those which are maximally recombined, because each male spawns regularly with the females of its group and each female spawns, in the main, with the dominant male only. The male genotype is the genotype best adapted to local conditions because the male is derived from the oldest female of the group. Individuals enter the group and gradually move up within it, with only the best adapted females eventually being able to reverse sex. Thus the social organization is a framework within which the selective process works. The social group is a self-perpetuating system which ensures the maintenance of the biased sex ratio by controlling sex reversal. Social control of sex reversal both maximizes the genetic advantages of the process and imparts considerable flexibility to it. Males are produced only when they are needed, and this method overcomes the possible precariousness of a strongly biased sex ratio maintained by endogenously controlled sex reversal.

D. R. Robertson
Zoology Department, University of Queensland, St. Lucia, Brisbane, Q. 4067, Queensland, Australia

References and Notes

1. J. W. Atz, in *Intersexuality in Vertebrates including Man*, C. N. Armstrong and A. J. Marshall, Eds. (Academic Press, London, 1964), pp. 145–232; R. Reinboth, *Zool. Jahrb. Abt. Allg. Zool. Physiol. Tiere* **69**, 405 (1962).
2. J. H. Choat, thesis, University of Queensland (1969), part 1; R. Reinboth, *Z. Naturforsch. B* **23**, 852 (1968).
3. J. E. Randall, *Pac. Sci.* **12**, 327 (1958).
4. L. Fishelson, *Nature* **227**, 90 (1970).
5. R. R. Sokal and F. J. Rohlf, *Biometry: The Principles and Practice of Statistics in Biological Research* (Freeman, San Francisco, 1969).
6. I thank R. Bradbury, A. Cameron, J. Choat, J. Connell, D. Dow, and J. Kikkawa for criticizing a draft of the manuscript; the Great Barrier Reef Committee for the use of Heron Island Research Station facilities; and the University of Queensland for financially supporting this research.

1 June 1972

Conditioned Approach and Contact Behavior toward Signals for Food or Brain-Stimulation Reinforcement

Abstract. *When presentation of a retractable lever always preceded food delivery, rats licked or gnawed the lever. They also approached but seldom orally contacted a lever signaling brain-stimulation reinforcement; instead, subjects sniffed, pawed, or "explored" the lever. Therefore, a Pavlovian conditioned stimulus evoked directed skeletal responses whose specific form depended on the forthcoming unconditioned stimulus.*

In their experiments on "autoshaping," Brown and Jenkins (*1*) found that hungry pigeons will consistently peck a small lighted disk whose illumination signals the imminent presentation of grain, even though the pecks never affect the delivery of grain. Furthermore, Williams and Williams (*2*) showed that such pecking persists even if it actually prevents scheduled grain deliveries. These results are difficult to incorporate within the framework of operant conditioning or other types of learning in which responses are assumed to be strengthened by their consequences.

However, the results do parallel several phenomena of Pavlovian conditioning, which involves pairings of an originally irrelevant event, the conditioned stimulus (CS), with some biologically significant event, the unconditioned stimulus (UCS). In autoshaping, as in Pavlovian conditioning, the CS (illumination of a disk) comes to elicit a conditioned response that anticipates and resembles the unconditioned response to the UCS (pecking at grain), and response-produced omission of the UCS often does not eliminate or even greatly weaken the conditioned response (*3*). On the other hand, the conditioned response in autoshaping is directed toward a particular external stimulus (the lighted disk), whereas the responses typically studied in Pavlovian conditioning (for instance, visceral or glandular responses) cannot be directed at some environmental object or location. However, Pavlov and others (*4*) did notice and describe in detail a variety of motor behaviors that accompanied the conditioned responses under study (such as salivation).

If we assume, as Pavlov did, that the CS eventually comes to serve as a substitute or surrogate for the UCS, then the form of the motor behavior directed at the CS in the autoshaping situation ought to be strongly controlled by the particular UCS that follows it. Our experiments with rats, reported here, provide one test of this hypothesis, because we compared conventional food UCS with reinforcing electrical stimulation of the brain (*5*); brain stimulation, unlike the food UCS used in most prior autoshaping studies, does not involve an external object that must be approached, contacted, and consumed. In addition, we wished to determine whether the results for pigeons represent a relatively general phenomenon of animal learning; would rats also "autoshape," that is, approach and contact a signal for an appetitive UCS?

A well-illuminated Skinner box had a food chute centered on the front wall (width, 27.9 cm). Two identical stainless steel retractable levers (3.2 cm wide and 1.3 cm thick), one in the center of each of the two side walls (width, 23.2 cm) were 4.4 cm above the floor and protruded 1.6 cm when inserted into the chamber. Whenever a lever was inserted, light from four miniature lamps (6 volts, 0.2 amp, type 328) inside the lever was visible through four 2-mm holes in the front of the lever and two 2-mm holes on top.

