Rats’ Behavior during an Interfood Clock Is Altered by the Temporal Pattern of Interfood Stimuli

Kathleen M. Silva and William Timberlake

Indiana University

Rats exposed to a basic interfood clock (a sequence of four different 12-s lights) during a 48-s interfood interval (IFI) showed a characteristic distribution of behavior: responses near the feeder peaked after food presentations, locomotion away from the feeder peaked in the middle of the IFI, and nosing in the feeder peaked just before food. Rats (Group Shorter) receiving interfood stimuli that got progressively shorter (24 s–12 s–8 s–4 s–food) showed sharper increases in nosing in the feeder across the last half of the IFI than rats (Group Longer) receiving interfood stimuli that got progressively longer (4 s–8 s–12 s–24 s–food). Although locomotion away from the feeder increased in the middle of the IFI for Group Shorter, activity in front of the feeder increased at the beginning of the IFI for Group Longer. Overall, the data support a behavior systems view that motivational modes underlying IFI behavior have timing characteristics that fit better with some temporal patterns of interfood stimuli than with others. Specifically, a sequence of progressively longer duration cues controls increased activity near the feeder at the beginning of the IFI, but a sequence of progressively shorter duration cues facilitates locomotion in the middle of the IFI and feeder-related responses at the end of the IFI.

The behavior of rats and pigeons changes predictably during the interfood interval (IFI) between periodic presentations of reward. For example, rats generally search near the feeder after eating, then drink, run in a wheel, and return to the feeder near the time of the next food presentation (Lucas, Timberlake, & Gawley, 1988; Reid, Bacha, & Moran, 1993). Pigeons gradually move away from the feeder after a food presentation and then progressively engage in more behavior directed toward the feeder wall as the time of the next reward approaches (Staddon, 1977; Staddon & Simmelhag, 1971; Timberlake & Lucas, 1985).

Researchers have used interfood clocks (a sequence of different interfood...
stimuli that fill the IFI) to examine the control of multiple responses across an IFI (Dinsmoor, 1994; Dinsmoor, Dougan, Pfister, & Thiels, 1992; Dinsmoor, Lee, & Brown, 1986; Ferster & Skinner, 1957; Matthews, Bordi, & Depollo, 1990; Palya, 1985; Palya & Pevey, 1987). For example, Matthews and Lerer (1987) showed that pigeons exposed to a key light that became increasingly brighter across a 30-s IFI developed a consistent distribution of responses between food presentations. Circling away from the feeder area (i.e., ‘‘re- treat’’) predominated after food presentations, when the key light was dimmest. Pacing along the chamber walls predominated in the middle of the IFI, when the key light was of a medium intensity. Pecking the key predominated just before food presentations, when the key light was brightest.

Using rats as subjects, Silva and Timberlake (1998a) explored the control of multiple responses during an IFI by comparing behavior when periodic food was and was not predicted by interfood stimuli. The interfood stimuli consisted of a sequence of four equal-duration lights flashing at different rates (i.e., S1–S2–S3–S4–food). Over a wide range of IFI durations, rats showed a consistent distribution of responses. Activity near the feeder was highest after food presentations during S1; locomotion away from the food site was highest in the middle of the IFI during S2; and nosing in the feeder was highest immediately before food presentations during S4.

The results reviewed above are mostly consistent with a behavior systems view of appetitive strings of behavior (Timberlake, 1983, 1994; Timberlake & Lucas, 1989; Timberlake & Silva, 1995). Drawing from ethology, this view relates the form of behavior during an IFI to a sequence of appetitive search modes (states) that control different repertoires of perceptual–motor mechanisms that depend on the spatial–temporal distance to reward. The portion of the rat’s feeding system described below represents a set of hypotheses and assumptions based on naturalistic observations and experiments of many researchers (Barnett, 1975; Ewer, 1971; Steininger, 1950; Telle, 1966; Timberlake & Washburne, 1989). The behavior systems view hypothesizes that an animal searching for food progresses through a sequence of search modes, each of which, in conjunction with external stimuli, controls a particular repertoire of preorganized food-related responses. For example, immediately after food, a rat is presumed to enter a postfood focal search mode, characterized by behavior directed around the feeder area (Lawler & Cohen, 1992; Lucas et al., 1988; Silva & Timberlake, 1998a; Silva, Timberlake, & Cevik, 1998a). During the middle of the IFI, the rat enters a general search mode characterized by locomotion around the experimental chamber (Silva & Timberlake, 1997, 1998a). As the time to food delivery approaches, the rat enters a focal search mode characterized by behavior directed toward the food site (Lucas et al., 1988; Silva & Timberlake, 1997, 1998a,b). Finally, the animal enters a handling/consuming mode consisting of chewing and ingesting the food.

