A reevaluation of the CS— hypothesis for schedule-induced polydipsia under intermittent schedules of pellet delivery

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Lashley and Rosellini (1980) have recently suggested that schedule-induced polydipsia (SIP) is determined by the occurrence of absolute periods within schedules of periodic food delivery which are associated with a low probability of food delivery, that is, CS— periods. To assess this hypothesis, SIP was examined in the present experiments under three schedules—fixed time, variable time, and random time (RT)—which differed in probability of occurrence and/or duration (Experiment 1), and under a range of RT schedules in which the CS— period was systematically varied by changing the interpellet interval (Experiment 2). In both experiments, the level and temporal distribution of SIP did not seem to be related to the absolute period associated with the absence of food. Instead, SIP was more systematically related to the average length of the interpellet interval and, therefore, to the average period associated with no food. It was suggested that drinking under intermittent schedules of pellet delivery, that is, SIP, is determined by an average CS— period and not by an absolute period associated with the unavailability of food.

Falk (1961) demonstrated that if water is made continuously available to a rat leverpressing for food under an interval schedule, the rat develops a characteristic temporal distribution of drinking following each pellet delivery (Staddon, 1977). Typically, this schedule-induced drinking occurs immediately following the delivery of food and greatly exceeds home-cage consumption under similar conditions of food deprivation (Riley, Hyson, Baker, & Kulkosky, 1980).

While the majority of explanations of schedule-induced polydipsia (SIP) have focused on physiological or motivational mechanisms (see Freed, Zec, & Mendelson, 1977; Roper, 1981), a Pavlovian conditioning account of SIP was recently presented (Lashley & Rosellini, 1980). According to this view, within reinforcement schedules that generate polydipsia the delivery of a pellet signals a period during which the probability of food is unlikely. As a result of this predictive relationship between the postpellet period and the reduced probability of food, this period becomes an inhibitory conditioned stimulus (CS—) for food, inhibiting food-related activities. As such, other behaviors are free to occur in the postpellet interval. Because of the salience

of the water tube, drinking typically occurs in, and is restricted to, this CS— period.

Different reinforcement schedules that generate different patterns of food delivery are likely to differ in the probability of occurrence and/or duration of these periods associated with no food (Lashley & Rosellini, 1980; Millenson, Allen, & Pinker, 1977). For example, under a fixed-time (FT) schedule, food is delivered to the animal with a constant interpellet interval, independently of its behavior. Thus, the period following pellet delivery is never associated with food; that is, this period is a CS— for food. One can also determine the duration of the CS— period on an FT schedule by the duration and the temporal distribution of licking. Since licking is restricted to the first third of the interpellet interval (IPI), the CS— period is presumably of the same duration. Under a variable-time (VT) schedule, food is also delivered independently of the animal's behavior. Although, within VT schedules, the IPI is variable, there is always a period immediately following pellet delivery which is never associated with food; that is, there is always some minimal CS— period. This minimal CS— period is presumably of shorter duration than that on an FT schedule (Catania & Reynolds, 1968; Ferster & Skinner, 1957). Finally, under a random-time (RT) schedule, food is also delivered with a variable IPI and independently of the animal's behavior. Unlike the VT schedule, however, there is no postpellet period differentially correlated with the absence of food delivery; that is, there is no minimal CS—

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period. Within an RT schedule, food is delivered with a constant probability throughout the IPI (Millenson, 1963).

Since, according to the CS- hypothesis, drinking is induced by periods associated with no food, SIP should differ under schedules that differ in the probability and/or duration of these CS- periods. Because the CS- period is longer under FT schedules than under VT schedules, the absolute level of consumption should be higher under the FT schedule and the temporal distribution of licking should extend further into the IPI. Similarly, since CS- periods do not occur under RT schedules, SIP should not develop.

