in the cervical region and spreads caudally, involving eventually all parts of the body. Movements of the limbs are performed at first only in conjunction with the body; they become independent a few days after the inception of motility. Motility is periodic in both forms; activity phases alternate with inactivity phases. Embryos become sensitive to exteroceptive stimulation a few days after the onset of motility, a demonstration of the nonreflexogenic nature of early motility. In both forms, movements are apparently random; the right or left, fore or hind limbs move without evidence of coordination. In brief, this pattern seems to be characteristic of these two amniote groups, reptiles and birds.

The main difference between chick and turtle embryos is in the profile of percentages of activity during incubation. The chick reaches high levels of activity, 80 percent by day 13, which are maintained until just before hatching. In the turtle maximum activity is reached about halfway through the incubation period and has a mean value of only 50 percent; it is not sustained.

Periodic activity declines from this point until shortly before hatching.

The attenuated incubation period of the turtle, coupled with its low levels of total activity, make it an excellent animal for use in studies of the qualitative as well as the quantitative aspects of embryonic behavior.

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References and Notes

- 1. H. Tuge, Proc. Soc. Exp. Biol. Med. 29, 52
- (1931). K. U. Smith and R. S. Daniel, Science 104, 2. K. U 154 (1946).
- Yntema, Anat. Rec. 149, 577 (1964). 3. C. L. V. Hamburger, Proceedings Comparative Neurochemistry 5th Int. Symposia (Perga-
- . Sym_P. 1964), pp. 21-. ch Wisconsin. do em mon Press, New York, 1964), pp. 21-34. The Lemburger Co., Oshkosh, Wisconsin. C. L. Yntema, staged series of turtle em-
- bryos, in progress. 7.
- V. Hamburger, M. Balaban, R. Oppenheim,
 E. Wenger, J. Exp. Zool. 159, 1 (1965).
 G. E. Coghill, Anatomical Problems of Be-8. haviour (Cambridge bridge, 1929). Cam-Univ. Press,
- 9. R. Oppenheim, *Science* **152**, 528 (1966). 10. This study was made in Viktor Hamburger's laboratory of neuroembryology. I thank him for his advice and for critically reading this eport. I also thank Fortune B. Decker for echnical assistance. Supported by PHS grant report. 5R01 NB 05721 03.

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Training and Maintenance of Keypecking in the Pigeon by Negative Reinforcement

Abstract. Pigeons were trained to peck a key to escape a pulsing shock of linearly increasing intensity. As the rate of increase was varied from 0.0374 milliamperes per minute to 37.4 milliamperes per minute, the intensity at which most pecking occurred varied from 2.2 to 5.0 milliamperes.

Although pigeons are routinely trained to peck a key for food, they have not been so easily trained to peck a key to escape or avoid electric shock. The difficulty seems to be due, at least partly, to variations in the pigeons' sensitivity to shock. In previous studies with a simple response such as headlifting to escape and avoid shock, the shock intensity had to be adjusted daily in order to maintain responding (1). With key-pecking it was necessary to continually adjust shock intensity, even from moment to moment (2).

Yerkes and Dodson (3), using rats, found that as a task becomes more complex a given criterion of learning can be attained only with a progressively narrower band of shock intensities. Intensities below this band presumably do not sufficiently motivate the response while intensities above the band elicit responses, emotional or othing in the pigeon is too narrow for informal adjusting procedures to keep the intensity of shock within it. The present experiment was designed to permit automatic adjustment to the effective band of shock intensities. Trains of brief shocks of gradually increasing intensity were presented. Since the tensity increased gradually, several shocks were presented within any band of reasonable width. If fluctuating sensitivity to shock were the main source of difficulty in shaping escape responding in the pigeon with manual adjustment of intensity, such responding should be easily shaped and maintained by this procedure, and the birds' responding should reveal the range and stability of the lower limit of the effective band.

erwise, that interfere with the response

being learned. Perhaps the band of intensities which could support key-peck-



Fig. 1. Normalized cumulative distrbutions for subject 319. The distributions represent the percentage of total responses made at or before each interval of pulses on the abscissa. Different slots are for different rates of increase. Due to the range of interresponse times at different rates of increase of shock, the distributions are based on geometrically increasing intervals of pulses. The abscissa values are given in terms of pulses of shock. Since these occurred at the constant rate of two per second, the abscissa values can be converted to seconds if they are divided by two.

Four pigeons, allowed free feeding in their home cages, were run once a day in a chamber containing an overhead light and a response-key. Shock pulses (35 msec long) were delivered at a rate of two per second through gold wires imbedded under the pigeon's pubis bones. The shocks increased linearly in intensity from 0 to 8.5 ma. Pecks on the key, while the shock was increasing or after it had reached maximum, reset the shock to zero and turned off the overhead light for 3 seconds. Then the light came back on and shock began to increase again.