According to a behavior systems view, search modes (and related behav-
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Behaviors can be conditioned to external stimuli that predict food. The extent to which an external stimulus controls a particular search mode should depend on, among other things, the temporal proximity of the stimulus to food. Thus, a stimulus immediately preceding food should come to evoke a focal search mode and appropriate responses, a stimulus presented temporally distant from food should come to evoke a more general search mode and related responses, and a stimulus presented immediately following food should evoke a postfood search mode and related responses (Silva & Timberlake, 1997, 1998a,b; Silva, Timberlake, & Koehler, 1996; Silva, Timberlake, & Gont, 1998b; Timberlake, 1994; Timberlake & Lucas, 1989).

Data produced using interfood stimuli are consistent with the behavior systems view of IFI responding. In Matthews and Lerer’s (1987) study described above, retreat can be viewed as postfood activity related to area-restricted searching for food, pacing is a general search activity related to searching for food more broadly, and pecking is a focal search response related to the imminent procurement of food (Timberlake & Silva, 1995; see also Papadouka & Matthews, 1995). Similarly, the order of responses found by Silva and Timberlake (1998a) are consistent with the behavior systems view. Activity near the feeder, a measure of postfood search, peaked during S1 (the time period after food presentations). General search behavior, in the form of locomotion away from the food site, peaked during S2 (the time period approximately in the middle of the IFI). Focal search behavior, in the form of nosing in the feeder, peaked during S4 (the time period immediately before food presentations).

The present study examined the behavior systems assumption that the different search modes are characterized not only by different activities, but by differential sensitivity to various stimuli. To test for this differential sensitivity, Timberlake and Silva (1995) suggested that it was important to understand how the rat’s underlying foraging mechanisms map to the experimental procedures (Silva et al., 1998a,b; Timberlake & Silva, 1994). According to this view, a sequence of stimuli that gets progressively shorter in duration should fit better with the rat’s species-typical foraging sequence (see also Dinsmoor, 1994). In a naturalistic sequence, animals are more likely to encounter diffuse, general cues temporally far from food. However, as the time to food approaches, they encounter more punctate or localizable cues. For example, consider a cat hunting for prey. It may use the change in daylight as a cue to begin searching. When it sees a cluster of trees it may approach them. As it approaches, it might encounter more localizable cues, such as the sound of a mouse moving in the underbrush. As it approaches the sound, it then may see even more localizable cues such as the mouse moving (see also Tinbergen, 1951). In should be noted that the behavior systems approach incorporates information based on the animal’s ecology. Although increasingly shorter and more focused cues may fit with the rat’s underlying motivational modes (Silva & Timberlake, 1998a; Timberlake & Washburne, 1989),
this sequence of cues may not fit with the modes of species with different feeding ecologies. For example, a sequence of stimuli that becomes progressively longer may fit better with the modes of a species for which the mode preceding food is relatively long (e.g., a squirrel cracking open an acorn).

In the present experiment, the role of stimulus duration and the order in which the different-length stimuli are presented was investigated by systematically altering the length of the individual interfood stimuli to be either more or less congruent with the typical relative durations of the underlying search modes. The notion was that the focal search mode is more likely to come under control of short-duration stimuli presented temporally close to food and the general search mode is more likely to come under control of long-duration stimuli presented more temporally far from food. One group of rats (Group Shorter) received a sequence of interfood stimuli in which each stimulus was of a shorter duration than the preceding one (24 s–12 s–8 s–4 s–food). A second group (Group Longer) received a sequence of interfood stimuli in which each stimulus was of a longer duration than the preceding one (4 s–8 s–12 s–24 s–food). A third group (Group Basic) received a sequence of interfood stimuli in which all stimuli were of equal duration (12 s–12 s–12 s–12 s–food).

