Responses induced by stimuli that predict lateral hypothalamic stimulation

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Four experiments attempted to establish conditioned consummatory behavior in rats using lateral hypothalamic (LH) stimulation as US. In the first, a light CS that predicted LH stimulation came to produce increased activity, but not eating, drinking, or gnawing. In the remaining three experiments, a different model of Pavlovian conditioning, derived from auto-shaping, was used. Presentation of an illuminated drinking tube served as the stimulus that predicted LH stimulation. Many rats increased contact with and drinking from this predictive stimulus. Various controls showed that these increases were at least partly based on the contingency between tube presentation and LH stimulation. LH stimulation that induced a consummatory behavior was more likely to support increased drinking from the predictive tube than was LH stimulation that induced only increased activity. However, the kind of consummatory behavior the LH stimulation induced did not affect the occurrence of drinking from the predictive tube. This finding supports the hypothesis that LH stimulation in rats does not activate neural circuits associated with specific consummatory behaviors.

Attempts to condition appetitive drive states as inferred from conditioned consummatory behaviors have met with limited success (see Cravens & Renner, 1970, and Huston, 1975, for reviews). Early studies attempted to demonstrate increased consummatory behavior in the presence of environmental stimuli that had been associated with deprivation-induced drive states. Although most studies reported negative results, Grant and Milgram (1973) obtained success with this paradigm when eating, but not drinking, was the dependent measure. They suggested that the critical factor in their success was the use of animals selected for low emotionality. In some of her experiments, Mineka (1975) observed small increments in food consumption and in responding during extinction of a food-reinforced leverpressing task in the presence of flavors that had been associated with food deprivation. Lovibond (1980) and Zamble (1973) were able to produce a modest but reliable increase in the amount of food rats consumed during their regular feeding period when it was preceded by a long-lasting CS. This history of

limited success led to the suggestion that the failures were due to the slow development of deprivation-induced drives. Conditioned consummatory behavior might be more successfully demonstrated if the neutral stimuli were associated with or predicted the onset of brain stimulation or other intervention that induced consummatory behaviors rapidly and under relatively precise control (Miller, 1973; Mowrer, 1960).

Several experiments have attempted to test this possibility. Successful conditioning of insulin-induced hyperphagia has been reported by Balagura (1968), but Siegel and Nettleson (1970) have argued that an alternative interpretation was possible in terms of a conditioned avoidance of the stress induced by the insulin. A similar alternative explanation has been offered (Mineka, Seligman, Hetrick, & Zuelzer, 1972; Wayner & Fraley, 1973) for the apparent conditioned drinking induced by a CS associated with injections of hypertonic saline and procaine (Seligman, Ives, Ames, & Mineka, 1970). Two apparently successful attempts both used rather unconventional methods of inducing consummatory behavior. Milgram, Grant, and Stockman (1975) found that sated rats ate significantly more in the test chamber where they had previously been induced to eat after self-produced hippocampal stimulation. Siegfried, Waser, Borbély, and Huston (1975) found that rats ate more in a chamber in which they had previously been induced to eat by cortical, caudate, or hippocampal spreading depression. A number of other experimenters have attempted, without success, to induce consummatory behavior with a neutral stimulus which had been paired with lateral hypothalamic stimulation that induced eating or drinking (Andersson & Larsson,

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1956; Bindra, 1969; Bindra & Campbell, 1967; Huston & Brozek, 1972; Milgram et al., 1975). Successful conditioning of the increased activity induced by LH stimulation has, however, been demonstrated (Bindra, 1969; Bindra & Campbell, 1967).

The present report presents four additional attempts to establish consummatory responding to stimuli that predicted LH stimulation. In Experiment 1, a light was presented preceding LH stimulation in the presence of food and water. This procedure largely replicated earlier findings, producing only a conditioned elevation in activity. The problem was then analyzed in terms of the insights provided by the autoshaping phenomenon (Hearst & Jenkins, 1974) into the nature of classical conditioning, and a new design was developed in which the predictive stimulus was the insertion of a drinking tube into the test chamber. Promising preliminary findings (Experiment 2) were replicated (Experiments 3 and 4), but the data suggested that factors in addition to the predictive relationship between conditioned stimuli and brain stimulation were involved. Furthermore, the nonspecificity of the relation between the behavior induced by LH stimulation and the behavior that the predictive stimulus became capable of inducing suggests that the brain stimulation itself had nonspecific effects (Valenstein, 1969, 1976; Valenstein, Cox, & Kakolewski, 1969).

EXPERIMENT 1

Method

Subjects. The subjects were nine adult male albino rats of Sprague-Dawley descent. They were individually housed and had free access to food and water throughout the experiment.

Apparatus. Testing was conducted in a chamber housed in a ventilated refrigerator shell which had a window covered with clear acrylic cut into the door to permit direct observation of the animals during testing. The chamber itself had a 30×30 cm floor area and 60-cm-high walls, of which three were made of sheet aluminum and one, which also served as the door, of clear acrylic. Mounted above the chamber were a commutator and cable assembly to deliver brain stimulation and a 7½-W, 110-V lamp, which provided dim illumination throughout testing. Two lamps (28-V, .48-W in series with a 47-Ω resistor), covered by 2.5-cm-diam green lamp jewels, were mounted 15 cm apart on the back wall of the chamber 7.5 cm from the floor. Fifteen to 20 food pellets, identical to those available in home cages (Purina Rat Chow), were scattered on the chamber floor, and a glass drinking tube containing tap water protruded 2.5 cm into the chamber through a hole in the middle of one side wall of the chamber 7.5 cm above the floor.

The chamber floor was supported independently of the walls on four arms, which extended 4.1 cm beyond each corner. The end of each arm was fastened to a shock-absorbing spring assembly that allowed the platform floor to move, primarily in a vertical plane, when a transient force was applied to it. The maximum floor displacement was about 1.2 cm, which required approximately 500 g to produce. A small cylindrical magnet was fastened underneath the center of the floor just above the hollow core of a stationary coil of wire (5-kΩ impedance), so that movements of the floor induced small voltages in the coil. These

signals were amplified by a dc amplifier that was capacitatively coupled to an emitter follower and Schmitt trigger. The Schmitt trigger advanced a printing counter which could follow up to 10 counts per second. It was programmed to print at the end of each experimental interval to provide a measure of activity for the preceding interval.

At the beginning of the experiment, the Schmitt trigger was adjusted to fire at what was judged to be a moderate level of activity. This setting remained the same for all subjects throughout all sessions. Behaviors such as sniffing, nosing, rearing, grooming, and walking fired the Schmitt trigger, but very small movements, such as heartbeat or respiration, did not. The rate of floor displacement determined whether a movement was recorded. Quick, abrupt movements were readily detected, but slower movements were also recorded if they were large enough. Two other printing counters, also programmed to print out at the end of each experimental interval, were driven by multivibrators controlled by an observer who watched the animals through the window in the refrigerator shell. He recorded the time spent eating and drinking in each experimental interval by activating the appropriate multivibrators.