Shock was 400-v alternating current passed through a fixed resistance of 25 kohms and a motor-driven variac. A gear-changer and a clutch were arranged so that the shock intensity increased from 0 to 8.5 ma at a constant rate (set by means of the gear-changer).

One subject (436) was trained previously to peck a key for food. Two other subjects (270 and 319) were trained to peck a key for food, and then the response was extinguished. They did not peck the key when first tested with the present procedure. Keypecking was established by setting the rate of increase of shock at 20 ma/min, increasing the maximum intensity from 8.5 ma to 15 ma, and reinforcing successive approximations to key-pecking by reducing the shock suddenly to zero for about 5 seconds. A fourth subject (499) had not been in any previous experiments. Key-pecking for escape was

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established as it was for subjects 270 and 319, except the key had mounted on it a clear plastic extension protruding into the chamber 1.3 cm; this extension was removed after training.

After training, the rate of increase of shock was changed every 5 days through a series of values that varied between 0.0374 ma/min and 37.4 ma/min, except for subject 499 who was not tested at low rates of increase. This procedure maintained stable keypecking behavior in all subjects. Only at the highest and lowest rates of increase in shock intensity was key-pecking irregular for some subjects. At 0.187 ma/min and below, subject 270 responded randomly with respect to shock intensity. At the highest rates of increase, subjects 319 and 436 stopped pecking (319 at 37.4 ma/min and 436 at 7.48 ma/min). Data from these birds at these extreme values are not included in the figures.

Performance after initial training is shown by the set of curves in Fig. 1 which describes a set of normalized cumulative distributions of interresponse times for a typical subject. In order to show all the functions for one subject in a single figure, the class intervals increase in width geometrically.

For the more rapid rates of shock increase, the slopes of these curves are quite steep; the spacing of responses was relatively precise. For the slower rates of shock increase (0.187 and 0.0374 ma/min), the slopes were less steep, indicating that the spacing of responses was more varied. The displacements of these curves along the abscissa indicate that the subjects' responding was largely determined by the instantaneous shock intensity, rather than by the time since the last response. If the subjects had tended to respond at equal time intervals, disregarding the rate of increase of shock, the distributions would have been superimposed.

Although shock intensity was the main determiner of responding, the occurrence of a response was not independent of the rate of change in shock intensity. Figure 2 shows the relationship between time and intensity more clearly. The heavy line shows the mode of interresponse time distributions (such as in Fig. 1) for each subject as a function of the rate of increase of shock. The curve fits a straight line of slope -0.92. The mode interresponse time ranges from about 10 minutes at 0.0374 ma/min to about 3 seconds at 37.4



Fig. 2. A log-log plot of the modes of the distributions of interresponse time (heavy line, left ordinate) and intensity at which responding occurred (thin line, right ordinate) as a function of rate of increase of shock intensity. 25 AUGUST 1967

ma/min. The slight deviation of this slope from 1 indicates that the shock intensity producing most responding changed slightly with the rate of shock increase. The path of this change is shown directly by the thin line. The intensity producing the most key-pecking ranges from about 2.2 ma, for slow rates of increase, to about 5 ma, for high rates of increase. In general, the more rapid the rate of increase in shock intensity, the higher the level of shock tolerated within a small range. This confirms the findings of Weiss and Laties (4) that rats, monkeys, and humans tolerate more shock when they must respond more frequently to reduce shock.

Two main features of the present procedure may contribute to the effective maintenance of key-pecking. First, the procedure permits continuous tracking of the shock intensities that can maintain pecking. However, this may be of minor importance except when shock onset is extremely gradual, for this range appears to have remained quite stable under most conditions. More important appears to have been the second feature, the presentation of shock by gradual increase instead of by sudden onset. However, although rate of shock intensity increase is established as a variable that controls responding, the present experiment does not establish conclusively that gradual rates of increase are essential for escape conditioning with the pigeon. For example, although key-pecking was not maintained at very high rates of increase, this may have been because the critical intensities were passed over before the subjects had a chance to respond. Or it may have been because the periods of "escape"-that is, periods of subaversive shock intensity-were too short to provide adequate reinforcement for the maintenance of responding.

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References and Notes

H. S. Hoffman and M. Fleshler, J. Exp. Anal. Behav. 2, 213 (1959).
 N. H. Azrin, *ibid.*, p. 260.
 R. M. Yerkes and J. D. Dodson, J. Comp. Neurol. Psychol. 18, 458 (1908).
 B. Weiss and V. G. Laties, J. Exp. Anal. Behav. 6, 563 (1963).
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- 5. Research
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