The behavior systems view predicts that longer duration interfood stimuli should fit better with general search behavior (locomotion) occurring in the middle of the IFI than shorter duration cues, which should more readily come to control focal search behavior (nosing in the feeder) at the end of the IFI. That is, progressively shorter cues are compatible with more focused responses. Thus, a sequence of interfood stimuli that gets progressively shorter should produce different results from a sequence in which the stimuli get progressively longer or when the stimuli are of equal length (see also Akins, Domjan, & Gutierrez, 1994; Dinsmoor et al., 1992; Matthews et al., 1990; Matthews & Lerer, 1987; Timberlake & Lucas, 1989). Support for this possibility comes from data showing that general search responses are more strongly evoked by temporally distant CSs that are greater than 20 s in duration (Akins et al., 1994; Silva & Timberlake, 1997; Timberlake, Wahl, & King, 1982), and focal search responses are more strongly evoked by temporally proximate CSs about 4 s in duration (Silva & Timberlake, 1997; Silva et al., 1998b).

Based on the behavior systems’ view, it was predicted that nosing in the feeder should increase rapidly across the last half of the IFI for rats receiving progressively shorter stimuli (Group Shorter) and increase gradually or remain the same for rats receiving progressively longer stimuli (Group Longer). Locomotion should peak in the middle of the IFI for Group Shorter, which receives the long-duration cues earlier in the IFI, and increase or remain the same for Group Longer, which receives the long-duration cues at the end of the IFI. The behavior systems framework does not explicitly predict the length of cue that should most strongly control postfood responding
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(though see Silva et al., 1998b). However, it does predict that responses occurring temporally close to food presentations are more compatible with short-duration cues than with long-duration cues. Since standing in front of the feeder (a postfood response) typically occurs immediately after food, then this response should show significant increases near the beginning of the IFI for Group Longer, but remain unchanged for the other groups.

METHOD

Animals

Twenty-four naive female Sprague–Dawley albino rats, approximately 90 days old at the start of the experiment, were maintained at 85% of their free-feeding weights throughout the experiment. The rats were housed in individual home cages in a colony room regulated by a 12-h:12-h light:dark cycle. They were fed approximately 12 g of commercial rat chow in their home cages after each experimental session to maintain them at 85% of their free-feeding weight. Water was always available in their home cages. The 24 rats were divided into three groups of 8 rats each, and the groups were matched according to weight.

Apparatus

Rats were tested in four identical chambers. Each chamber was a rectangular sheet metal box 60 × 30 × 30 cm with a Plexiglas top and front. The food receptacle was 2.0 × 5.0 × 1.8 cm deep and located on a side wall 12 cm toward the back of the chamber. Food reward was delivered by a Waltke feeder (Waltke Scientific Enterprises, Psychology Department, Indiana University), which delivered two 45-mg Noyes pellets into the feeder. An infrared beam projected across the entrance of the feeder, an 11.0 × 10.0 cm platform was located on the floor in front of the feeder, and a 9.0 × 14.0 cm platform was located on the floor along the back of the chamber. A retractable lever was located on the feeder wall, 5 cm from the back of the chamber and 4 cm above the floor. The interfood stimuli were presented on a green jewel light 2 cm above the lever. A schematic of the apparatus is shown in Silva and Timberlake (1998a,b).

The experimental room also contained a video camera that monitored the experimental chambers. For closed-circuit observation, the video camera was connected to a Panasonic monitor located in an adjacent room.

Procedure

Experimental sessions were conducted at the same time daily, 6 days per week. There were 20 IFIs. Each session terminated immediately following the 20th IFI. The experimental procedure consisted of chamber adaptation, feeder training, and interfood clock training.
Chamber adaptation. The rats were put in the chambers for 10 min on 2 successive days. No food or stimuli were presented. In their home cages, the rats were fed the same food pellets that they received during subsequent phases.

Feeder training. Five food pellets were placed on the platform in front of the feeder at the beginning of a session, and 20 pellets were placed in the feeder. A session terminated after the rats had eaten all the pellets or after 30 min had elapsed, whichever occurred first. A rat was considered trained when it ate 20 food pellets within a 30-min session for 2 consecutive days.