Procedure. Bipolar electrodes, made of .175-mm-diam Teflon-insulated stainless steel wire, bared only in cross-section, were stereotactically implanted under pentobarbital anesthesia (50 mg/kg) bilaterally in the lateral hypothalamic area. Coordinates referred to bregma (top of skull horizontal) were 3.0 to 3.5 mm posterior, 1.3 to 1.6 mm lateral, and 8.4 to 9.0 mm ventral. Beginning 1 week after surgery and continuing throughout the experiment, the animals were weighed, and their food and water intake in the home cage was measured daily before testing. Three weeks after electrode implantation, the subjects were tested for baseline levels of eating, drinking, and activity in the chamber. Each subject was placed in the chamber with the stimulating cable attached for 30 min each day for 4 days (Sessions 1-4, Baseline 1). Although no external discriminative stimuli or hypothalamic stimulation were delivered, activity counts and time spent eating and drinking were recorded on the same schedule that was used in the later conditioning sessions. Total amount of food and water consumed was also recorded for each session. The chamber floor was vacuumed and wiped with a damp paper towel after each subject was tested.

Following initial baseline testing, the subjects were screened in the chamber in one 30-min session (Session 5) for stimulation-induced eating and drinking. A procedure similar to that of Valenstein, Cox, and Kakolewski (1969, 1970) was used. Stimulation, which consisted of biphasic rectangular pulse pairs (10-150 μ A peak amplitude, 60 Hz, .5-msec pulse width), was alternately turned on for 30 sec and off for 60 sec in the presence of food pellets, a drinking tube, and wood blocks. Stimulation intensity was initially 10 μ A and was increased in 10- μ A steps until the animal displayed either stimulation-induced eating, drinking, or gnawing or what was judged to be a disorganized aversive reaction to stimulation. If a stimulation-induced behavior was observed, the subjects were given five more 30-sec stimulation tests at that site and intensity. Both electrode implantations were tested in each animal. Stimulation sites and intensities determined during this session were used in subsequent stimulation sessions. Baseline measures of activity and food and water consumption were then obtained for 4 more days (Sessions 6-9, Baseline 2).

For the next 10 days (Sessions 10-19, conditioning), the subjects were treated just as in the baseline sessions, except that during each session they were given 10 pairings of a light signal with brain stimulation. The mean intertrial interval was 100 sec. The signal consisted of turning on for 20 sec the two lamps mounted on the chamber wall. Brain stimulation began with the signal termination and lasted 20 sec. For each pairing, the counters, which recorded activity and time spent eating and drinking, printed out every 20 sec, beginning 20 sec before the signal was turned on and continuing 20 sec after the hypothalamic stimulation

terminated. Thus, activity counts were recorded for four periods on each trial: presignal, signal, stimulation, and poststimulation. Food and water were available during all sessions for all subjects except one (K5). To assess the effects of consummatory behavior elicited by the US on conditioning, this rat received no food or water in the test situation. Total amount of food and water consumed was measured, and time spent eating and drinking was again recorded. The last 4 days (Sessions 20-23) consisted of extinction identical to the preceding conditioning sessions except that brain stimulation was not delivered.

At the end of experimentation (these subjects also were used in Experiment 2), all subjects received an overdose of pentobarbital and were perfused intracardially with saline followed by 10% Formalin in saline. The brains were stored in the Formalin solution for at least 1 week before frozen sections were cut at 40 μ . Photographic records were made of selected sections prior to being mounted on slides and stained with cresyl violet.

Results and Discussion

Only two animals, K4 and K5, exhibited stimulation-induced eating in the initial screening session; none showed stimulation-induced drinking. K4 continued to exhibit stimulation-induced eating throughout the conditioning sessions, consistently spending over 50% of the stimulation period eating. Food and water were not available to K5 during conditioning, but on a test following the extinction, this animal ate and drank during stimulation. Of the seven that failed to show stimulation-bound eating or drinking, five exhibited locomotor-exploratory behavior for the duration of stimulation. All these animals, except K7, developed stimulation-induced eating or drinking behaviors in the course of the experiment, one animal (K1) as late as Session 17. Animals K9 and K2 eventually showed drinking, and K1 and K6, eating. The two remaining animals (K3, K10) showed overt aversive reactions (e.g., squealing, rearing, backing-up, shivering) to stimulation and received no further testing. Thus, six of the seven rats receiving the conditioning procedure eventually showed consummatory behavior induced by the LH stimulation.

None of the animals exhibited any significant anticipatory eating or drinking during the 20-sec signal periods during conditioning or extinction, nor was the amount of time spent eating and drinking greater during extinction than during the two baseline tests prior to conditioning. The only influence that brain stimulation had on eating or drinking in its absence was a nonspecific one. The screening for stimulation-induced behaviors (Session 5) increased the amount of time spent eating and drinking on the immediately following baseline session (Wilcoxon test, $p < .05$).

The activity measure, on the other hand, showed orderly changes over the course of the experiment. Figure 1 presents mean activity during different periods of the trials plotted as a function of daily sessions. Total activity did not change significantly over the 4 days of the first baseline, but the interpolated stimulation-induced behavior test in Session 5

significantly elevated activity between Sessions 4 and 6 (Wilcoxon test, $p < .05$). Total activity counts declined significantly across the 4 days of the second baseline test to reach the level of the first baseline test [$F(6,18) = 18.27$, $p < .001$]. There were no differences in activity between the four successive periods of the "pseudotrials" in which the counters were activated according to the sequence that was to come during conditioning even though no stimuli were presented.

Clear evidence for conditioned increase in activity was obtained when light predicted LH stimulation (Sessions 10-19). The signal did not merely energize ongoing behaviors, but, rather, elicited a consistent specific pattern of sniffing and forward locomotion similar to that elicited by LH stimulation prior to the emergence of consummatory behavior. The animals were most active during the 20-sec hypothalamic stimulation period and least active during the 20-sec presignal and poststimulation periods [$F(3,18) = 18.08$, $p < .001$]. More importantly, as conditioning continued, the activity during the 20-sec signal period increased from the presignal and poststimulation level to the level the animals exhibited during the hypothalamic stimulation periods [session $\times$ period interaction, $F(27,162) = 2.84$, $p < .001$]. Activity declined across trials within sessions [$F(5,54) = 3.29$, $p < .025$], but the decline was greater in the presignal and poststimulation periods than in the stimulation period [trial $\times$ period interaction, $F(27,162) = 1.85$, $p < .025$].

