*SPACED FOOD BUT NOT ELECTRICAL BRAIN
STIMULATION INDUCES POLYDIPSIA
AND AIR LICKING¹*

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An attempt was made to induce polydipsia in rats whose lever pressing was reinforced with food pellets or electrical brain stimulation. Nine food-deprived, water-sated rats drank water excessively during sessions in which food pellets were delivered. When brain stimulation was substituted for food, drinking immediately ceased. Delivering brain stimulation according to a variety of schedules, pairing brain stimulation with food reinforcement, and substituting an air stream for water, each failed to produce polydipsic licking. These results show that polydipsia is not induced by all reinforcers.

Key words: polydipsia, air licking, food-pellet reinforcers, electrical brain-stimulation reinforcers, lever pressing, licking, rats

If food-deprived but water-sated rats receive small dry-food reinforcers that are temporally spaced, they will often drink as much as or more than their normal daily intake of water in a period of a few hours. This high rate of consumption, labelled "schedule-induced polydipsia" (SIP), appears to result from the rat's drinking a small draught (about 0.5 ml) after most of numerous pellet deliveries (Falk, 1961). (See Falk, 1964, 1971, 1972 for reviews of the literature on this effect).

One recent line of research on SIP has attempted to isolate the factors associated with reinforcer deliveries that produce drinking. Food reinforcers have several properties: reinforcing, discriminative (signalling reinforcement unavailability under periodic schedules, for example), and eliciting (taste, chewing, *etc.*). The general strategy in this line of research has been to ascertain if reinforcers other than dry food induce SIP. Differences between

reinforcers that do or that do not produce SIP may suggest some determinants of the phenomenon.

It is not yet clear if electrical brain-stimulation (ESB) reinforcement schedules (Pliskoff, Wright, and Hawkins, 1965) produce SIP. Cohen and Mendelson (1974) arranged both food and ESB schedules within daily sessions and reported little drinking after ESB deliveries. Since their rats drank a large volume of water after food reinforcers, it is possible that arranging both food and ESB reinforcement schedules within the same session militated against finding drinking after ESB reinforcement. Such a potential problem was absent in the experiments of Atrens (1973), who exposed rats only to ESB reinforcement schedules, and Wayner, Greenberg, Fraley, and Fisher (1973), who switched rats from food to ESB reinforcement schedules. While some water consumption was found in both these experiments, the data are equivocal. Atrens found drinking in two of five rats. In both cases, however, drinking ceased after several sessions. Only one of Wayner *et al.*'s four rats continued to drink after the schedule was changed from food to ESB. This subject drank less under the ESB than the food schedule and was tested for only a few sessions.

The present experiments were undertaken to provide more definitive evidence on whether ESB reinforcement schedules produce SIP.

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GENERAL METHOD

Subjects

Two Wistar albino rats (S1 and S2) obtained from Woodlyn Breeding Laboratories, Guelph, Ontario, and seven black hooded rats (S3 through S9) obtained from Canadian Breeding Laboratories, La Prairie, Quebec, served; they were males and weighed between 300 and 350 g at time of surgery.

Surgery and Histology

The rats were anesthetized with sodium pentobarbital (Nembutal, 50 mg/kg), injected intraperitoneally, and chronically implanted with a Plastic Products bipolar 0.25-mm electrode aimed at the medial forebrain bundle in the lateral hypothalamus. The coordinates for implantation were 2 mm posterior to bregma, 1.8 mm lateral to the sagittal suture, and 8.6 mm ventral to the dura. Electrodes were held in place with acrylic cemented to machine screws embedded in the skull. The electrodes protruded from the acrylic to permit connection to a Plastic Products lead. Following surgery, all rats were injected intramuscularly with 0.2 ml penicillin, and allowed at least one week to recover.

At the end of the experiment, the rats were asphyxiated with carbon dioxide, and their brains fixed in formal saline and frozen. Forty- μ thick brain sections were cut and stained with thionin. Histological inspection verified that, except for Rat S3, electrodes had been implanted at sites in the medial forebrain bundle. Rat S3's electrode was located in a more posterior section within the substantia nigra. Figure 1 illustrates these placements according to the stereotaxic coordinate system used by Pellegrino and Cushman (1967).