Interfood clock training. Three groups of rats (Groups Basic, Longer, and Shorter) were exposed to 16 sessions with an interfood clock consisting of a sequence of four lights flashing at different rates. The first light (S1) did not flash; the second light (S2) flashed on:off at a rate of 1 s; the third light (S3) flashed on:off at a rate of 0.5 s; the fourth light (S4) flashed on:off at a rate of 0.1 s. Two food pellets were presented immediately after the offset of the last stimulus (i.e., S1–S2–S3–S4–food). The present experiment did not counterbalance for the order of flashing rates. However, previous research has shown that the pattern of responses during the interfood clock is the same whether the interfood stimuli flash progressively faster, progressively more slowly, or when the flashing rate is mixed (Silva, 1996).

The groups differed in the duration of the interfood stimuli that comprised the interfood clock (see Fig. 1 for a visual representation of the different interfood clocks). Group Shorter received an interfood clock in which the duration of the stimuli became progressively shorter. S1 was presented for 24 s, S2 for 12 s, S3 for 8 s, and S4 for 4 s. The rats in Group Longer received

![FIG. 1. A graphic representation of the interfood clocks received by Groups Shorter, Longer, and Basic.](image-url)
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an interfood clock in which the duration of the stimuli became progressively longer. S1 was presented for 4 s, S2 for 8 s, S3 for 12 s, and S4 for 24 s. The order of interfood stimuli was constant from trial to trial. Group Basic received an interfood clock in which the interfood stimuli were of equal length. That is, each of the interfood stimuli was presented for 12 s. The “basic” condition was included in the present study so that the patterns generated by a sequence of stimuli that became progressively longer or shorter could be compared to a clock condition whose pattern was already known (e.g., Silva & Timberlake, 1998a). To make the onset of the interfood stimuli more salient, the lever moved in and out of the chamber at stimulus changes.

Dependent measures and data analysis. Four dependent measures were automatically recorded by computer-controlled devices: the duration of (a) nosing in the feeder, (b) activating a platform located far from the feeder (i.e., the Far platform), (c) activating a platform located in front of the feeder while not nosing in the feeder (i.e., the Near platform), and (d) contacting the lever located beside the feeder. All rats reached stable levels of responding for all dependent measures by the 10th day of acquisition. Because contacting the lever was a relatively rare event with marked individual differences, these data were not reported.

Because it was very rare that the rats nosed in the feeder without standing on the Near platform, the time spent standing on the Near platform initially reflected the total time the rats spent standing on the platform while nosing in the feeder and while not nosing in the feeder. To separate “standing-on-the-platform-nosing in the feeder” from “standing-on-the-platform-not-nosing in the feeder,” the amount of time spent nosing in the feeder was subtracted from the amount of time spent standing on the Near platform. Thus, the amount of time that the rats spent on the Near platform excludes the amount of time that the rats were on the platform while nosing in the feeder.

As a measure of stimulus control, we measured changes in the amount of responding at the transition between one interfood stimulus and another compared with responding during an interfood stimulus. The type of statistical analyses that were used are described under Results. All statistically significant effects are reported at the \( p < .05 \) level.

RESULTS

One purpose of the present experiment was to compare the patterns of responding across the IFI generated by different orders of interfood stimuli durations. Figure 2 shows the duration per second spent nosing in the feeder and activating the Far and Near platforms for each group plotted across the absolute time since food in 4-s bins for Groups Shorter, Longer, and Basic. The durations of individual interfood stimuli are denoted by a continuous line with breaks between stimuli. These data indicate whether a particular interfood stimulus controlled a particular response. For example, if an in-
FIG. 2. The duration per second spent nosing in the feeder and activating the Far and Near platforms for each group averaged over the last 4 days of interfood clock training and plotted across the absolute time since food was presented in 4-s bins for Groups Shorter, Longer, and Basic. Different clock stimuli are denoted by the breaks in the data. Each Plus (+) symbol denotes the average duration of responding averaged over each interfood stimulus.
terfood stimulus controls nosing in the feeder, then a likely effect would be that the level of nosing should be relatively unchanged within an interfood stimulus, but show a change between interfood stimuli. Furthermore, graphing the data over time clarifies how responses not controlled by the interfood stimuli change across the IFI. The statistical analyses described below were conducted on data that were divided into 4-s bins. However, each graph also contains Plus (+) symbols that denote the value of each response averaged over the duration of a particular stimulus. Averaging the data over each interfood stimulus provides additional data showing how the order of the clock stimuli affected the level of the responses during the different interfood stimuli and how responding changed between interfood stimuli.

