mously with "sex pheromones." Most authors now use "sex attractants" to denote chemicals which are similar in biological activity to sex pheromones in that they attract only one sex, but which have not been identified as occurring in the opposite sex.
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8. We used a sample of propylure synthesized by A. I. Meyers and E. W. Collington, *Tetrahedron* **27**, 5979 (1971). We thank Dr. Meyers for this sample. Our GLC analysis (*12*) of the sample on a 2 percent Apiezon L column (240 by 0.2 cm, inside diameter) at 130°C and a flow rate of nitrogen of 76 ml/min ($N = 2700$ theoretical plates) showed the presence of six compounds with relative retention times of (percentage composition based on peak areas): 0.66 (0.1 percent); 0.80 (0.1 percent); 0.85 (0.1 percent); 0.91 (0.9 percent); 1.00 (97.3 percent); and 1.14 (1.5 percent). Thus the sample of propylure was 97.3 percent *trans* with the maximum single minor component being 1.5 percent. However, the most probable peak representing the *cis* isomer of propylure is the one with a relative retention time of 0.91 (0.9 percent). Under identical conditions, the relative retention times of *cis*- and *trans*-7-hexadecenyl acetates were 1.70 and 1.82, respectively (the retention time of *cis* isomer was 137 minutes).
9. Purchased from Aldrich Chemical Co. and redistilled before use to 99 percent purity.
10. The hexalure was obtained from Farchan Division, Story Chemical Corporation, and used without further purification. Gas-liquid chromatography, nuclear magnetic resonance, and thin-layer chromatography indicated that the sample consisted of more than 95 percent 7-hexadecenyl acetate (of which more than 90 percent was the *cis* isomer).
11. The moths used for extracts, bioassays, and lures in traps were obtained from larvae reared on a modified wheat-germ diet [P. L. Adkisson, E. S. Vanderzant, D. L. Bull, W. E. Allison, *J. Econ. Entomol.* **53**, 759 (1960)], using the individual rearing method of R. Patana, *U.S. Department of Agriculture, Agricultural Research Service, Production Research Report* (1969). The sexes were separated as pupae, which were placed for emergence into 4-liter paper cartons with screen tops. The cartons were placed in rearing units at 28°C under a light : dark cycle of 14 hours of light and 10 hours of darkness, synchronized with that occurring in the field. Rearing units holding males and females were kept in separate rooms.
12. We used an F & M Hewlett-Packard dual channel gas chromatograph, model 402, equipped with an all-glass inlet system and glass columns (50 by 0.2 cm, inside diameter). The columns were operated at 135° to 150°C, with nitrogen flow rates of 50 to 70 ml/min. The liquid phases (Table 1) were absorbed on 80–100 mesh AW, hexamethyldisilazane-treated Chromosorb W.
13. The two legs of the splitter were heated and adjusted in size so that the effluent arrived at the hydrogen flame detector and the biological detector simultaneously. At the biological detector, an air purge of 5000 ml/min picked up the effluent and circulated it through the 1000-ml volume container enclosing the cage of male moths. Details of our splitting technique have been described [L. K. Gaston, T. R. Fukuto, H. H. Shorey, *Ann. Entomol. Soc. Amer.* **59**, 1062 (1966)].
14. Adult female pink bollworms had been reported to contain 0.06 to 0.60 mg of deet each (*3*). Since females weigh 12 to 20 mg, deet should make up 0.3 to 5 percent of their total body weight. Our GLC method can detect 5 ng, but we could find no deet at this level.
15. We thank W. O. Ridgway for shipments of frozen pink bollworm moths originating from a mass rearing facility of the U.S. Department of Agriculture, Phoenix, Ariz.
16. Pupae were collected by hand from rosetted cotton blooms in the field. The pupae were separated according to sex (*11*). Emerged female moths were held for 3 to 5 days before their abdomen tips were removed and extracted with ether.
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19. The purified biologically active material showed two partially overlapping peaks in GLC analysis (4 percent diethylene glycol succinate, at 175°C). Collection of this active material, followed by reductive ozonization, gave three compounds: 1-pentanal, 1,4-butanedial, and 7-acetoxy-heptanal. The two compounds constituting the biologically active material had relative retention times of 1.40 and 1.46 (*n*-hexadecyl acetate = 1.00). The *cis*-7,*trans*-11 and *cis*-7,*cis*-11 synthetic isomers of 7,11-hexadecadienyl acetate had relative retention times of 1.41 and 1.47, respectively. The two active peaks were collected separately. The infrared spectrum of the earliest collected active peak (1.40) showed absorption at 966 cm^{-1} (*trans*-double bond) and was identical to the spectrum of synthetic *cis*-7,*trans*-11-hexadecadienyl acetate. The infrared spectrum of the later collected active peak (1.46) showed no absorption in the 960 cm^{-1} region and was identical to the spectrum of synthetic *cis*-7,*cis*-11-hexadecadienyl acetate. Gas-liquid chromatographic analysis by coinjection of the earliest collected active peak with synthetic *cis*-7,*trans*-11-hexadecadienyl acetate gave a single peak; likewise, coinjection of the later collected active peak with *cis*-7,*cis*-11-hexadecadienyl acetate gave a single peak. These synthetic compounds were prepared and supplied by Farchan Division, Story Chemical Corporation.
20. This is paper No. 40 of a series entitled "Sex pheromones of Lepidoptera." We thank S. U. McFarland, S. Eubanks, and B. Wilk for assistance. Supported in part by grants from the Rockefeller Foundation and Cotton Incorporated.