Although there have been individual investigations of SIP under each of the aforementioned intermittent schedules of food delivery, that is, FT, VT, and RT (Hamm, Porter, & Kaempff, 1981; Hawkins, Schrot, Githens, & Everett, 1972; Lashley & Rosellini, 1980; Allen & Weidinger, Note 1), there are few data on the acquisition of SIP under VT schedules (Hawkins et al., 1972), there are inconsistencies regarding the occurrence of SIP under RT schedules (Hamm, Porter, & Kaempff, 1981; Lashley & Rosellini, 1980; Allen & Weidinger, Note 1), and there are no investigations of the aforementioned schedules under the same experimental conditions. Thus, there has been no systematic evaluation of the absolute level of consumption and temporal distribution of licking under these three schedules and, therefore, no systematic test of the CS- hypothesis. Experiment 1 assessed the consumption and temporal distribution of drinking under FT, VT, and RT schedules in order to provide a more direct comparison of these schedules and a test of the CS- hypothesis.

EXPERIMENT 1

Method

Subjects. The subjects were 12 experimentally naive, female rats of Long-Evans descent, approximately 120 days of age at the beginning of the experiment. They were individually housed in wire-mesh cages and maintained on a 12-h-light/12-h-dark cycle (lights on at 0800 h) for the duration of the experiment.

Apparatus. Four identical chambers (26.5 × 19.2 × 16.0 cm) were used throughout the experiment. The sides and the ceiling of each chamber were made of .6-cm clear Plexiglas, while the grid floor was constructed of .4-cm-diam stainless steel rods spaced 2 cm center to center. A 1 × 3 cm food hopper was centered on the front wall 3 cm above the grid floor. A graduated Nalgene drinking tube located outside the chamber was positioned such that the Girton metal drinking spout was flush with the outer wall 3 cm above the grid floor and 7 cm to the left of the food hopper. Licks were detected with a drinkometer (Lafayette Model 55008). A continuously illuminated 28-V houselight was centered on the front wall of each chamber 13.5 cm above the grid floor. Electromechanical circuitry located in the same room recorded licks and automatically delivered food.

Procedure. All rats were given ad-lib access to water and fed 3-5 g of Purina Rat Chow daily until they reached 85% of their free-feeding weights. At this point, they were divided into three

groups matched on body weight ($n=4$ per group). On Day 1, each rat was placed in the experimental chamber, where it received 60 45-mg Noyes food pellets delivered, independently of its behavior, according to the following schedules. Group FT was presented with a single pellet once a minute on a FT 60-sec schedule. Group VT received pellet presentations on an average of once a minute on a VT 60-sec schedule. This VT schedule was composed of 13 possible IPIs (100, 5, 56, 50, 68, 12, 109, 80, 20, 120, 40, 90, and 30 sec) taken from Falk (1967). Although the order of this interval sequence was constant over sessions, the initial IPI varied randomly from session to session. Group RT received pellet deliveries on an average of once a minute on a RT 60-sec schedule determined by a Scientific-Prototype probability generator (4020J). Every .9 sec, the probability of food delivery was .015. The resultant range of IPIs on the RT schedule was .9-415 sec.

Following delivery of a food pellet, a 1-sec time base was initiated with cumulative time and licks registered separately in six consecutive 10-sec intervals. For Group FT, a pellet was delivered at the 60th second (termination of the sixth 10-sec interval). For Groups VT and RT, pellet delivery was variable and random, respectively, such that food delivery could occur before or after 60 sec. If the pellet was delivered after 60 sec, licks and time were registered in the sixth 10-sec interval until a pellet was delivered. For all groups, delivery of a food pellet reset the time base to zero (and back to the beginning of the first 10-sec interval).

If necessary, the animals were supplementally fed Purina Rat Chow in the home cage to maintain their body weights at 85% of initial baseline values. The experimental procedures and maintenance conditions were continued for 18 consecutive days.

Results

All determinations of statistical significance were made at $p < .05$, two-tailed.