For each group, a one-way analysis of variance (ANOVA) examined the influence of time (in 4-s bins) in the IFI (Bin 1 versus Bin 2 . . . Bin 12) to determine if there was any main effect of time in the IFI for any of the dependent measures. If a significant main effect was found, Scheffe tests were conducted to determine between which bins the differences occurred.

The top row of graphs show that nosing in the feeder changed across the IFI for each group, a result confirmed by a main effect of time in the IFI for each group $[F_{s}(11, 77) > 12.23]$. Scheffe’s test revealed that nosing in the feeder decreased during the first 8 s and remained near that level until the middle of the IFI for all groups. Furthermore, during the last half of the IFI for all groups, nosing increased at stimulus changes but remained constant within an interfood stimulus. Since the groups appeared to systematically differ in their level of nosing in the feeder toward the end of the IFI, ANOVAs were conducted that examined the influence of group type (Groups Shorter vs. Longer vs. Basic) on nosing during each 4-s bin. The groups differed in the amount of nosing during the last three bins $[F_{s}(2, 21) > 3.97]$, and Scheffe’s test revealed that Group Shorter nosed in the feeder more than the other groups. In sum, the interfood stimuli during the last half of the IFI controlled nosing in the feeder for all groups. However, rats exposed to a sequence of stimuli that became progressively shorter showed sharper increases in nosing in the feeder toward the end of the IFI and nosed in the feeder more than rats exposed to the other sequences of interfood stimuli.

The second row of graphs show that, overall, activity on the Near platform decreased as the IFI elapsed for all groups. An ANOVA confirmed that activity on this platform changed across the IFI $[F_{s}(11, 77) > 6.18]$. Scheffe tests revealed that, in general, activity on the Near platform was lower during the last bin than the second, third, and fourth bins for Groups Shorter and Longer and was lower during the last bin than the second bin for Group Basic. Most importantly, Group Longer was the only group that showed a statistically significant increase in platform activity from the first bin (which corresponds to S1) to the second bin (which corresponds to the beginning of S2). Responding during the second and third bins was the same. The increases between the first and second bins shown by the other groups were not statisti-
cally significant. Thus, activity on the Near platform, a measure of postfood search, showed a significant increase from S1 to S2 only when the shortest of the interfood stimuli were presented immediately after food. This suggests that stimuli presented after food can control increases in postfood responses when short stimuli serve as the interfood stimuli.

The third row of graphs shows that activity on the Far platform peaked in the middle of the IFI for Groups Shorter and Basic. Although there was a main effect of time for each group \( F_s(11, 77) > 2.51 \), there were no significant changes across the IFI for Group Longer according to the Scheffe tests. Groups Shorter and Basic spent significantly more time on the Far platform during the fifth and sixth bins than during the first and last bins. Although the data for Group Longer showed a slight peak in the middle of the IFI, there was considerable individual variation. In sum, these data indicate that changing the duration of individual interfood stimuli can affect the pattern of activity on the Far platform, a general search response, resulting in significant peaks of responding in the middle of the IFI when the interfood stimuli get progressively shorter or when they are equal in length. However, unlike nosing in the feeder, this response appeared to be less tightly controlled by individual stimuli (Silva & Timberlake, 1998a). That is, the increase in responding occurred more during an interfood stimulus than at changes between stimuli.

DISCUSSION

Overall, for all groups, nosing in the feeder decreased during the first 8 s and remained near that level across the first half of the IFI. Nosing in the feeder increased during the last half of the IFI, but the groups differed in their absolute levels of nosing near the end of the IFI. A group receiving a sequence of stimuli that became progressively shorter (Group Shorter) nosed in the feeder more than groups receiving a sequence of stimuli that became progressively longer (Group Longer) or that were of equal length (Group Basic). Dinsmoor et al. (1992) observed a similar effect with pigeons. Lengthening a final interfood stimulus from 30 to 120 s reduced the number of key pecks during the final stimulus.