26 April 1973; revised 3 July 1973

Pavlovian Conditioning with Heat Reinforcement Produces Stimulus-Directed Pecking in Chicks

Abstract. *In a cooled chamber, chicks approached and pecked a small disk whose illumination preceded heat lamp activation, even when pecks prevented heat lamp onset. These behaviors did not occur when the disk and heat stimuli were randomly presented. Approach and contact of conditioned stimuli may develop even though these behaviors are not (i) evoked by the reinforcing stimulus, (ii) necessary for reinforcer reception, or (iii) ever followed by the reinforcer.*

Pavlovian conditioning involves the presentation of stimulus events irrespective of an organism's behavior. As a result of this experience, a formerly ineffective stimulus [conditioned stimulus (CS)] may come to evoke a response whose form often resembles that elicited by the reinforcing stimulus [unconditioned stimulus (US)].

Unlike conventional Pavlovian procedures that restrict the subjects' locomotor behavior, recent conditioning experiments have permitted subjects unrestrained access to CS's (*1–3*). Under these circumstances, subjects not only evidence similar conditioned responses (CR's) and unconditioned responses (UR's), but they frequently draw near to the CS and they may even contact it. For example, Jenkins and Moore (*3*) found that freely moving pigeons exhibited conditioned "eating" and "drinking" behaviors to visual CS's which preceded food and water US's, respectively. Not only were skeletal components of the UR (such as licking and swallowing) elicited by the small visual CS, but they were integrated into a complex sequence of skeletal behaviors beginning with approach and culminating in physical contact with the CS.

Most reports of approach and contact of CS's have involved appetitive US's that, like food and water, must be approached and physically contacted in order to be received (*4*). The possible importance of these obligatory skeletal behaviors to the development of CS approach and contact has not yet been extensively investigated. To this end, thermal stimulation was used as the US in the present study. This reinforcer requires no instrumental behavior for its reception; accordingly, conditioned approach and contact of a CS could not readily be attributed to a similar preconsummatory sequence for the heat US. Furthermore, most previous experiments have utilized CS's and US's that often give rise to similar or compatible behaviors (*5*). Birds frequently peck at small visual features. They also peck at kernels of grain and thrust their beaks into puddles of water. Would birds also peck a small visual CS if the subsequent US evoked highly dissimilar behaviors? Here again, thermal stimulation is an interesting US. The stereotypical behaviors evoked in chicks by heat (such as immobility and wing extension) are not only topographically different from stimulus-

directed pecking, but they are quite possibly incompatible with pecking as well.

In the first experiment, 16 male chicks 3 days old were individually placed in a lidless chamber (17.8 cm wide, 17.8 cm deep, and 32.1 cm high) housed in a cooled incubator (*6*). At intervals averaging 1 minute, an overhead infrared lamp (240 volts, a-c; 275 watts) was activated for 4 seconds. For the eight chicks that began training in the paired (P) condition, heat lamp activation was always preceded by an 8-second illumination of a green key light (24 volts, d-c; 2.8 watts) located behind a small circular opening (1.9 cm in diameter, 6 cm above the floor) in the aluminum chamber wall. The remaining eight subjects were initially administered a nonassociative control treatment (*7*). These birds received the same number of daily key light and heat lamp presentations, but these occurrences were scheduled completely independently of one another. In this so-called random (R) condition, CS's and US's were programmed on two identical but separate variable-interval 1-minute schedules. Daily sessions ended after 50 US's. During the 3 days of phase 1, training was conducted as described. During the following 3 days of phase 2, subjects that had first received P training were switched to R training (P-R), and subjects that had first received R training were switched to P training (R-P). The primary behavior recorded was the number of contacts of a transparent plastic key placed just behind the key light opening. The specific form of the contact behavior was noted as well as other skeletal activities and vocalizations.