During extinction (Figure 1, Sessions 20-23), activity decreased over sessions during all four periods [$F(3,18) = 4.91$, $p < .025$], but differences remained between the periods [$F(3,18) = 6.03$, $p < .005$]. The activity level during the presignal period did not dif-

Figure 1. Mean activity counts (arbitrary units) during the four periods (presignal, signal, stimulation, poststimulation) in each trial as a function of sessions under each testing condition (baseline, conditioning, extinction) (Experiment 1).

for significantly from that during the poststimulation periods or the "stimulation" period (20-sec periods when stimulation would have been delivered), but was significantly less than during the signal period [$F(1,6) = 12.12$, $p < .025$]. Activity counts decreased across trials within sessions for all four periods in the extinction phase [$F(9,54) = 10.80$, $p < .001$]. Unlike in the conditioning phase, the trial $\times$ period interaction was not significant, showing that the various periods did not differ in the rate of decrease of activity over trials.

Figure 2 illustrates the location of the ends of electrode tracks determined following Experiment 2. Placements that induced eating or drinking were generally dorso-lateral to the fornix at the level of the lateral hypothalamus. Although K7's placement was in this vicinity, this animal displayed a stimulation-induced locomotor-exploratory behavior that never developed into eating or drinking. Placements in animals K10 and K3, which evoked an aversive reaction when stimulated, were in or near the zona inserta, dorsolateral to placements that induced locomotor-exploratory and consummatory behaviors.

In sum, a light that predicted LH brain stimulation became capable of inducing increased activity but not increased consummatory behavior, even though the LH stimulation induced consummatory behavior or became able to induce it over the course of training.

This finding simply confirms the results of earlier investigators (Andersson & Larsson, 1956; Bindra, 1969; Bindra & Campbell, 1967; Huston & Brozek, 1972; Milgram et al., 1975).

EXPERIMENT 2

The design of Experiment 1 assumes an S-R theory of classical conditioning (Mackintosh, 1974) in which the predictive CS acquires the capacity to elicit responses like the UCR. That is, the light is supposed to acquire the capacity to elicit responses towards the food or water like those the brain stimulation induced in most animals. An alternative conception of classical conditioning, stimulus substitution or S-S theory (Mackintosh, 1974), proposes that the predictive CS becomes treated as if it were a surrogate of the US (Hearst & Jenkins, 1974; Peterson, 1975; Peterson, Ackil, Frommer, & Hearst, 1972). Considerable support for this position can be derived from the autoshaping literature, although it by no means accounts for all of the data derived from this experimental paradigm (Boakes, 1977; Hearst & Jenkins, 1974; Mackintosh, 1974).

The basic autoshaping experiment (Hearst & Jenkins, 1974) consists of presenting a stimulus (such as illuminating a key in a pigeon chamber or inserting a lever

Figure 2. Approximate location of electrode tips for rats in Experiments 1 and 2 represented on drawings derived from DeGroot's (1959) atlas.

into a rat box) that reliably predicts presentation of a reinforcing event (such as grain to a hungry pigeon or a food pellet to a hungry rat). The presentation of the reinforcing event is contingent only on the presentation of the predictive stimulus and is independent of the subject's behavior. Hence, this procedure has the form of the typical Pavlovian conditioning experiment, even though the responses resemble ones ordinarily associated with instrumental conditioning.

A common finding is that subjects direct toward the predictive stimulus responses which often resemble the responses elicited by the UCS. Pigeons begin to peck at an illuminated key that predicts access to grain. Rats lick and bite a bar, insertion of which predicts delivery of a food pellet. However, the predictive stimulus contributes to the configuration of the response as well (Timberlake, *in press*; Timberlake & Grant, 1975; Timberlake, Wahl, & King, 1982; Wasserman, 1973). Thus, the rats in Experiment 1 may have responded to the predictive light stimulus by approaching it, sniffing it, or directing other kinds of exploratory or consummatory behaviors towards it. Such behaviors were, in fact, observed during Experiment 1, but no systematic records were kept. They are specifically predicted by Bindra (1974; Lajoie & Bindra, 1976) from his incentive motivational account of associative learning. The role of the CS in defining the configuration of the CR has also been described in other forms of classical conditioning (Holland, 1977, 1980). Such considerations led us to the conjecture that making the insertion of a drinking tube the predictive stimulus for motivating brain stimulation would provide the conditions for the development of conditioned drinking. To test this possibility, the seven rats trained in Experiment 1 were tested in this situation.

Method

Subjects. The subjects were the seven rats used in Experiment 1. During final screening for stimulation-induced behavior after that experiment, three animals (K4, K6, and K1) exhibited stimulation-induced eating, two (K2, K9) drinking, one (K5) both eating and drinking, and one (K7) only locomotor exploration. All animals were individually housed and had free access to food and water in their home cages throughout experimentation.

Apparatus. All testing was carried out in a chamber similar to that used in Experiment 1. A 25-W, 110-V houselight mounted above the chamber remained on throughout testing. A retractable glass drinking tube (signal tube) was mounted 7.5 cm above the floor in the middle of a side wall of the chamber. When available, the tube was .6 cm behind a 1.3-cm-diam hole in the wall. When not available, the tube was retracted 5.0 cm behind the hole. Mounted on the water tube was a lamp (28 V, .4 A) which was illuminated whenever the tube was available to the subject. Another identical drinking tube with a lamp (fixed tube) was mounted behind a similar hole in the opposite wall of the chamber. Contacts with each tube were detected with two drinkometers (BRS-Foringer) and recorded on printing counters. The brain stimulation circuit was isolated from the drinkometer circuit to prevent any inadvertent hypothalamic stimulation. Because the tubes were

still outside small holes in the chamber walls when made available, tube contacts were confined mainly to tongue or nose contacts. During sessions in which a particular tube was never made available, its access hole was covered.

Procedure. All animals were tested on 39 consecutive daily 30-min sessions, each consisting of 15 trials with intertrial intervals of 60, 90, or 120 sec. The number of drinking tube contacts per trial and the total amount of water consumed during each session were recorded. For the first four sessions, the water-filled signal tube was illuminated and made available for 20 sec on each trial, but the animals did not receive hypothalamic stimulation. During Sessions 5-9, the animals were tested for stimulation-induced drinking. The fixed tube filled with water was available continuously, while the signal tube was never available. The subjects received 15 20-sec periods of unilateral hypothalamic stimulation, the intensity and site of which were the same as those which induced behaviors in Experiment 1. For the next 14 days (Sessions 10-23), each trial consisted of presenting the illuminated tube for 20 sec and delivering the brain stimulation for 20 sec following the signal tube's retraction. Hence, the signal tube was never available during hypothalamic stimulation, but was always available for the 20 sec prior to stimulation. During Sessions 24-27, signal-tube/hypothalamic-stimulation pairings continued, but in addition the fixed tube was available continuously. Sessions 29-31 were identical to Sessions 10-23 (signal-tube/hypothalamic-stimulation pairings only). In Sessions 32-35, the subjects received the 15 signal-tube presentations without subsequent hypothalamic stimulation, reproducing conditions in Sessions 1-4. For the last 4 days (Sessions 36-39), a dry stainless steel tube replaced the water-filled signal tube, and hypothalamic stimulation followed its 20-sec presentation. After the last training session, all animals were again tested for stimulation-induced drinking with the fixed tube available. Following experimentation, histological verification was made of electrode placements as described in Experiment 1.