Activity on the Far platform peaked in the middle of the IFI for Groups Shorter and Basic, but there were no significant changes in this response across the IFI for Group Longer. This latter group showed an increase in activity on the Near platform between the first 4-s bin and the second 4-s bin, which corresponds to the change in stimuli from S1 to S2. The other groups failed to show any significant increases in this response between S1 and S2 or between the first and second bins.

Overall, the data suggest that rats are sensitive to the temporal characteristics of interfood stimuli and their order in the IFI. Activity on the Near platform and nosing in the feeder peaked just after and before food, respectively, and showed the ability to be controlled differentially by brief stimuli. The
shorter stimuli, either following food in the case of Near platform activity or preceding food in the case of nosing in the feeder, resulted in a significant increase in responding between adjacent stimuli. More specifically, rats receiving shorter stimuli at the beginning of the IFI (Group Longer) increased their activity on the Near platform between S1 and S2, whereas rats receiving the shorter stimuli at the end of the IFI (Group Shorter) increased their nosing in the feeder between S2 and S3 and between S3 and S4. In contrast, the peak in Far platform activity appeared to be less related to the changes in interfood stimuli. The implications of these results are discussed below.

Behavior Systems Account

One purpose of the present experiment was to determine if the order of different length interfood stimuli affected the pattern of different responses across the IFI. According to a behavior systems view (Timberlake & Lucas, 1989; Timberlake & Silva, 1995), an animal progresses through a sequence of search modes entrained by food presentations. Immediately after food, a rat enters a postfood search mode, characterized by behavior near the feeder. During the middle of the IFI, the rat enters a general search mode characterized by locomotion around the experimental chamber. As the time to food delivery approaches, the rat enters a focal search mode characterized by behavior directed at the feeder. According to this view, if an animal is provided with external predictive stimuli signaling the presentation of food, appropriate search modes should come to be controlled by these stimuli after extended training. The extent to which a stimulus controls a particular search mode and related responses should depend on the temporal proximity of the stimulus to food. A stimulus immediately preceding food should come to evoke nosing in the feeder (a focal search response); a stimulus presented in the middle of the IFI should come to evoke locomotion (a general search response); and a stimulus presented immediately following food should evoke behavior around the food site (a postfood search response).

While previous research by Silva and Timberlake (1998a) showed that an interfood clock composed of equal-length interfood stimuli generates a sequence of responding consistent with the behavior systems framework, they found that only the pattern of nosing in the feeder was differentially controlled by interfood stimuli. Stimuli immediately preceding food facilitated nosing in the feeder above that of a group that did not receive interfood stimuli, but locomotion away from the feeder in the middle of the IFI and activity near the feeder at the beginning of the IFI were similar in the presence and the absence of interfood stimuli and so appeared to be related primarily to the passage of time. One assumption of the behavior systems view is that the optimal stimulus length for the different search modes should be longer for the general search mode and shorter for the focal search mode. Thus, behaviors reflecting these modes are more likely to be maximally expressed under different progressions of interfood stimuli. General search be-
haviors are more likely to peak during the middle of the IFI and focal search behaviors at the end when interfood stimuli grow progressively shorter. Consistent with this view, Group Shorter nosed in the feeder during the last half of the IFI more than Group Longer, which displayed a flatter temporal pattern of nosing in the feeder than Group Shorter. In addition, locomotion peaked in the middle of the IFI for Group Shorter, but showed a flatter temporal pattern of responding for Group Longer.

The behavior systems approach also assumes that after food is eaten rats enter a postfood search mode characterized by behavior focused around the food site. The present results provide a novel finding that this postfood mode fits best with short cues presented immediately after food: Activity on the Near platform increased from S1 to S2 for Group Longer, but not for any other groups. These other groups also failed to show significant increases during the corresponding time period at the beginning of the IFI.

Finally, it is worth noting that care must be taken in the behavior systems approach to incorporate information based on the animal’s ecology before making predictions. Although increasingly shorter and more focused cues may fit with the rat’s underlying motivational modes (Silva & Timberlake, 1998a; Timberlake & Washburne, 1989), this sequence of cues may not fit with the modes of species with different feeding ecologies. For example, a squirrel that encounters an oak tree may spend a short time searching for an acorn. However, once it finds one, it may spend a long time cracking it open. Therefore, a sequence of stimuli that becomes progressively longer may fit better with a squirrel’s underlying modes than a sequence that becomes progressively shorter.