When first placed in the refrigerated chamber, the chicks showed highly agitated behavior, racing to and fro and cheeping loudly. The activation of the heat lamp produced a marked change in their behavior. The chicks stopped scurrying about, extended their wings, and often emitted twittering sounds. Sometimes the birds would stiffen into a "head up" posture; at other times they would lower their bodies and occasionally rub the floor with their chests.

The behavior of the chicks toward the lighted key differed under the two CS-US contingencies (Fig. 1). During phase 1, substantial pecking emerged and was maintained only with sequential CS-US pairings. Paired subjects began pecking the key after a median of eight CS-US pairings. When the

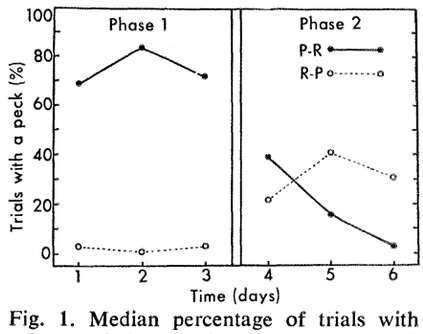

Fig. 1. Median percentage of trials with a key peck in experiment 1. During both phases 1 and 2, *P* refers to paired CS and US presentation and *R* refers to random presentation of CS and US. The two treatment groups (*P-R*, filled circles and solid lines; *R-P*, open circles and dashed lines) received paired and random training in reversed order.

paired subjects pecked at the CS, they generally struck the key three to six times per 8-second presentation. Occasionally, twittering vocalizations accompanied the pecking, but lowering of the body and wing extension did not. Subjects exposed to the random treatment in phase 1 contacted the CS for the first time after a median of 33 CS presentations—more trials than required by paired subjects [Fisher exact $P = .056$, one-tailed (*8*)]. Furthermore, random subjects contacted the CS on many fewer trials than did paired subjects on days 1, 2, and 3 [all U's < 8.0, P's $< .005$, one-tailed Mann-Whitney test (*8*)]. Under reversed conditions in phase 2, the P-R subjects decreased and the R-P subjects increased their levels of responding [T's ≤ 2.0, P's $\leq .025$, one-tailed Wilcoxon test (*8*)]. In order to assess the control of key responding by the CS, response rates were separately computed during key light "on" and "off" periods. Under paired training, response rates were high during key light "on" periods and low during "off" periods. When CS's and US's were randomly presented, however, response rates were very low and not differentially controlled by CS presentation.

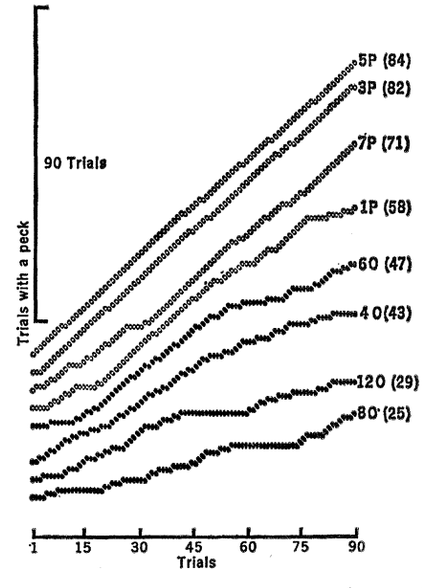

Fig. 2. Cumulative response records of eight representative subjects in experiment 2. Trial 1 denotes the first trial with a key peck CR. Subsequent trials are depicted along the abscissa. Each trial with a key peck increments the ordinate 1 unit. The numbers in parentheses next to the individual subject numbers denote the number of trials with at least one key peck out of the 90 trials; *P* and open circles, paired CS and US presentation; *O* and solid circles, omission training procedure.

The CR topographies were also of considerable interest. Until the second or third session, pecks for subjects in the paired group were quite forceful and aimed directly at the key. These "true" pecks generally gave way to a modified response form: The chicks approached even closer to the key and pushed their beaks into it, shaking their heads from side to side. The total pattern of behavior can perhaps be described as "snuggling." This snuggling appeared to occasion less efficient manipulation of the key. Key responses not only became less forceful, but their directedness was also reduced as the chicks frequently nudged their beaks along the wall surface just adjacent to the key. These observations were paralled by a general decline in the mean number of pecks per trial with a peck: 6.74 on day 1, 4.07 on day 2, and 3.79 on day 3 for paired subjects (*9*).

In the first experiment, key responding emerged and persisted under paired training despite the fact that heat reinforcers were contingent only upon prior key illuminations and not upon any of the chicks' behaviors. Nonetheless, the logical possibility still exists that responding to the key light might have been adventitiously reinforced by the heat lamp activations that inevitably followed the key light stimuli and incidentally followed key responses (*10*). To assess this possibility, chicks in a second experiment were trained on a procedure in which key responses could never be followed by thermal stimulation (*11*). If key responding were to emerge and continue under these circumstances, then adventitious response-reinforcer (operant) contingencies must be relatively unimportant

in the conditioning of CS approach and contact behaviors such as those observed in the initial experiment.