Illumination and insertion of a lever lasted 15 seconds and occurred independently of presentations of the other lever. The interval between successive presentations of a given lever ranged from 45 to 135 seconds (mean, 90 seconds). Lever depressions and all contacts of the levers with bare skin (such as the palms of forepaws, or nose or mouth) were recorded separately. Videotape records enabled us to examine various qualitative characteristics of the conditioned responses.

All rats, whether trained with food or brain-stimulation UCS, were exposed to the same five successive experimental treatments. Each daily session consisted of 40 presentations of each lever. First, the rats received a baseline (operant level) session during which the levers were presented without any food or brain stimulation. In the second phase (acquisition), presentations of one lever, designated the positive stimulus (CS+) for a particular rat, were immediately followed by delivery of a food pellet in the food group and by intracranial stimulation in the other group. The second lever (CS^0) was presented randomly with respect to presentations of food, brain stimulation, or CS+.

In the third phase (extinction), each lever was still presented 40 times daily, but no food or brain stimulation was delivered. In the fourth phase (reac-

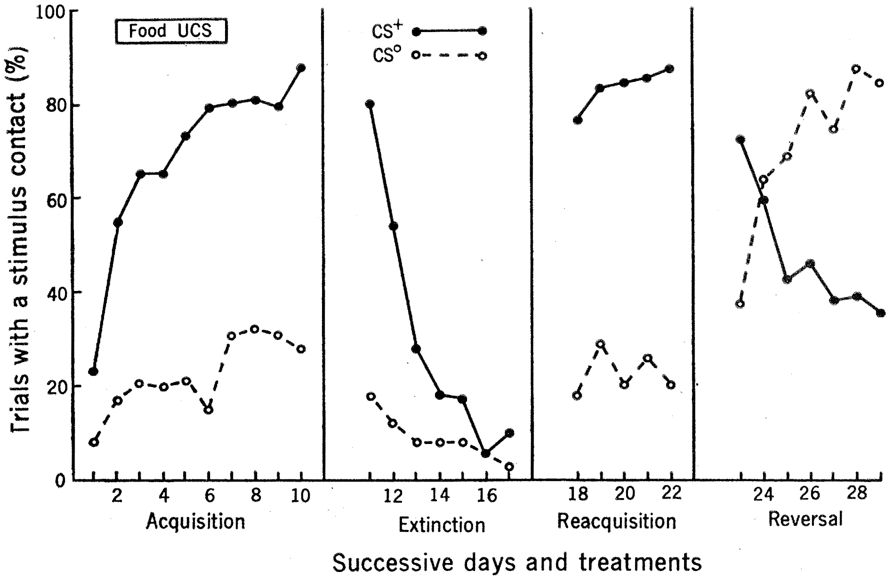

Fig. 1. Mean probability of a lever contact during successive treatments in the group of rats ($N = 6$) trained with food as the unconditioned stimulus. During acquisition and reacquisition phases, CS^+ signaled food, whereas CS^0 occurred randomly. During extinction phase no food was given. During reversal phase CS^0 signaled food and the former CS^+ occurred randomly.

quisition), the original acquisition conditions were reinstated. Then, in the fifth phase (reversal) the functions of the two levers were reversed for each rat so that CS+ became CS^0 and CS^0 became CS+. At no time in these experiments did approach toward or contact with the levers, or any other behavior of the subject, affect the presentation of either CS's or UCS's.

In the food experiment, six male Long-Evans pigmented rats, approximately 1 year old, were maintained on a 22-hour food deprivation schedule. Each rat first received two 30-minute sessions during which the feeder mechanism intermittently dispensed 97-mg food pellets. The levers were never inserted during this preliminary period. The subjects then proceeded through the above five phases, which lasted 1, 10, 7, 5, and 7 days, respectively. All subjects contacted at least one lever in the operant level session, but these responses occurred, on the average, during fewer than 15 percent of the total daily trials.

Figure 1 displays the group mean percentage of daily trials on which each lever was contacted in the food experiment. Every individual rat showed similar general effects. During acquisition there was a large increase in contacts of CS+, while contacts of CS^0 increased only slightly. During extinction there was a rapid decrease in contacts of CS+. Strong recovery of responding to CS+ occurred during the reacquisition phase. During the reversal phase, contacts of the former CS^0 increased markedly while contacts of the former CS+ decreased.

Visual observation and the videotape records revealed that contacts of CS+ were almost exclusively oral and consisted mainly of licking responses and gnawing behavior. Typically, subjects would approach and contact CS+ very soon after its insertion, lick and gnaw at it throughout the period when it was available, and then go to the food chute when CS+ was removed. Actual depressions of the lever during presentation of CS+ occurred fairly frequently but appeared to be incidental byproducts of the licking and gnawing behaviors.