Results

During Sessions 1-4, when the signal tube was presented alone, none of the animals contacted the signal tube on more than 2 of the 15 trials during any of the sessions. In Sessions 5-9, two animals (K5 and K9) exhibited LH-stimulation-induced drinking, but the other five did not, including one animal (K2), which had exhibited stimulation-induced drinking in Experiment 1. All animals did exhibit a typical locomotor-exploratory behavior when stimulated. Thus, all rats showed little, if any, contact with the inserted tube prior to its pairing with LH stimulation, and all showed at least the typical activating effects of the LH stimulation.

Four of the seven subjects (K4, K5, K6, K7) began contacting the signal tube and consuming some water (.5 to 4.0 cc/session) during the 14 sessions in which signal tube preceded brain stimulation. Only one of these animals (K5) had shown any previous drinking. Periodic observations suggested that even those animals that did not actually contact the signal tube did orient toward it between trials and often approached it when it was lighted and available prior to stimulation. The contacts, when they occurred, were made up almost entirely of licks. Figures 3 and 4 show the percent of trials on which either the signal tube or the fixed tube (when available) was contacted

Figure 3. Percent of trials on which signal tube and fixed tube were contacted by Rat K4 as a function of sessions under different test conditions (Experiment 2).

and the number of contacts made on both tubes by one animal (K4). Generally, across sessions, animals increased the percentage of trials on which they contacted the signal tube and the total number of contacts per session.

When the fixed drinking tube was made available along with the signal tube (Sessions 24-27), the animals reduced their responding on the signal tube in various degrees. Rat K5, the only animal to show stimulation-induced drinking and also to respond to the signal tube, stopped contacting the predictive signal tube completely and drank from the fixed tube during each 20-sec hypothalamic stimulation. The other three animals continued to contact the signal tube, though less consistently than when the fixed

tube was absent, but they seldom contacted the fixed tube during hypothalamic stimulation. Removal of the fixed tube (Sessions 28-31) reinstated rates of responding on the signal tube in all four animals.

When hypothalamic stimulation was not delivered (Sessions 32-35) but signal tube presentations continued, three animals (K5, K6, K7) not only continued contacting the signal tube, but also consumed between 1 and 3 cc of water during the 1st day. Between the 2nd and 3rd days of extinction, their signal tube contacts declined abruptly to zero. The fourth animal (K4) stopped responding almost immediately. Thus, the increased drinking from the predictive tube was extinguished when the tube no longer predicted the LH stimulation.

Figure 4. Number of contacts with signal tube and fixed tube by Rat K4 as a function of sessions under different test conditions (Experiment 2).

When presentation of a dry stainless steel tube served as the signal for brain stimulation (Sessions 36-39), contacts with the signal tube reappeared. The percent of trials on which a contact was made with the signal tube was approximately the level attained when the water-filled tube had served as the signal for hypothalamic stimulation, but the number of contacts per signal tube presentation was much lower, because contact with the dry tube consisted primarily of touching the tube with a paw or the nose rather than licking it.

During the final test for stimulation-induced drinking following Session 39, only Animal K5 (which had drunk on all previous tests) and Animal K9 (which did not drink from the signal tube, but had previously exhibited stimulation-induced drinking) drank during stimulation.

Discussion

Four of the seven rats in Experiment 2 showed increased contact with the drinking tube which appeared to depend upon the predictive relationship between presentation of the illuminated tube and delivery of brain stimulation. Tube-stimulation pairings resulted in more contacts and more water consumption than did presentation of the tube alone either before training or in extinction afterwards. Presence of another tube during tube-stimulation pairings reduced the contacts and water consumption in all four animals.

Nevertheless, four points make interpretation of these observations difficult. First, there was no apparent relation between the behavior induced by brain stimulation and the occurrence or nonoccurrence of increased contact with and drinking from

the predictive tube. Only one of the three animals that had shown drinking induced by brain stimulation in the screening tests preceding Experiment 2 contacted and drank from the predictive tube. Conversely, three of the four rats that responded to the predictive tube did not show brain-stimulation-induced drinking. Second, three of the four animals continued extensive contact with the predictive tube in the presence of a fixed, continuously available water-filled tube from which they drank little. Third, an empty predictive tube was contacted almost as much as a water-filled one. These two points suggest that the tube contacts did not necessarily represent approach to water. Fourth, all rats had served in Experiment 1 and therefore had had extensive experience with neutral-signal/brain-stimulation pairing before starting Experiment 2.

EXPERIMENT 3

Because of the problems in interpreting the results of Experiment 2, Experiment 3 was designed to describe the effect of predictable-tube/brain-stimulation pairings more satisfactorily. To this end, naive animals were trained under several different contingency relations between presentation of the drinking tube, contact with the drinking tube, and LH stimulation. Although evidence was obtained for an increase in contact with and water consumption from a drinking tube that predicted LH stimulation, this effect was dwarfed by an overall tendency to lick the drinking tube regardless of the contingencies.

Method

Subjects. Fifty-two adult male and female albino rats derived from the Sprague-Dawley strain served as subjects. They were individually housed in plastic breeding cages with sawdust on the floor. Food and water were available at all times, and testing was carried out during the light phase of a 12:12-h light-dark cycle.

Apparatus. The training apparatus resembled that used in Experiment 2. It was slightly smaller ($25 \times 25 \times 37.5$ cm) and was illuminated less brightly (7-W lamp). The hole for the predictive drinking tube was closer to the grid floor (5 cm) and was slightly off center (10 cm from the back wall). Instead of being recessed slightly behind the plane of the wall, the signal tube extended .6 cm into the chamber when presented. A different lickometer, one drawing approximately 12 μ A, was used.

Procedure. Using the procedure described in Experiment 1, 46 animals were implanted bilaterally with bipolar stimulating electrodes aimed for LH. Seven to 10 days after implantation, the animals were screened for stimulation-induced drinking, eating, gnawing, and exploration, using a protocol that differed from the one used in Experiment 2 in that once the effective site and intensity of stimulation were identified, the animals were sometimes retested on 1 or 2 subsequent days (up to 60 extra 30-sec trains of stimulation), using those stimulus parameters. Stimulation parameters were the same as those used in Experiments 1 and 2, the amplitude of the pulse pairs ranging between 25 and 400 μ A (mostly 50-100 μ A). From this point on, each daily session lasted for 20 trials, which consisted of 12-sec insertions of the illuminated drinking tube, 12-sec trains of brain stimulation, or some combination of both. The intertrial intervals were 60, 90, or 120 sec.

