced by the periodic food schedule.

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