Apparatus

Two experimental chambers were used. The first was constructed three sides of metal and one of Plexiglas and measured 25 by 25 by 38 cm high. A Scientific Prototype lever was centrally mounted on one metal wall, 6 cm above the grid floor. A ball drinking spout protruded 1 cm through a 1.5-cm diameter hole 2.5 cm to the left of the lever, 3 cm above the floor. A food cup connected to a Davis Scientific pellet dispenser was mounted to the right of the lever, 3 cm above the grid floor. A 21 by 27

by 40 cm high plywood chamber served as the second chamber. A lever, food cup, and drinking spout were similarly mounted on one wall of this chamber. Both chambers were enclosed within illuminated, ventilated, sound-attenuating shells.

Electrical stimulation of the brain was delivered from a 60-Hz sine wave generator. A commutator, which connected leads from the generator to the stimulating electrodes, allowed the rats unrestrained movement within the chamber.

Experimental conditions were arranged by solid-state and electromechanical circuits.

Bar presses, reinforcements, and licks detected by a drinkometer circuit connected between the brass grid floor and the spout, were recorded by a cumulative recorder and digital counters. The drinkometer circuit was electrically isolated from the ESB circuit by a series of relays.

Procedure

Following food deprivation to 80% of free-feeding weights, an attempt was made to shape bar pressing with ESB reinforcement. Only those animals whose bar pressing was conditioned by ESB were employed. Current levels were then held constant for the duration of the experiment. During initial bar-press training, ESB was delivered for 0.25 sec contingent on each press. Once bar pressing was established, the ESB reinforcer in Chamber 1 consisted of five equally spaced 0.25-sec pulses. The interval between each pulse was 0.25 sec. Rats tested in Chamber 2 received one 2.5-sec pulse. Initially, each response produced an ESB reinforcer. Then, over the first two or three sessions, the schedule parameters were changed gradually until ESB followed pressing according to the schedules described below. Except as noted, the reinforcer was always contingent on a bar press.

Following bar-press training with ESB reinforcement, all rats received a few sessions in which 45-mg Noyes food pellets were substituted for ESB.

All experimental sessions, with designated exceptions, were 90 min long. Sessions generally occurred six days per week, at about the same time each day. Purina rat chow was given after each experimental session to maintain the rat at 80% weight. Except as noted, water

Fig. 1. Electrode sites in the nine subjects and two rats (10 and 11) from a related, unreported experiment. Drawings were taken from Pellegrino and Cushman (1967).

was continuously available in the subject's home cage.

Data are presented for the last five sessions for conditions that lasted more than five sessions. When a condition lasted only five sessions, data from all sessions are included. Data from single sessions are included when conditions alternated daily.

EXPERIMENT I

Drinking was monitored as rats were exposed to a variety of food- and ESB-reinforce-

ment schedules. Food and ESB schedules alternated by sessions or blocks of sessions.

METHOD

Subjects and Apparatus

Rats S1 through S8 were tested in Chamber 1.

Procedure

The reinforcement schedules are listed in order in Table 1. Parameter values of the differential-reinforcement-of-low-rate (DRL), fixed-interval (FI), and variable-interval (VI) schedules are given in seconds.