On the first 3 days, the animals received brain stimulation in the experimental chamber. The drinking tube was illuminated

and available throughout the sessions. The next phase established the baseline rate of contact with and consumption from the drinking tube during the 20 12-sec presentations that would occur in the subsequent training. No brain stimulation was delivered at any time. This phase usually lasted 3 days, but was extended in some cases to up to 9 in an attempt (sometimes unsuccessful) to reduce the number of trials on which the rat contacted the tube to two or fewer for 2 consecutive days.

At this point the animals were assigned to one of four treatment groups. The forward-pairing group (CS-US; $N = 15$) had the tube presentations immediately preceding, but not overlapping, the LH stimulations. The backward pairing group (US-CS; $N = 5$) received the stimulations immediately preceding, but not overlapping, the tube presentations. The omission group (Omit; $N = 8$) received brain stimulation immediately after the tube was withdrawn, but only if no contacts with the tube had been recorded on that trial. The CS-only group ($N = 18$) received the tube presentations, but no brain stimulation. Six rats that had no implanted electrodes also received this treatment, but they are treated as a separate group. For most animals, this training phase lasted 20 days, but the number of sessions varied from 14 to 33, depending on stability of performance. After this "acquisition" phase was completed, 34 animals were shifted to one of the other contingencies for an additional 15-20 days, and a few were shifted again one or more times to still other contingency relations. These shifts served as within-subject controls for the role of forward pairing between tube insertion and LH stimulation in establishing and maintaining responding on the tube. All animals, except the six unoperated ones and nine that showed no reliable drinking behavior, received 14-20 sessions of extinction. Finally, the effectiveness of the brain stimulation in inducing eating, drinking, gnawing, and exploration and in supporting self-stimulation at the currents used in the preceding sessions or at currents up to 700 μ A was tested. After all testing was complete, the rats were anesthetized, perfused, and prepared for anatomical verification of the location of the electrode tips as described in Experiment 1.

Results

Figure 5 presents the data from a single rat (13) initially trained in the forward-pairing condition. The top and bottom show the amount of water consumed and the percent of trials on which contacts were recorded. These measures increased over the 20 sessions of forward pairing (CS-US), so that as much as 5.0 ml was consumed in the 240 sec during which the tube was available within a single session. Consumption and probability of contact declined over the course of subsequent omission training (Omit), but the mean consumption on the last 3 days was still about .5 ml/session. However, during backwards pairing (US-CS), consumption returned to the level obtained at the end of the initial forward-pairing phase. Ten additional sessions of forward pairing elevated consumption and increased the probability of tube contacts further. These measures declined again when the backward pairing condition was reinstated. However, even though intervals of 6 or 18 sec were interposed between brain stimulation and insertion of the illuminated tube, contacting the tube and drinking from it still remained strong. Twenty sessions of extinction had little, if any, effect on either response measure.

Although this rat's consummatory behavior does reflect the effect of the contingencies between signal tube and hypothalamic stimulation and does resem-

Figure 5. Amount of water consumed and percent of trials on which signal tube was contacted by Rat 13 as a function of sessions under different testing conditions (Experiment 3).

ble those found in Experiment 2, a pattern of extensive drinking independent of the contingencies is prominent. This pattern is representative of all four groups of rats. Approximately half (25/52) of all rats tested drank more than .5 ml/session from the signal tube and contacted it on more than 20% of its presentations during the last half of acquisition. If one of these criteria was met, the other was also met. If the forward-pairing condition contributed to the probability of drinking, one would expect the forward-pairing group to have a higher proportion of subjects showing drinking. Table 1 shows that this was not the case. Among the animals that did meet the criteria for drinking, those in the forward-pairing group contacted the signal tube or drank from it no more or no sooner than did those in the other groups. Analysis of variance on the percent of trials on which contact was made and the amount of water that was consumed showed only a significant increase in these measures across the four quarters of acquisition [$F(3,45)=22.29$ and 12.64 , $p < .001$] from all training conditions.

One additional analysis provides a more sensitive test of the role of forward pairing in the maintenance of contact with, and drinking from, the tube during its 12-sec presentations. Most animals were shifted to at least one new contingency after acquisition. The 63 shifts of this sort can be divided into three groups. Twenty-seven shifts went from forward pairing to some other contingency ($\text{CS-US} \rightarrow \text{CS-US}$), 21 went in the opposite direction, from some other contingency to forward pairing ($\text{CS-US} \rightarrow \text{CS-US}$), and the remaining 15 did not involve forward pairing ($\text{CS-US} \rightarrow \text{CS-US}$). Figure 6 presents these three comparisons

Table 1
Proportion of Animals in Each Acquisition Condition Meeting Criterion of $>20\%$ Tube Contact Trials and $\geq .5$ ml/Session in Last Half of Acquisition

CS Only				
CS-US	Implanted	Normal	US-CS	Omit
6/15	8/18	6/6	2/5	3/8

for percent of trials on which contacts occurred (left) and for mean volume consumed (right). Each measure is plotted as the mean difference between the last quarter of testing before the shift and the last quarter after the shift. Shifting to the forward-pairing contingency produced a reliable increase on both measures [$t(20) = 3.74$ and 2.55 , $p < .01$ and $.02$, respectively], shifting away produced a decline [$t(26) = 3.30$ and 2.36 , $p < .01$ and $.05$, respectively], but shifts not involving forward pairings had no reliable effect [$t(14) < 1.0$, $p > .10$ for both].

The preceding analysis pooled together all animals, regardless of the behavior induced by brain stimulation. Table 2 presents the number of animals in each acquisition condition divided according to the kind of behavior induced by brain stimulation during screening and pretraining and according to the occurrence of drinking from the illuminated tube during "acquisition." Animals in the forward-pairing condition were more likely to drink from the illuminated tube if the brain stimulation had induced drinking, eating, or gnawing than if it had induced only searching activity (Fisher's exact test, $p < .05$). No systematic effect of stimulation-induced activity was found for the other pairing conditions whether treated separately or combined. Because of the small number

Table 2
Number of Animals in Each Acquisition Condition That Drank From Predictive Tube as a Function of Behavior Induced by Brain Stimulation

	CS-US		CS Only		US-CS		Omit	
	D	$\bar{D}$	D	$\bar{D}$	D	$\bar{D}$	D	$\bar{D}$
Drink	4	0	2	1	0	0	1	0
Other	2	2	4	6	1	2	1	3
Search	0	7	2	3	0	2	1	2

Note—Criterion for drink or other consummatory behavior: $>10\%$ of test trials and/or drinking during initial test with fixed tube. D = drinking from predictive tube; $\bar{D}$ = no drinking from predictive tube.

of observations available, it was necessary to pool the data for all animals that showed any consummatory behavior, and it is not possible to determine whether different consummatory behaviors differed reliably in their association with acquisition of drinking from the illuminated tube.