Figure 1 presents the mean consumption for Groups FT, VT, and RT over the 18 days of polydipsia training. As can be seen from the figure, all groups drank less than 5 ml of water on Day 1. Over training, consumption for all groups gradually increased, reaching asymptote at approximately 34, 26, and 28 ml for Groups FT, VT, and RT, respectively, by Day 14 of exposure to free food. There were no significant differences among the groups during the acquisition of drinking [$H=5.59$, 3.04, and 2.23 for Days 1, 6, and 12, respectively, or at asymptote (Day 18), $H=4.24$]. This similarity is further illustrated in Figure 2, which presents the

Figure 1. Mean water consumption for Groups FT, VT, and RT throughout polydipsia training.

Figure 2. Total water consumption for individual animals in Groups FT, VT, and RT throughout polydipsia training.

absolute consumption for individual rats in each group over the 18 days of polydipsia training. While there were individual differences in acquisition and at asymptote, these differences were not specific to any particular schedule of pellet delivery (see Figure 2).

Figure 3 presents the postpellet distribution of licking for each group on Days 1, 6, 12, and 18 of polydipsia training. As seen in the figure, licking was not distributed differentially in time following food delivery on Day 1. By Day 6, however, all groups were licking in a postpellet pattern typical

Figure 3. Mean postpellet lick-rate distribution for Groups FT, VT, and RT on Days 1, 6, 12, and 18.

of SIP, that is, maximal lick rates in the first two 10-sec intervals following pellet delivery. This post-pellet distribution of licking was maintained on Days 12 and 18. At no point in training was the distribution of licking different for these three groups of rats (all $H_s < 1.70$).

Discussion

The aforementioned Pavlovian conditioning account of SIP (Lashley & Rosellini, 1980) states that because of a direct relationship between the period following pellet delivery and a low probability of food, this period becomes a CS— for food, inhibiting food-related behaviors and allowing for the development of postpellet licking, that is, SIP. Since, according to this model, SIP is elicited by and restricted to the CS— period, there should be a direct relationship between the probability and/or duration of these periods and the development and asymptotic level of SIP. Thus, SIP should differ under schedules that differ in the probability and/or duration of CS— periods, as do FT, VT, and RT. As described, however, there were no statistically significant differences among groups in total water consumption at any point in training. The fact that differences among groups were not statistically different may be a result of the small sample size in each group; significant differences may have been obtained with larger samples. As previously described, however, there was considerable overlap among individual animals in the level of consumption, with excessive drinking evident in all rats regardless of the schedule condition. Furthermore, the temporal distribution of postpellet licking was identical across groups.

Since Groups FT, VT, and RT were virtually iden-

tical in their absolute consumption and in the temporal distribution of licking, differences in the absolute CS— periods during intermittent schedules of pellet delivery may not be important in determining the development of SIP. Instead of absolute CS— periods, a more important factor in the development of SIP may be the average interval between pellet deliveries, that is, the average IPI. Since, in the present study, the average IPI under the VT and RT schedules is of the same temporal length as the constant IPI of the FT schedule, that is, 60 sec, similar average CS— periods may be generated among all groups, accounting for the similarities in SIP.

Other reported data, however, are less supportive of an averaging hypothesis (Bond, 1976; Freed & Mendelson, 1979). For example, Bond (1976) delivered pellets to rats independently of their behavior, with the interval between pellet deliveries either increasing (progressive time) or decreasing (retrogressive time) systematically over the session. The range of IPIs was 5-300 sec. In the progressive-time sequence, there was little licking at the lower IPI values. As IPI values increased initially, licking increased; however, it decreased with even longer IPI values. A similar, but reversed, pattern was evident in the retrogressive-time sequence. That levels of SIP were influenced by specific IPI values suggests that the average IPI is not controlling SIP, a result necessary for the CS— averaging hypothesis. In a related experiment (Freed & Mendelson, 1979), the effect of specific IPI values on SIP was also examined. In this report, a single pellet delivery was followed 20 sec later by a second pellet, this pellet was then followed by a third pellet 80 sec later, and a fourth pellet was delivered 80 sec after the third (i.e., sequential IPIs of 20, 80, and 80 sec). This sequence occurred 20 times over the session for 10 sessions. Similar to what Bond (1976) found, the animals displayed differential levels of SIP, depending upon the specific IPI (i.e., 20 or 80), again suggesting that local IPIs rather than average IPIs determine SIP.