Six control chicks were trained similarly to paired subjects in the first experiment. On each of three consecutive days, these subjects received 40 CS-US conditioning trials with the chamber temperature set at 15°C, 10°C, and 5°C on days 1, 2, and 3, respectively. To assess the possible contribution of accidental peck-heat pairings, six other subjects were given omission training (O) in which the heat lamp was activated provided that subjects did not peck the key light stimulus; one or more pecks to the key light caused omission of the 4-second heat lamp presentation at the termination of the 8-second trial stimulus.

Within 70 trials, all 12 chicks began pecking the key light. Cumulative response records of four subjects in the paired condition and four subjects in the omission condition are shown in Fig. 2 (*12*). Omission subjects all acquired the key pecking response and persisted despite response-dependent nonreinforcement, although they responded with a generally lower rate than did paired subjects. Over the course of the 90 trials beginning with the first CR, the four omission subjects in Fig. 2 responded on 25 to 55 percent of the trials. Under similar experimental conditions, even higher response frequencies have been observed in additional subjects (data not included in this report). As in the first experiment, the change in topography from pecking to snuggling was observed in both paired and omission subjects.

The present data support the following conclusions: (i) Approach and contact of conditioned stimuli is under the control of Pavlovian reinforcement contingencies. Only paired (but not random) presentations of the key light and the heat lamp were effective in producing and sustaining key responding (experiment 1). Furthermore, key responding emerged and persisted even when contacts of the key actually prevented the heat lamp from being activated (experiment 2). (ii) Instrumental approach and contact of US's are unnecessary for the emergence of CS approach and contact. The chicks approached and contacted the lighted key even though no instrumental behaviors were required to receive the heat lamp stimulation. (iii) Approach and contact of CS's does not depend on similar or compatible CS- and US-controlled responses. The chicks approached and pecked or snuggled with the lighted key even though the heat stimulus evoked none of these behaviors. (iv) The topography of the conditioned response is not immutable and may undergo transformation during the course of conditioning. The pecking of paired and omission chicks tended to evolve into snuggling on successive days of training.

The form of the conditioned behaviors observed in these experiments raises an important issue concerning CR determination in Pavlovian conditioning. Here the chicks engaged in energetic approach, pecking, and snuggling activities toward the key light CS even though the heat lamp US elicited generally unenergetic and undirected postures and movements. If the topography of the conditioned response were primarily determined by the reinforcing stimulus and if the CS were merely a substitute or surrogate for the US (*1–3*), then the CS should have evoked the latter behaviors rather than the former ones. That this did not occur points to conditioned stimuli as potentially important determinants of conditioned response form and direction in conditioning studies (*13*).

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References and Notes

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6. The chamber temperature was set at 15°C on days 1, 2, and 3; 10°C on day 4; and 5°C on days 5 and 6. The chamber temperature was reduced in an attempt to maintain the effectiveness of the heat reinforcer because the subjects appeared to be adapting to the cold chamber by day 3 and would occasionally "nap" during experimental sessions. The reductions in chamber temperature did not entirely eliminate cold adaptation, however.
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9. Interpretation of these data as well as the lowered pecking probability for P-R animals in phase 2 (Fig. 1) is complicated somewhat by the decline in responsiveness to cold (*6*). Therefore, (i) as far as the present data are concerned, only trials with at least one peck were considered, and (ii) R-P animals actually increased their response frequencies in phase 2.
10. Baby chicks will also peck a key when pecks immediately produce heat and light stimulation [J. F. Zolman, S. D. Chandler, D. Black, *Develop. Psychobiol.* **5**, 181 (1972)].
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4 December 1972; revised 30 April 1973

Disparity Detectors in Human Depth Perception: Evidence for Directional Selectivity

Abstract. *Viewing a target moving in depth depresses visual sensitivity to depth when test and adapting stimuli simulate motion along closed paths with the same directions of rotation. However, for opposite directions of rotation, sensitivity is either unaffected or increased. This points to two classes of disparity detectors. Either eye's input to a single class of disparity detector consists of the physiological responses to a single direction of horizontal movement.*

Stationary objects appear to be in motion if objects moving in one direction are first viewed for some time. The direction of the illusory motion is opposite to the direction of movement of the first-viewed objects. This aftereffect of seen motion has been cited as evidence for the presence of directionally selective motion detectors in the human visual system (*1*). According to this explanation, the human visual system contains motion detectors that respond preferentially to a retinal image that is moving in a specific direction. The "preferred" direction differs for different motion detectors. The particular detectors that are excited by a moving stimulus provide a physiological representation of the direction of movement. The balance between the