The reinforcement properties of the brain stimulation were tested in 32 of the 46 implanted rats. Almost two-thirds showed self-stimulation at currents equal to ($N=6$) or greater than ($N=15$) that needed for stimulation-induced activity. Of the 11 rats that did not show positive reinforcing effects, 4 did show consummatory behavior and 7, searching induced by the stimulation. The rats showing self-stimulation were equally distributed among the four acquisition conditions, and self-stimulation was not systematically related to the appearance or absence of drinking on the signal tube.

The approximate positions of the electrode tips for 41 of the 46 implanted rats are represented in Figure 7. The reconstructions are grouped according to whether the stimulation induced drinking (D), other consummatory behaviors (O), or only searching (S) during the pre- and postexperimental screening. Electrode placements in the lateral hypothalamic area and the subthalamus immediately dorsal to it induced consummatory behaviors. Placements that induced only searching tended to be more medial, dorsal, or lateral in the brain. Animals that developed contacting with and drinking from the signal tube (solid symbols) tended to have the electrode tips nearer the center of the area from which consummatory behaviors were more likely to be induced, regardless of acquisition condition.

Discussion

Approximately half the rats drank from the signal tube when it was inserted, but drinking was not restricted to the condition in which tube insertion predicted brain stimulation. Some aspects of the data did differentiate the forward-pairing contingency from the others. Probability of contact with the tube

Figure 6. Mean change in amount of water consumed and percent of trials on which the signal tube was contacted as a function of switching contingency to forward pairing (to CS-US), away from forward pairing (from CS-US) and not involving forward pairing (CS-US to CS-US) (Experiment 3).

Figure 7. Approximate location of electrode tips for rats in Experiment 3 represented on drawings derived from DeGroot's (1959) atlas. Placements at which stimulation induced drinking, other consummatory behaviors, or only searching are represented on top, middle, and bottom sets of drawings, respectively. Locations are coded according to whether the rats contacted and drank from the signal tube (solid) or not (open) and according to the contingency between signal tube and LH stimulation during acquisition.

and amount drunk reliably increased when the contingency shifted to forward pairing from some other contingency. These measures both fell when the contingency shifted from forward pairing to some other contingency. In addition, the proportion of animals that acquired the drinking response was higher in the forward-pairing acquisition condition when the US induced a consummatory behavior than when the US induced only exploratory behavior. However, the consummatory response elicited by the brain-stimulation US did not have to be drinking. In the other contingency conditions, the effectiveness of

the brain stimulation in inducing consummatory behavior did not influence the proportion of animals developing the drinking response.

An unexpectedly high proportion of animals in Experiment 3 drank from the tube when it did not predict brain stimulation. Several explanations for this finding can be offered. The drinking may have been adjunctive behavior associated with the intermittent presentation of reinforcing brain stimulation. However, this seems unlikely because reliable adjunctive drinking has not been demonstrated with reinforcing brain stimulation (Atrens, 1973; Cohen,

Mendelson, & Bramble, 1974). Furthermore, many control animals in Experiment 3, including ones without implanted electrodes, made many tube contacts even though they did not receive LH stimulation. Two properties of the signal tube appear to be more important. First, contacts with and drinking from the signal tube may have been elevated by the salience of the illuminated tube, which was inserted .6 cm into an otherwise barren environment. The animals in Experiment 2, in which the signal tube remained .6 cm behind the chamber wall and was accessible through a 1.3-cm-diam hole, made few baseline contacts and during extinction stopped contacting the tube and drinking from it. Second, the drinkometer sensing current was about 12 μ A, well above threshold for it to serve as a positive incentive (Slangen & Weijnen, 1972).

The failure of some animals in the forward-pairing condition to develop drinking behavior may reflect properties of the brain stimulation. It is a common finding that LH stimulation is ineffective in inducing consummatory behaviors in a substantial proportion of rats. Mittleman and Valenstein (1981) found stimulation-induced consummatory behavior in about 25% of the albino rats and 50% of the hooded rats they tested. They summarized several hypotheses about the processes which may produce these individual (and strain) differences. Whatever these processes may be, one may presume they would also affect the development of the specific consummatory response of drinking from the signal tube as well. Instead, other responses, more compatible with the stimulation-induced searching behavior such as orientation, approach, sniffing, and light touches, may have been conditioned but not detected. Just such responses were observed in Experiment 1 and have been described when insertion of a bar predicted LH stimulation (Peterson, 1975; Peterson et al., 1972). The apparatus in the present experiment did not detect orienting responses or light touches directed to the dry walls of the glass tube. When the rats were observed during testing, they were seen to make orienting responses towards the predictive tube without touching it. Experiment 4 was designed specifically to examine these behaviors.

EXPERIMENT 4

In Experiment 4, the animals were systematically observed to determine whether orienting responses and light touches became directed at a signal tube that predicted brain stimulation. Three modifications were made to maximize detection of associatively established responding to the predictive tube and minimize nonassociative responding to it. First, a new drinkometer circuit that drew less current was used. Pretests showed that it did not significantly elevate

consumption above baseline. Second, the rats were presented two tubes. One predicted brain stimulation, and the other was explicitly unpaired with it. Third, the tubes remained behind the plane of the wall when accessible.

Method

Subjects. Eight adult male albino rats of Sprague-Dawley descent served as subjects. They were individually housed and had free access to food and water in their home cages throughout the experiment. Testing was carried out at approximately the same time each day for each rat during the light phase of a 12:12-h light-dark cycle.

Apparatus. The training chamber was similar to that used in Experiment 3. An additional movable drinking tube was added to the chamber on the other side wall. Drinking-tube contact-sensing current was reduced to less than 3 μ A, and the drinking tubes remained .6 cm behind the plane of the wall when accessible.

Procedure. The animals were implanted with single bipolar electrodes aimed for LH, using the procedure described in Experiment 1. One week later, they were screened for stimulation-induced drinking, eating, gnawing, and locomotor exploration in a chamber different from the one subsequently used in conditioning. The screening consisted of a single session in which stimulation intensity was adjusted to elicit vigorous locomotor exploration characteristic of LH stimulation (Christopher & Butter, 1968). Two animals were discarded because stimulation elicited aversive reactions. The other six were given 20 trials of 20 sec of LH stimulation alternated with 60 sec of no stimulation and were observed for the display of LH-stimulation-induced behaviors. Stimulation parameters were the same as those used in Experiments 1-3. The effective intensities ranged from 15 to 30 μ A.