Although these two studies question the CS— averaging hypothesis, it should be noted that in each of these studies the sequence of multiple IPIs was fixed over sessions—progressive and retrogressive (Bond, 1976) or sequential 20, 80, and 80 (Freed & Mendelson, 1979)—rather than variable or random as in the present study. Thus, it may be that, in schedules that permit the learning of specific IPI sequences, postpellet licking may directly track each IPI length, whereas in schedules that do not permit the learning of specific sequences, that is, variable and random schedules, postpellet licking may track the average IPI. Consequently, a CS— averaging mechanism could still account for the present data.

EXPERIMENT 2

If absolute consumption and temporal distribution of SIP under intermittent schedules of pellet delivery are determined by the average IPI, and the accompanying average CS- period, then SIP should be differentially affected by manipulations that affect the duration of the average CS- period. One method of varying the duration of the average CS- period would be to vary the average IPI. When the IPI is varied under fixed and variable schedules of pellet delivery, both absolute consumption and the temporal distribution of licking are affected. For example, in relation to absolute consumption, as the IPI increases, consumption increases. With further increases in the IPI, however, consumption decreases (Falk, 1966; Flory, 1971; Hawkins et al., 1972). On the other hand, within the range of IPIs that produce polydipsia, the distribution of licking is simply displaced into the interval as the IPI increases (Rosellini & Burdette, 1980).

Accordingly, since SIP under intermittent schedules of pellet delivery may be determined by an average CS- period, the relationship of IPI to consumption and the temporal distribution of licking under RT schedules should be similar to the relationship described for FT and VT schedules. Experiment 2 examined this relationship under a range of RT schedules.

Method

Subjects and Apparatus. The subjects were 28 rats of the same sex, strain, and approximate age as in Experiment 1. They were also maintained under the same conditions. The apparatus was the same as that described in Experiment 1.

Procedure. All rats were given ad-lib access to water and fed 3-5 g of Purina Rat Chow daily until they reached 85% of their free-feeding weights. At this point, they were divided randomly into seven groups ($n = 4$ per group). On Day 1, each rat was placed in the experimental chamber, where it received 60 45-mg Noyes food pellets delivered, independently of its behavior, according to the following schedules. Group RT-10 received pellet presentations on the average of once every 10 sec under a random-time 10-sec schedule. Similarly, Groups RT-20, RT-60, RT-120, RT-180, RT-300, and RT-480 received pellet presentations, independently of their behavior, under random time 20, 60, 120, 180, 300, and 480 sec, respectively. The RT schedules for all groups were determined by a probability generator and a recycling timer, with the probability that any pulse from the recycling timer would deliver a food pellet set at .015. Thus, in order to generate average IPI values of 10, 20, 60, 120, 180, 300, and 480 sec, the recycling timer pulse occurred every .15, .30, .90, 1.8, 2.7, 4.5, and 7.0 sec for the seven schedules of pellet delivery, respectively. These recycling timer values also defined the minimum IPI for each RT schedule of pellet delivery.

Following each session, absolute water consumption and the temporal distribution of licking were recorded for each rat, as described for Experiment 1. As above, Purina Rat Chow was given to maintain body weight at 85%. The experimental and maintenance procedures were continued for 10 consecutive days.

Results

Unless otherwise specified, all determinations

of statistical significance were made at $p < .05$, two-tailed.

Although consumption was low on the 1st day of free-food presentations, drinking gradually increased over sessions, reaching asymptote on Days 9 and 10. Figure 4 presents the mean consumption averaged over Days 9 and 10 for each group. As illustrated, while all groups drank during the free-food presentations, the amount consumed was a function of the schedule ($H = 15.15$). Groups RT-10 and RT-20, which did not differ significantly from each other, drank significantly less than the remaining groups. No other comparisons were significant (multiple comparisons; see Conover, 1980).