Other Accounts

The results of the present experiment also bear some relation to other accounts of learning and behavior. For example, according to Scalar Expectancy Theory (SET) (Gibbon & Balsam, 1981), the animal compares the length of the time between food presentations, C, with the length of the stimulus predicting food, T, and calculates the C/T ratio. If C is kept constant, the shorter the stimulus just before food the larger the ratio will be and, hence, the greater responding will be during this stimulus. The present results were consistent with SET. The Plus (+) symbols in Fig. 2 that denote the average level of responding during interfood stimuli showed that Group Shorter nosed in the feeder more than the other groups during S4. However, according to SET, Group Basic should have nosed in the feeder more than Group Longer during the final interfood stimulus. These groups, however, nosed in the feeder similarly during S4. One-way ANOVAs that compared the groups’ (Groups Longer vs. Shorter vs. Basic) level of nosing during each interfood stimulus showed that the groups spent different amounts of time nosing in the feeder during each stimulus \( [Fs(2, 21) > 9.53] \). Subse-
sequent Scheffe tests confirmed that Group Shorter spent more time nosing in the feeder than the other groups during S2, S3, and S4.

Moreover, although SET can account for Group Shorter’s heightened level of nosing in the feeder, it does not explain well other results. For example, SET can only account for the pattern of a terminal response and applies only to procedures that partition a trial into one component during which no food is presented and another component that is contiguous with food. Thus, it makes no specific predictions applicable to multistimulus situations like the interfood clock (Palya & Pevey, 1987), nor can it explain why a nonterminal response such as activity in front of the feeder increased between S1 and S2 for Group Longer.

The difference in the pattern of nosing in the feeder between Groups Shorter and Longer is also consistent with a higher order conditioning account. According to this view, the final stimulus (S4) acquires the most associative strength, which diffuses back to the earlier stimuli such that each successively earlier stimulus has less associative strength than the one that follows it. Because it is more contiguous with the forward presentation of food, a short-duration final stimulus should accrue more associative strength than a long-duration final stimulus, thereby spreading more associative strength to the preceding stimuli than a long final stimulus. As a result, responding should be higher throughout the IFI for Group Shorter than the other groups. Partially consistent with this view, Group Shorter nosed in the feeder more than the other groups during the final three interfood stimuli. However, like SET, the higher order conditioning account does not explain why other nonterminal responses, such as activity in front of the feeder, are controlled by short stimuli at the beginning of the IFI.

**Stimulus Control**

The present research adds to previous research (e.g., Silva & Timberlake, 1998a,b; Silva et al., 1996, 1998a,b) in providing evidence for the stimulus control of motivational modes. The terminal response of nosing in the feeder was facilitated by the interfood stimuli during the last half of the IFI, a result consistent with previous experiments showing that terminal responses are facilitated by stimuli presented during the last half of the IFI but not the first half (Gibbon & Balsam, 1981; Palya, 1985; Palya & Bevins, 1990; Silva & Timberlake, 1998a). However, the present experiment added to previous studies (e.g., Dinsmoor et al., 1992) by showing that the amount of responding during the last half of the IFI depends on the temporal characteristics of stimuli and their order in the IFI. More specifically, a sequence of stimuli that became progressively shorter evoked more responding than a sequence that became progressively longer.

The present research also provides information about the extent to which interfood stimuli control different responses within an IFI. A previous study
that exposed rats to an interfood clock composed of equal-length interfood stimuli suggested that nosing in the feeder was the only response differentially controlled by interfood stimuli (Silva & Timberlake, 1998a). In that study, nosing in the feeder was facilitated by the stimuli immediately preceding food, but locomotion away from the feeder in the middle of the IFI and activity near the feeder at the beginning of the IFI were similar in the presence and absence of the interfood stimuli. However, the present study showed that these latter two responses are sensitive to the temporal characteristics of stimuli and their order in the IFI. Although locomotion peaked in the middle of the IFI filled with equal length stimuli and also when the interfood stimuli became progressively shorter, it did not peak when the interfood stimuli became progressively longer. However, it is important to note that this response was not under as strict stimulus control as nosing in the feeder. Unlike the nosing response, locomotion did not show systematic increases or decreases during stimulus changes. It is also unclear at present why the pattern of locomotion across the IFI is similar during interfood clocks that become increasing shorter and those that contain equal length stimuli. Perhaps it might be argued that responses later in a behavior sequence need to reach a certain level before earlier responses display a peak in responding.