Two days later, training sessions lasting about 60 min began in the conditioning chamber. The right and the left tubes were individually presented 20 times for 20 sec with intertrial intervals of 60, 90, or 120 sec. A minimum of 20 sec separated the availability of the two tubes. During all sessions, the number and total duration of tube contacts were recorded with printing counters. The first four sessions served as a baseline, during which the animals received tube insertions but no LH stimulation. During subsequent conditioning sessions, the tube contacted less during baseline was designated CS+ and predicted LH stimulation, which started with the CS+ tube's retraction. The other tube became CS- and was never followed by stimulation. During Phase 1 of conditioning, the first 6 to 9 training sessions, the parameters of stimulation for five rats were the same as those used when they were screened for stimulation-induced behaviors. In Phase 2 (8 to 10 sessions), the intensity was reduced by 4-12 μ A, and in Phase 3 (6 to 10 sessions), the train duration was also reduced to 5 sec. The sixth rat's training began with Phase 3.

Systematic observations of the rat's behavior were made on the last day of each phase. The single observer used a scoring system similar to that employed by Peterson (1975). On each CS+ and CS- presentation, the animals were scored on whether or not each of the following categories of reactions occurred: (1) orient toward—rat points its nose in the direction of the tube in reaction to its insertion; (2) face away—rat points its nose away from the tube in reaction to its insertion; (3) approach—rat moves its nose to within approximately 3 cm of the tube port sometime during tube presentation; (4) withdrawal—rat moves away from inserted tube; (5) sniff—rat sniffs at tube and tube port, touches port with vibrissae; (6) lick—rat contacts tube with tongue; (7) nose—rat contacts tube with nose; (8) paw—rat contacts tube with paw.

Approximately 1 week after their last conditioning session, the animals were again screened for LH-stimulation-induced behavior and were tested for the reinforcing effects of LH stimulation by attempting to shape a leverpress response using LH stimulation

at both intensities and durations used in the previous conditioning sessions. The animals were subsequently sacrificed, and electrode locations were histologically verified as described in Experiment 1.

Results and Discussion

During the initial screening, the six experimental animals increased exploration and sniffing directed contralaterally to the side of LH stimulation. Some animals shuffled the wood blocks or food pellets when they were encountered during stimulation. Reliable stimulation-induced consummatory behavior appeared in two rats (4 and 8), which spent some portion of approximately half the stimulation periods gnawing on food or wood blocks and licking and gnawing on the cage floor. No animal drank during the screening session.

During the four baseline testing sessions, the mean number of trials on which a tube was contacted during the 40 tube insertions was less than two, and the rats drank almost no water. No consistent preference was found between the tubes. Informal observation indicated that approach and orientation to tube insertion decreased within and across sessions.

No animal increased tube contacts or drank significantly in Phase 1. During the observation session at the end of this phase, the rats oriented toward the inserted CS+ tube on 60%-90% of the trials and to the CS- tube on 20%-25% of the trials [$t(4) = 14.2$, $p < .001$]. All five animals also approached the CS+ tube more than the CS- tube [$t(4) = 3.74$, $p < .05$], but they usually halted and stood almost motionless, facing the inserted CS+ tube. No differences appeared in any other tube-related behavior. During the LH stimulation, the rats explored and sniffed vigorously or licked and gnawed the cage floor. No animal displayed these behaviors in the presence of the CS+ or CS-.

In Phase 2, Rat 4, which ate or gnawed during screenings, contacted the CS+ tube on 31% of the trials and drank as much as 5 ml of water from it during a session. Contacts on CS- were recorded on 10% of the trials, and 2 ml was the maximum consumed. The other rats showed no increase in drinking or contacts. During the observation session at the end of this phase, all animals continued orienting and approaching the CS+ tube more than the CS- tube [$t(4) = 21.96$ and 11.07 , $ps < .001$ and $.01$, respectively]. In addition, they began to sniff and nose at the CS+ tube more than they did at the CS- tube [$t(4) = 3.47$ and 2.96 , $p < .05$, respectively].

During Phase 3, Rat 4 continued to drink reliably from the CS+ tube, contacting it on 39% of the trials and drinking as much as 3.5 ml. In contrast, it touched the CS- tube on only 4% of the trials and drank no water. When the two tubes were reversed in their predictive relation to the brain stimulation, the drinking switched to the new CS+ . In

the final observation session, differences in behaviors directed toward the CS+ and CS- drinking tube became still greater. The animals oriented, approached, sniffed, nosed, and licked the CS+ tube more than the CS- tube [$t(4) = 19.33$, 13.68 , 10.20 , 9.79 , $ps < .001$, and 2.39 , $p < .05$, respectively].

In the final screening for LH-stimulation-induced behaviors, three rats exhibited consummatory behavior. Rats 4 and 8, which had eaten or gnawed during the initial screening, did so again, but more consistently. Rat 11 ate on half the stimulations. The other animals behaved much as they did in the initial screening session, showing vigorous locomotor exploration, some object shuffling, but no eating, gnawing, or drinking. All animals were successfully shaped to respond for LH stimulation, when stimulation duration was 500 msec at both the high and low intensities used in the conditioning sessions. Longer durations were much less effective.

These results generally confirm and extend the findings in the previous experiments. Only one animal showed reliable drinking from the signal tube, even though LH stimulation directly induced eating rather than drinking during the screening. No differences between this animal and others in terms of electrode location or stimulation effects were apparent. Direct observation of animals in this experiment revealed that all animals increased their orientation and approach to the signaling tube when the stimulation was at an intensity and duration later shown to be reinforcing. The drinking tube signal for higher intensity stimulation appeared to function as a warning signal eliciting a "freezing" reaction, while the signal for a lower intensity was responded to in an appetitive, investigative manner (Stellar, Brooks, & Mills, 1979). It is possible that these changes across sessions were due to an order effect rather than the change in stimulation parameters. However, the fact that these changes in behavior were largely qualitative suggests that stimulation parameters were important.

GENERAL DISCUSSION

It is clear from the present research, as well as from past studies, that a stimulus that reliably predicts LH stimulation acquires the capacity to elicit behaviors related to that stimulation. However, the behaviors that develop in response to a predictive stimulus depend, at least to some extent, on the properties of the predictive stimulus and on the effects of the brain stimulation as well. In addition, the apparent outcome of the pairings depends on what responses are selected for measurement.

Experiment 1 confirmed several previous studies (Andersson & Larsson, 1956; Bindra, 1969; Bindra & Campbell, 1967; Huston & Brozek, 1972; Milgram

et al., 1975) by showing that rats became more active in the presence of a light that predicted LH stimulation. This finding with brain stimulation resembles the effect on behavior of signals that predict presentation of more conventional incentives, such as food (Hyde & Trapold, 1975; Lovibond, 1980; Sheffield & Campbell, 1954). However, even if they predicted LH stimulation that induced consummatory behavior, light signals failed to increase consummatory behavior. This consistent observation suggests three possible hypotheses: that a consummatory behavior itself cannot be conditioned at least when LH stimulation serves as US, that the LH stimulation induces processes only indirectly related to consummatory activity, and/or that an inadequate model of classical conditioning was used in designing the experiments.