Figure 5 presents the absolute consumption averaged over Days 9 and 10 for individual rats in each group. The aforementioned difference between Groups RT-10 and RT-20 and the other groups is further illustrated in this figure. As shown, SIP was minimal for rats in Groups RT-10 and RT-20. Subjects in the remaining groups, however, acquired polydipsia at a substantial level, that is, greater than 11.0 ml, although a single rat in each of the RT-300 and RT-480 groups resembled rats in Groups RT-10 and RT-20 in that they failed to display polydipsia.

Further differences among groups are illustrated in Figure 6, which presents the distribution of post-pellet licking averaged over Days 9 and 10. A Kendall tau test¹ indicates that, as the average IPI increased from 10 to 480 sec, more licking was likely to occur later in the postpellet interval ($\tau = .26$, $z = 1.71$, $p = .044$, one-tailed). That this difference among groups was not simply due to a difference between Groups RT-10 and RT-20 and the remaining groups (a pattern evident in consumption; see above) is supported by the fact that as the IPI increases from 60 to 480 sec, more licking was again likely to occur later in the postpellet interval ($\tau = .32$, $z = 1.82$, $p = .034$, one-tailed).

Discussion

As described, if the absolute level of water consumption and temporal distribution of licking under

Figure 4. Mean water consumption for Groups RT-10, RT-20, RT-60, RT-120, RT-180, RT-300, and RT-480 averaged over Days 9 and 10 of polydipsia training.

Figure 5. Total water consumption for individual animals in all groups averaged over Days 9 and 10 of polydipsia training.

intermittent schedules of pellet delivery are determined by the average CS- period, then manipulations that affect the duration of these periods, that is, changes in interpellet interval, should affect the occurrence of SIP. Furthermore, if the mechanism determining SIP is the same under FT, VT, and RT schedules, then such manipulations should affect SIP similarly under these three schedules.

As illustrated in the present study, at the short and intermediate IPIs absolute water consumption under RT schedules was similar to that seen under FT and VT schedules with similar IPI values; that is, while drinking was minimal at the shorter IPIs, consumption increased at the more intermediate intervals. At the longer IPIs, that is, 300 and 480, absolute consumption under the RT schedules was not significantly reduced, but was maintained at levels similar to those obtained at the more intermediate values, an effect inconsistent with the reduced drinking reported under FT and VT.

In order to illustrate how the average CS- hypothesis could account for this apparent inconsistency, it is first necessary to indicate why, according to the average CS- hypothesis, a bitonic function

in absolute consumption would be expected as IPI increased. As described, at short IPIs within a schedule of food delivery, SIP is minimal, presumably because the average CS- period is too short to initiate and maintain drinking. As the IPI increases, the duration of the CS- period increases to a value sufficient to produce polydipsia. With further increases in the IPI, polydipsia is again reduced. This reduction in SIP at the longer IPIs may be due, in part, to the fact that CS- periods are no longer established under such schedules. Recent work by Killeen (1975) supports this interpretation. Killeen reports that, as the IPI increases, there is a reduction in the ability of a food delivery to signal a subsequent period during which food delivery is unlikely. Given this reduction in the ability of food to signal nonfood periods, the probability of establishing CS- periods is reduced and SIP is minimal at these extended IPIs.

Although a bitonic function in consumption can be accounted for by the average CS- hypothesis, it remains unclear why in the present experiment SIP was not reduced at the longer RT schedules in which average CS- periods are presumably also less likely to be established. It should be noted, however, that under RT schedules, IPI values are exponentially distributed (Millenson, 1963). As such, under an extended RT schedule, for example, RT 480, the relative occurrence of short and intermediate IPIs is greater than that of long IPIs. Because of a high frequency of short and intermediate IPI values, food's ability to signal subsequent nonfood periods may not be significantly reduced, allowing CS- periods to be established and, consequently, to produce SIP. Accordingly, in order for consumption under long RT schedules to be reduced, the average IPI would have to be increased to a point at which the number of short intervals is reduced below the point that maintains food delivery as a reliable signal for subsequent nonfood periods.