In the brain-stimulation experiment, four male rats (three pigmented Long-Evans and one Holtzman albino), approximately 4 months old, received bilateral implants of bipolar electrodes aimed at the lateral hypothalamus (*6*). After at least 2 weeks of postoperative recovery, the subjects were screened for the positive effects of electrical stimulation in these brain sites. The rats were placed in a box with no levers, and the experimenter adjusted the current until stimulation elicited reactions (such as sniffing or locomotor exploration) that are known to correlate highly with the reinforcing effect of intracranial UCS's (*7*).

The rats then received the same general treatment given rats in the food experiment, except that they were not deprived of food and the UCS was intracranial stimulation delivered through a commutator and a flexible cable attached to the subject's head. The UCS was five trains of biphasic rectangular-wave pulse pairs at 100 hz. Each pulse of the pair lasted 0.5 msec, and each train lasted 0.25 second, with a 1.0-second interval between trains. Follow-

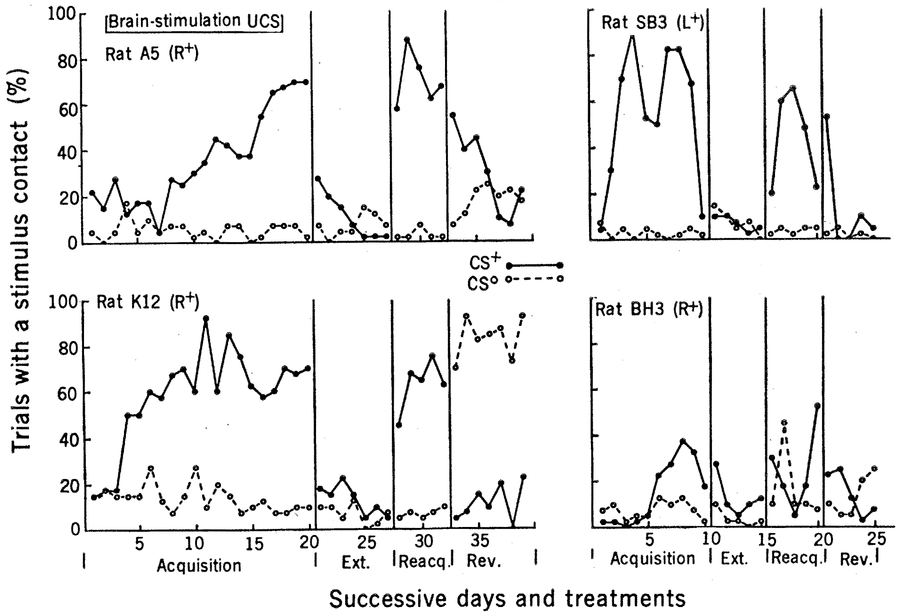

Fig. 2. Lever contacts for four rats trained with brain stimulation as the unconditioned stimulus. The different treatments indicated on the abscissa correspond to those described for Fig. 1. The CS^+ was the right lever for three rats (R^+) and the left lever for one (L^+).

ing completion of the five experimental phases, the rats were tested for rewarding effects of the brain stimulation in a standard operant lever-pressing, self-stimulation task (*5*), which confirmed the original judgments of the stimulation's positive value for all the rats.

Figure 2 shows data for the four rats with intracranial stimulation as UCS. Each subject approached and contacted CS+, but the effects of the various treatments were generally less pronounced and more variable than in the food experiment. However, visual observation and videotape records revealed that the brain-stimulation subjects were directing their behavior toward CS+ much more than their recorded contacts would suggest. On most presentations the subjects moved very close to CS+, but sometimes contacted it only with their whiskers as they sniffed or explored near it; these responses were not detected by our sensing devices. The rats seldom approached CS^0 when it was presented. We believe, therefore, that the less clear-cut performance of the brain-stimulation animals was probably due more to relatively insensitive measures of their approach and contact behavior than to any attenuation of the basic phenomena observed in the food experiment.

The brain-stimulation subjects seldom licked or gnawed the CS+. They tended to engage in "exploratory" behavior—sniffing at the lever, touching it lightly with their forepaws, and so forth—patterns of behavior which, although relatively consistent for a given rat, differed among individuals. There seemed to be a definite relation between the behaviors directed at CS+ and those elicited by the brain stimulation; if an animal sniffed or displayed certain postural adjustments during UCS presentation, we often noticed fragments of the same general pattern during presentation of CS+ (*8*).