In Experiments 2, 3, and 4, an S-S, or stimulus substitution, model replaced an S-R model of classical conditioning (Mackintosh, 1974), which was implicitly assumed in Experiment 1 and by previous investigators. The autoshaping literature has provided many instances in which animals respond to the predictive stimulus as if it was a substitute or surrogate for the unconditional stimulus (e.g., Hearst & Jenkins, 1974; Peterson, 1975). In our experiments, the predictive stimulus was the presentation of a drinking tube illuminated to make it more salient. If the LH stimulation induced consummatory behavior, especially drinking, then consummatory behavior should be directed toward the predictive drinking tube. That behavior should appear as drinking, at least if LH stimulation itself induced that response.

At least some rats in Experiments 2, 3, and 4 showed the expected increase in tube contacts and water consumption, although, in Experiment 3, this effect was partially masked by an unusually high probability of drinking on the inserted drinking tube regardless of the contingency between tube presentation and LH stimulation. Nevertheless, in that experiment probability of tube contact and volume of water consumed increased when animals were shifted to forward pairing between tube insertion and LH stimulation, and these measures decreased when animals were shifted away. In Experiment 2, the animals stopped contacting the tube entirely when it was not followed by brain stimulation and promptly resumed drinking when the forward-pairing contingency was reinstated. In Experiment 4, the one animal that drank consistently from the predictive tube did not drink from the explicitly unpaired tube. When the contingency relations were reversed, the drinking response was redirected towards the now predictive tube. These results clearly demonstrate that consummatory behaviors can be conditioned, which shows that the first hypothesis listed above is clearly false.

Several features of our data support the second hypothesis, that LH stimulation induces processes

only indirectly and nonspecifically related to consummatory behavior. Most importantly, there was no necessary relation between the response that LH stimulation induced directly and the occurrence of drinking on the predictive tube. Although drinking was more likely to appear if the stimulation induced some form of consummatory behavior, rather than just exploratory behavior, the nature of the consummatory behavior did not matter. Animals in which the stimulation induced eating, gnawing, or drinking began to drink from the predictive tube. Even some rats that only explored during stimulation drank from the predictive tube. Furthermore, consummatory behavior, even drinking, induced by the LH stimulation did not guarantee that drinking would appear on the predictive tube. What did appear consistently in all animals in which it was sought was increased activity or increased orienting and approach. The latter confirms Peterson's (1975; Peterson et al., 1972) earlier observation using insertion of a retractable lever as the predictive stimulus. The former confirms the findings of Bindra (1969; Bindra & Campbell, 1967).

Valenstein (Bachus & Valenstein, 1979; Mittleman & Valenstein, 1981; Valenstein, 1969, 1976; Valenstein, Cox, & Kakolewski, 1970) has also argued that LH stimulation induces nonspecific effects, based on observations of behaviors induced in the rat by LH stimulation itself. He proposed that LH stimulation induces a generalized excitation which is guided towards one or another behavioral activity by some sort of prepotency process or behavioral hierarchy. This hypothesized process is characteristic of the individual animal, its past history, and other factors. LH stimulation is not the only kind of event that induces generalized excitement. Killeen, Hanson, and Osborne (1978) showed that delivery of food to hungry pigeons increases arousal as measured by activity. Hanson (1980) demonstrated a connection between this arousal of behavior and its diversity, which appears to complement the variability that Valenstein finds with LH stimulation. Various manipulations of the food delivery schedule modified arousal level and degree of behavioral diversity inversely. These effects appeared consistently in all three birds Hanson tested, even though the individual birds' behavioral hierarchies differed both in absolute amounts and in specific behaviors.

The present data imply that the predictive stimulus for a motivating and reinforcing event, LH stimulation, also becomes capable of inducing a generalized excitatory process which is manifested in different ways, depending on the properties of the signal, the characteristic of the individual subject, the nature of the test environment, and the characteristics of the stimulating event as well. Whatever process the LH stimulation induces becomes associated with the predictive stimulus, which uniformly becomes able

to induce activity and orientation. Whether the predictive stimulus becomes able to support a specific consummatory response, drinking, is only weakly predictable from the responses that the LH stimulation induces.

In the preceding interpretation, responses to the predictive stimuli are held to reflect processes induced by the reinforcing LH stimulation, an approach proposed by Hogan and Roper (1978) to investigate the motivational states associated with brain stimulation. This approach must be tempered by the apparent complexity of the autoshaping phenomenon. As our third hypothesis suggests, available models of autoshaping are inadequate to specify the conditions under which consummatory behaviors will appear, because several variables affect the form that responding takes. Both the configuration of the predictive stimuli and the nature of the unconditioned stimulus contribute to the configuration of the conditioned response. When food is predicted by a stimulus rat (Timberlake, in press; Timberlake & Grant, 1975), a ball bearing rolling down a trough (Timberlake, Wahl, & King, 1982), or insertion of a bar (Peterson, 1975), the conditioned responses appeared as social responses, manipulatory responses, or licking and biting, respectively. The appearance of a keypecking response depends on whether the predictive stimulus is localizable (Hearst & Jenkins, 1974; Wasserman, 1981). Furthermore, a localized keylight stimulus can elicit pecking responses when the US does not elicit a pecking response (warmth, food or water in the mouth) as well as when the US does (Wasserman, 1981; Woodruff & Starr, 1978). Conversely, the configuration of a peck directed at a predictive keylight resembles the species-specific configuration of the response directed at the US, food or water (Jenkins & Moore, 1973), even when the US itself was never allowed to release the full species-specific response in the animals' lifetime (Woodruff & Starr, 1978). Similarly, the configuration of the response made to the predictive insertion of a bar or presentation of a rolling ball bearing depends on whether a food pellet or reinforcing brain stimulation serves as US (Peterson, 1975; Peterson et al., 1972; Ackil & Timberlake, Note 1). These results from the autoshaping literature, as well as many other findings in the literature on classical conditioning (e.g., Hearst & Jenkins, 1974; Mackintosh, 1974), demonstrate that a comprehensive account of classical conditioning has not been available to guide the search for the specific conditions under which consummatory behavior might be conditioned. Timberlake's (in press) recent behavior systems model of conditioning attempts to account for the complex relations that have been observed between properties of predictive stimuli, reinforcing events, and conditioned responses by including the species-typical

ecological relationships between the predictive stimuli and reinforcing events. The capacity of this model to account for the present data depends, however, on understanding the action of LH stimulation, the specific features of which are highly variable between individuals.

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