In terms of activating the Near platform after food, previous research that exposed rats to an interfood clock comprised of equal-length interfood stimuli failed to find evidence that the interfood stimuli after food controlled this response (Silva & Timberlake, 1998a). However, the present experiment showed that this response is controlled by the interfood stimuli in some circumstances. Animals receiving a short-duration stimulus after food followed by a slightly longer stimulus showed a significant increase in platform activity after food presentations.

It may be possible to make generalizations about stimulus control based on the present and previous data. For example, Silva and Timberlake (1997) suggested that general search responses occurring in the middle of the IFI may not be as tightly controlled by external stimuli as focal search responses. Similarly, Domjan (1994) suggested that general search behaviors may be more controlled by contextual cues than discrete stimuli. In terms of postfood responses, Silva et al. (1996, 1998a) have found that a short CS presented immediately after food in a backward serial conditioning procedure controls a postfood search mode.

The general finding that stimuli at the beginning and end of IFI control responses more than stimuli in the middle of the IFI is consistent with Palya’s (1993) bipolar model of interfood clock performance. This model specifies that, with respect to terminal responses, stimuli correlated with the successive portions of the latter half of the IFI are increasingly positive, stimuli correlated with successively earlier portions of the IFI are increasingly negative or aversive, the stimuli in the middle of the IFI are relatively neutral,
and qualitative changes in behavior are expected to stimuli correlated with these various portions of the IFI. Previous studies that have measured only a terminal response have found support for this model by showing that pigeons will peck a key to produce the positive stimuli correlated with the last half of the IFI and peck a key that removes stimuli correlated with the first half of the IFI (Dinsmoor et al., 1986; Palya, 1993). The present results provide further support for this model by showing that stimuli during the last half of the IFI controlled nosing in the feeder, stimuli near the beginning of the IFI controlled the qualitatively different response of activity in front of the feeder, and locomotion in the middle of the IFI was not under as tight stimulus control as the responses at the beginning and end of the IFI.

That control by an interfood stimulus depends on the length of the stimulus and its position in the IFI might account for Silva and Timberlake’s (1998a) finding that the interfood stimuli controlled some responses and not others. Recall that animals in that study were exposed to a sequence of four 12-s interfood stimuli. While this stimulus length was sufficient for stimuli at the end of the IFI to control focal search responses, it might have been too short to control general search responses that were predominantly occurring in the middle of the IFI. Support for this possibility comes from data showing that general search responses are more strongly evoked by CSs that are greater than 20 s in length (Akins et al., 1994; Silva & Timberlake, 1997; Timberlake et al., 1982), and focal search responses are more strongly evoked by CSs near 4 s in length (Silva et al., 1998b). Similarly, Akins et al. (1994) showed that a 60-s CS facilitated locomotion, a general search response, whereas shorter interfood stimuli facilitated approach to the CS, a focal search response.

In sum, the present data provided information about the organization of behavior during periodic presentations of food and about how external cues and their timing control this organization. The results showed that rats’ behavior possesses a particular organization during periodic presentations of food. Locomotion around the chamber peaks in the middle of the IFI, behavior near the feeder peaks after food presentations, and nosing in the feeder peaks just before food is presented. The latter two responses are controlled most strongly by short external stimuli after and before food, respectively. Locomotion is affected most strongly by relatively long external stimuli in the middle of the IFI. The organization is consistent with a behavior systems view of appetitive behavior, which posits that the structure of responding during periodic presentations of food is related to a sequence of search modes entrained by predictable food presentations (Timberlake & Lucas, 1989; Timberlake & Silva, 1995; see also, Cohen, Looney, Campagnoni, & Lawler, 1985; Domjan, 1994; Fanselow, 1994; Hogan, 1994; Timberlake, 1994). These search modes can account for the temporal distribution of response patterns evident during an IFI as well as the effects of systematically changing the duration of stimuli that comprise an interfood clock.
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