Table 1
Summary of Procedure and Results, Experiment I

Subject	Schedule	Reinforcer	Number of Sessions	Number of Responses	Number of Reinforcements	Volume of Water (ml)
				Mean(Range)	Mean(Range)	Mean(Range)
S1	DRL 20	ESB	15	453(438-471)	31(28-36)	0.0
		Food	10	393(370-420)	142(126-157)	58.8(56-64)
		ESB	5	459(336-538)	54(41-66)	0.0
		Food	5	404(100-538)	120(100-139)	41.2(24-50)
		ESB	1	434	81	0.0
		Food	1	363	150	46.0
		ESB	1	352	90	0.0
		Food	1	513	137	60.0
		ESB	1	406	49	0.0
		Food	1	555	140	62.0
		ESB	10*	352(317-383)	74(55-89)	0.4(0-1)
	VI 30	ESB	7	1714(1306-2342)	186(177-199)	0.0
		Food	7	2240(1915-2575)	180	47.2(41-55)
		ESB	7	1653(1047-2752)	182(180-188)	0.2(0-1)
	FI 80	ESB	5	1114(945-1398)	67(67-68)	0.0
		Food	5	1340(1022-1683)	69(69-70)	37.3(35-39)
		ESB	5	1244(1100-1407)	69	0.0
	FI 160	ESB	5**	1321(1027-1433)	46	0.0
		Food	5**	1965(1765-2227)	46(46-47)	24.9(21-31)
S2	DRL 20	Food	15	480(465-510)	50(23-72)	10.5(6-17)
		ESB	10	629(571-696)	36(32-43)	0.0
		Food	5	486(453-519)	36(26-41)	8.0(6-10)
		ESB	5	412(382-470)	56(33-71)	0.0
		Food	1	435	62	11.5
		ESB	1	345	87	0.0
		Food	1	405	73	15.0
		ESB	1	297	122	0.0
		Food	1	423	97	13.0
		ESB	1	417	48	0.0
		ESB	10*	194(147-254)	116(91-142)	0.7(0-2)
	VI 30	ESB	7*	219(191-275)	124(110-138)	0.0
		Food	7	2052(1789-2349)	180	22.6(20-25)
		ESB	7	1187(595-1814)	178(171-180)	0.2(0-1)
	FI 80	ESB	5	1115(1019-1189)	69(68-69)	0.5(0-2)
		Food	5	1636(1414-1849)	70(69-70)	9.7(6-14)
		ESB	5	1362(1235-1509)	69	0.2(0-1)
	FI 160	ESB	5**	1438(1303-1677)	46(46-47)	0.0
		Food	5**	1994(1286-2328)	46	5.4(2-8)
S3	DRL 20	ESB	10	238(148-291)	129(102-145)	0.9(0-2)
		Food	10	290(211-326)	104(96-126)	11.1(5-16)
S4	DRL 20	Food	10	342(301-371)	146(138-152)	30.3(29-32)
		ESB	10	330(283-352)	94(84-121)	1.9(1-3)
	DRL 30	Food	10	254(228-275)	63(50-74)	16.9(15-20)
		ESB	10	230(208-253)	67(61-75)	0.6(0-1)
	DRL 40	Food	10	194(181-214)	41(35-51)	8.5(4-14)
		ESB	10	194(163-243)	47(25-62)	0.1(0-1)
	FI 30	ESB	10	916(749-1088)	175(166-193)	1.5(0-3)
		Food	10	1684(1275-2185)	168(163-171)	24.0(20-29)
S5	FI 90	ESB	10	698(577-804)	59(56-60)	0.7(0-2)
		Food	10	1420(1180-1871)	60(60-62)	6.4(5-8)
	FI 30	ESB	10	1274(1061-1402)	173(171-174)	1.2(1-2)
		Food	10	2153(1982-2300)	174(160-180)	16.7(15-18)

Table 1 Continued

Subject	Schedule	Reinforcer	Number of Sessions	Number of Responses	Number of Reinforcements	Volume of Water (ml)
				Mean(Range)	Mean(Range)	Mean(Range)
S6	FI 30	Food	10	1078(950-1189)	181(178-185)	40.4(36-45)
		ESB	10	714(581-862)	175(170-180)	2.5(0-4)
	FI 90	Food	10	1614(1325-1845)	62(61-63)	29.0(28-30)
		ESB	10	578(423-698)	60	1.8(0-3)
	FI 150	Food	10	1600(1327-1799)	38(36-39)	22.3(19-26)
		ESB	10	601(514-668)	37(36-38)	2.6(1-4)
	FI 120	Food	10	1760(1591-1905)	27(26-27)	16.1(15-17)
		ESB	10	433(397-465)	25(24-26)	0.3(0-1)
S7	FI 30	ESB	10	512(436-560)	172(167-179)	0.0
		Food	10	2315(1623-2693)	188(183-192)	32.4(30-34)
	FI 90	ESB	10	558(441-676)	64(63-65)	0.0
		Food	10	2675(2512-2900)	64(62-68)	21.3(20-22)
	FI 150	ESB	10	491(438-530)	37(35-39)	0.0
		Food	10	2335(2186-2563)	38(36-39)	8.5(7-12)
S8	FI 30	ESB	10	1923(1747-2144)	184(158-193)	0.0
		Food	10	1473(1193-1655)	184(182-186)	32.5(29-34)
	FI 90	ESB	10	1473(1141-1665)	63(60-67)	0.0
		Food	10	2000(1818-2116)	65(62-67)	23.3(20-25)
	FI 150	ESB	10	1634(1419-1838)	37(36-38)	0.2(0-1)
		Food	10	1448(1377-1538)	37(36-38)	20.3(19-21)

*100% body weight.