More direct support for the average CS- hypothesis can be seen in the effects of varying the IPI on the temporal distribution of licking. As described, as the average IPI increases, licking is displaced into the interval, with more licking occurring later in the IPI, a shift, presumably reflecting the fact that the average CS- period increases with increases in the IPI.

Together, the absolute level of consumption and the temporal distribution of licking generally parallel those seen under FT and VT schedules when the IPI is varied and support the position that SIP under schedules of periodic food delivery may be determined by an average CS- period. It is clear, however, that the patterns are not identical, indicating that factors other than an average CS- period may also be contributing to the initiation and maintenance of SIP.

Figure 6. Mean postpellet lick rate distribution for Groups RT-10 ($n=4$), RT-20 ($n=4$), RT-60 ($n=4$), RT-120 ($n=4$), RT-180 ($n=4$), RT-300 ($n=3$), and RT-480 ($n=3$) averaged over Days 9 and 10 of polydipsia training. To be included in this rate analysis, a rat had to meet at least one criterion of SIP (see Roper, 1981). In the present experiment, this was defined as displaying a differential pattern of licking with a minimum of .5 licks/sec in at least one of the 10-sec postpellet intervals.

GENERAL DISCUSSION

The CS- account of SIP (Lashley & Rosellini, 1980) states that because the delivery of a pellet signals a period during which the probability of food is unlikely, this period becomes a CS- for food which inhibits food-related behavior and allows for the development of postpellet licking, that is, SIP. Accordingly, since SIP should be elicited by and restricted to these CS- periods, there should be a direct relationship between the probability and/or the duration of these periods and the development and asymptotic levels of SIP. Thus, SIP should differ under schedules that differ in the probability and/or duration of these periods. As demonstrated, however, the absolute consumption and temporal distribution of licking was the same under different intermittent schedules of pellet delivery, that is, FT, VT, and RT.

While the CS- account does not explain the occurrence of SIP under RT schedules or the similarity in SIP under FT, VT, and RT schedules, as described, a modification of the CS- account—the average CS- period—does. According to this position, if the absolute consumption of water and the temporal distribution of licking are determined by an average CS- period, then manipulations that affect the duration of the average CS- period should

affect the occurrence of SIP. Furthermore, if the mechanism underlying SIP is the same under all intermittent schedules, that is, an average CS- period, then manipulations that affect the duration of CS- periods should similarly affect the level of water consumption and temporal distribution of licking under different intermittent schedules of pellet delivery. As seen in Experiment 2, the absolute level of consumption and the temporal distribution of licking under RT schedules were affected by variations in IPI in a manner generally similar to those occurring under FT and VT schedules (Hawkins et al., 1972; Rosellini & Burdette, 1980).

In summary, Experiments 1 and 2 suggest that an absolute CS- period may not be necessary for the occurrence of SIP. Instead, SIP may be produced by an average CS- period determined by the frequency of pellet delivery, an effect consistent with that found in other research indicating the rat's ability to average the frequency of reinforcement over time (see Anger, 1963; Herrnstein, 1969).

REFERENCE NOTE

1. Allen, J. P., & Weidinger, R. C. *Truly random reinforcement intervals do produce schedule-induced polydipsia*. Paper presented at the Psychonomic Society Meeting in St. Louis, Mo., November 1980.

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NOTE

1. In order to conduct this analysis, we transformed the temporal distribution of licking for each rat into a single composite index:

$$I = \frac{\sum_{i=1}^5 X_i Y_i}{Y_{\max}}$$

where X is the 10-sec interval (X having the value 1-5), Y is the average lick rate for a given interval, and $Y_{\max}$ is the maximum lick rate occurring within one of the five 10-sec intervals. Note that when licking occurs later in the postpellet interval, the value of I is large relative to that when licking occurs more immediately postpellet.

(Manuscript received February 23, 1982;
revision accepted for publication March 22, 1983.)