Our experiments demonstrate that rats, like pigeons, will approach and contact a localizable stimulus that signals the imminent presentation of a reinforcing stimulus. These conditioned movements may appear maladaptive because they have no effect on delivery of the UCS and, in fact, often require the subject to move away from the place where the UCS is delivered, thereby delaying reception and consumption of the UCS (*9*). Furthermore, the form of the conditioned contact response resembles the unconditioned movement patterns elicited by the forthcoming UCS. As Pavlov suggested, the CS seems to serve as a surrogate for the UCS. Wolin (*10*), using a conventional operant situation, and Jenkins and Moore (*11*), using an autoshaping situation, have observed analogous topographical differences in the pecking responses of pigeons at disks that signal either food or water. Eating movements (brief, forceful pecks) were directed at a food-correlated disk, whereas pecks at a water-correlated disk resembled drinking movements (sustained, relatively weak pecks, accompanied by occasional licking or swallowing).

Therefore, simple frequency measures of grossly defined responses such as key pecks or lever presses may mask important differences in response form that depend on the type of reinforcement. The key peck and lever press are not as "arbitrary" as they are frequently assumed to be by researchers who investigate the operant conditioning of skeletal responses. Directed motor responses of these kinds also emerge from the use of a classical conditioning procedure. In many situations, such responses probably combine or interact with responses established and controlled by their consequences [Law of Effect (*12*)] to determine the overall behavior displayed on a so-called "operant" task.

GAIL B. PETERSON*
JAMES E. ACKIL†
GABRIEL P. FROMMER, ELIOT S. HEARST
Department of Psychology,
Indiana University, Bloomington 47401

References and Notes

1. P. L. Brown and H. M. Jenkins, *J. Exp. Anal. Behav.* **11**, 1 (1968).
2. D. R. Williams and H. Williams, *ibid.* **12**, 511 (1969).
3. F. D. Sheffield, in *Classical Conditioning*, W. F. Prokasy, Ed. (Appleton-Century-Crofts, New York, 1965), p. 302; R. L. Patten and J. W. Rudy, *Psychonom. Sci.* **8**, 463 (1967).
4. I. P. Pavlov, *Conditioned Reflexes and Psychiatry* (International, New York, 1941), vol. 2, pp. 120, 150; K. Zener, *Amer. J. Psychol.* **50**, 384 (1937). An extensive discussion of Pavlov's views and data on these matters was given by B. R. Moore [thesis, Stanford University (1971)].
5. S. P. Grossman, *A Textbook of Physiological Psychology* (Wiley, New York, 1967), pp. 564–595.
6. The brain of one rat was inadvertently destroyed, but for the three others the locations of the electrode tips have been identified in photographic prints made from unstained frozen sections 40 μm thick. They were all located in the vicinity of the lateral hypothalamus, in sites that have previously been demonstrated to be reinforcing.
7. M. Christopher and C. M. Butter, *J. Comp. Physiol. Psychol.* **66**, 335 (1968).
8. Subsequent research [G. B. Peterson, thesis, Indiana University (1972)] has demonstrated the unimportance of several confounding factors in the experiments reported here. The same effects occurred reliably during between-subject and within-subject comparisons of food and brain-stimulation UCS in which all rats (i) received implanted electrodes aimed at lateral hypothalamic sites, (ii) were deprived of food, and (iii) were attached to the electrode cable during daily sessions. Thus, the differential response topographies to signals for food as compared to brain stimulation described in this report are not simply due to (i) the different drives dominating the two groups during training, (ii) biases toward particular types of behavior because of the repeated elicitation of specific unconditioned responses in the experimental situation, (iii) some restraining effect of the cable attachment such that sustained and vigorous gnawing was rendered less probable in the brain-stimulation group, (iv) the different ages of the two original groups of rats, or (v) some unknown brain damage that resulted from the surgical techniques used on the brain-stimulation rats.
9. "Maladaptive" behavior of this and other kinds are also described in a cogent article by K. Breland and M. Breland [*Amer. Psychol.* **16**, 681 (1961)].
10. B. R. Wolin, in *Contemporary Research in Operant Behavior*, A. C. Catania, Ed. (Scott, Foresman, Glenview, Ill., 1968), p. 286.
11. H. M. Jenkins and B. R. Moore, in preparation.
12. G. Kimble, *Hilgard and Marquis' Conditioning and Learning* (Appleton-Century-Crofts, New York, 1961).
13. Supported by PHS grants MH10852, MH-16046, and MH19300. We acknowledge the stimulating suggestions and valuable information concerning his own experiments provided by H. Jenkins. Reprints may be obtained from E.S.H.

* Present address: Department of Psychology, Dalhousie University, Halifax, Nova Scotia, Canada.

† Present address: Department of Psychology, Western Illinois University, Macomb 61455.

30 May 1972