**2-hr sessions.

RESULTS

Table 1 summarizes the number of lever presses, number of reinforcements, and volume of water consumed during each condition.

Both ESB and food reinforcement reliably maintained lever pressing in all rats. Food reinforcement often, but not always, maintained a higher response rate.

When food pellets served as reinforcers, SIP typically occurred. Only minimal drinking occurred when ESB reinforcers were delivered. Rats S1 and S2 were tested for several ESB sessions at 100% weight. Consistent with sessions at 80% weight, little drinking occurred. Usually, there was no measurable water consumption during ESB sessions. At most, 4 ml of water were consumed during one session, while water consumption at times exceeded 60 ml during 90-min food-reinforcement sessions. Figure 2 illustrates these large differences in water consumption during food- and ESB-reinforcement conditions. These data are from S1 during five sessions of ESB and five sessions of food reinforcement, followed by daily alternation of these conditions.

EXPERIMENT II

It is possible that SIP would occur with ESB reinforcement were it not for the extreme hydration that occurs in the absence of food consumption. The present experiment provided rats with an opportunity to engage in a drinking activity that circumvents this problem. Both air- (Mendelson and Chillag, 1970) and nitrogen-licking (Taylor and Lester, 1969) have been observed in rats under spaced-delivery food schedules.

METHOD

Subjects and Apparatus

Three rats (S5, S6, S7) in which food-associated SIP had occurred in previous experiments, and one naive rat (S9), were tested in Chamber 2. The drinking spout, connected to a regulated supply of compressed air, delivered a stream of air at a pressure of approximately 2.5 to 5.0 lb/sq in.

Procedure

An FI 90-sec schedule was in effect. Although three of the four subjects had previously acquired SIP, none air licked during the first

Fig. 2. Water consumption for Rat S1 during DRL 20-sec sessions in which either Noyes food pellets or ESB reinforcers were delivered.

few sessions with food reinforcement. Consequently, they were water deprived for 23 hr before each session. After three such sessions, during which air licking occurred at a high rate, water was again made freely available in the home cage, and the regular experimental regimen ensued. This procedure had to be re-

peated two or three times before all four animals would lick air reliably during the food condition. Four additional animals, some of which drank water excessively in previous experiments, failed to air lick and were excluded from the experiment. Table 2 summarizes the sequence of food and ESB schedules.

Table 2
Summary of Procedure and Results, Experiment II

Subject	Reinforcer	Number of Sessions	Number of Responses	Number of Licks
			Mean(Range)	Mean(Range)
S5	Food	10	1100(813-1362)	8374(4203-13013)
	ESB	10	1122(1078-1135)	9(1-14)
	Food	5	1328(963-1789)	5800(1972-8562)
S6	Food	10	2179(1634-3078)	7289(3497-14623)
	ESB	10	1182(1062-1308)	2(0-6)
	Food	5	2644(2340-2935)	6676(4062-13884)
S7	Food	10	2257(1716-2710)	14228(12950-15510)
	ESB	10	458(414-502)	10(4-16)
	Food	5	1716(1619-1930)	10977(3102-15880)
S9	Food	10	1225(1167-1322)	3489(2190-4804)
	ESB	10	516(466-614)	79(6-341)
	Food	5	1265(1023-1469)	6576(4005-8589)

RESULTS

As shown in Table 2, air licking occurred at a high rate during food sessions but was almost completely absent during ESB sessions.

EXPERIMENT III

Failure to demonstrate excessive postreinforcement licking with ESB may be attributable to the chronically implanted stimulating electrodes. Falk (1964) showed that small hypothalamic lesions have a marked attenuating effect on SIP. While the within-subject comparisons of the present study preclude this possibility, another possibility exists. Valenstein, Cox, and Kakolewski (1970) found that rather long (10 sec or more) trains of hypothalamic stimulation decreased normal deprivation-elicited food and water consumption following stimulation. It is possible that this post-ESB inhibition of drinking occurred in the present experiments, and precluded licking under ESB schedules. This possibility was evaluated in two ways in the present experiment. First, food and ESB reinforcers were delivered simultaneously for lever pressing. Second, water-deprived rats were stimulated while licking water or air.

METHOD

Subjects and Apparatus

Rats S4, S5, S6, S7, and S8, were tested in Chambers 1 and 2.

Procedure

As shown in Table 3, Rats S4 and S6 initially received 10 sessions of paired ESB and food reinforcement, followed by five sessions

of ESB reinforcement. During the first condition, a food pellet and an ESB reinforcer were simultaneously delivered according to an FI 90-sec schedule. (Since it took a fraction of a second for the rat to reach the pellet, ESB onset actually preceded ingestion of the food pellet.) Both rats were finally returned to the original condition, S4 having first received an additional 10 sessions of food reinforcement alone.

These rats as well as Rats S5, S7, and S8 were next water deprived for 22 hr before six sessions in which the lever was removed. During the first three daily 15-min sessions, the rats received no ESB. Stimulation identical to that delivered in previous conditions was delivered during the next three 15-min sessions according to a response-independent FT 90-sec (Rats S4, S6, S7, and S8) or FT 30-sec (Rat S5) schedule. Water (Rats S4, S5, S6, and S8) or air (Rat S7) was available throughout these six sessions.

RESULTS

As shown in Table 3, paired food and ESB, as well as food alone, reliably produced excessive drinking. When food reinforcement was removed, drinking was immediately and greatly reduced.

Stimulation produced only minor disruption of drinking elicited by water deprivation. The average number of licks of water or air per session during sessions without and with ESB was: 2209 and 1889, 435 and 449, 1976 and 2354, 4611 and 4311, 2387 and 2534 for Rats S4, S5, S6, S7, and S8, respectively. Post-ESB inhibition of licking, if present, does not appear large enough to account for the failures to observe SIP in the earlier experiments.

Table 3

Summary of Procedure and Results, Experiment III

Subject	Reinforcer	Number of Sessions	Number of Responses	Volume of Water (ml)
			Mean(Range)	Mean(Range)
S4	Food + ESB	10	1060(889-1261)	18.9(16-20)
	ESB	5	650(519-777)	0.6(0-1)
	Food	10	924(819-1052)	13.5(12-15)
	Food + ESB	10	848(685-1049)	16.4(15-18)
S6	Food & ESB	10	1846(1521-2196)	25.4(22-28)
	ESB	5	645(387-982)	0.5(0-1)
	Food + ESB	5	2098(1915-2294)	25.1(23-26)

GENERAL DISCUSSION

These experiments confirm and extend previous findings that drinking associated with the spaced delivery of reinforcers occurs with food but not with ESB reinforcers. While one can never state with certainty that SIP will not occur with ESB reinforcers, the present study rules out several of the more likely reasons for failing to observe SIP with ESB schedules. First, the use of a variety of schedules and parameter values decreases the chances that SIP failed to be observed because it is peculiar to certain schedules. Second, the opportunity to lick air shows that the absence of SIP with ESB reinforcers is not peculiar to water drinking nor due to excessive hydration that might occur in the absence of food. Third, arranging food and ESB in alternate blocks of sessions prevented drinking associated with one reinforcer from attenuating drinking by the other. Fourth, pairing ESB and food and delivering ESB to rats while drinking rules out the possibility that some aspect of ESB inhibits drinking. Fifth, it is unlikely that SIP failed to occur due to a peculiar site of neural stimulation: electrode placements were scattered throughout and even outside the medial forebrain bundle. Sixth, the within-subjects designs rule out the possibility that electrode-related brain damage was responsible for the absence of SIP with ESB reinforcers. Nor was the failure to observe SIP with ESB schedules due to the fact that food and ESB differed in reinforcing or discriminative properties. Both reinforcers reliably maintained operant responding and both signalled the unavailability of reinforcement equally on the various schedules.

The failure to observe SIP under ESB reinforcement schedules is consistent with the notion that SIP is due to some aspect of food other than its reinforcing or discriminative properties. The major difference between food and ESB reinforcers appears to be in what might be called an "eliciting" function. A distinction can be made (*cf.* Staddon and Simmelhag, 1971) between reinforcer-evoked behavior that does or does not require some additional stimuli for its occurrence. Thus, reinforcement might increase generalized nondirected activity in the post-reinforcement period (*cf.* Killeen, 1975) or, if appropriate stimuli are available, induce drinking. Our data suggest that the lat-

ter stimulus-dependent category of reinforcer-induced behavior might vary as a function of the reinforcer. Reinforcing hypothalamic stimulation might induce postreinforcement aggression (Huston and Desisto, 1971), but apparently not drinking.

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