

the rabbit (7), where the long interval between suckling visits of the female apparently functions to reduce predation.

In the tree shrews, a number of similarities to Primates can now be explained as convergent. The long intersuckling interval places an upper limit on the number of young, and the number of mammary glands is consequently reduced. In the Primates, on the other hand, the number of young (and of mammary glands in the female) has been reduced as a specific adaptation deriving from a greatly increased pregnancy period (60 to 65 days in the tiny *Microcebus*; 3 months or more in all other Primates). The interbirth interval of 45 days in *Tupaia* (4, 6, 8) is shorter than the pregnancy period of all Primates.

The reproductive anatomy of *Tupaia* is very different from that of all living Primates. Whereas the urethra and the vagina open separately to the exterior in all Primates (probably in connection with the advanced age of the young at birth), the urethra of *Tupaia* opens into the vagina at some distance from the common clitoric duct (as in *Lagomorpha* and other primitive placentals). The female *Tupaia* lacks the os clitoridis typical of basic Primates. In male tree shrews, the testes are anterior to the penis (as in *Marsupialia* and *Lagomorpha*) and not posterior as in Primates. Male tree shrews lack the os penis typical of male Primates.

Renewed studies of the pyramidal tracts (9), the tympanic region of the skull (10), the innervation of the skin (11), optical junctions in the brain (12), and of the supposed Tupaoid fossil *Anagale* (13) show that there are considerable differences between tree shrews

and Primates. Detailed consideration of all evidence now available (6) indicates that the tree shrews are best classified as a separate order of mammals (*Tupaioidea*), as suggested by Straus (14) and that they show significant similarities to the *Marsupialia*.

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References and Notes

1. G. H. Manley, *Symp. Zool. Soc. Lond.*, in press.
2. W. C. O. Hill, *Primates I: Strepsirhini* (Wiley, New York, 1953); W. Grassé, *Traité de Zoologie XVII: Mammifères* (Masson, Paris, 1955), pp. 1642-1694; W. K. Gregory, *Bull. Amer. Mus. Natur. Hist.* **27**, 269 (1910).
3. G. G. Simpson, *Bull. Amer. Mus. Natur. Hist.* **85**, 1 (1945); W. E. LeGros Clark, *The Antecedents of Man* (University Press, Edinburgh, 1962); A. Carlsson, *Acta Zool. Stockholm* **3**, 264 (1922); G. Elliot-Smith, *Essays on the Evolution of Man* (University Press, Oxford, 1924); F. G. Evans, *Bull. Amer. Mus. Natur. Hist.* **80**, 85 (1942).
4. H. Sprankel, *Z. Wiss. Zool.* **165**, 181 (1961).
5. M. W. Lyon, *Proc. U.S. Natur. Mus.* **45**, 1 (1913); J. H. Kaufmann, *Folia Primatol.* **3**, 50 (1965); M. W. Sorenson and C. H. Conaway, *Sabah Soc. J.* **2**, 77 (1964); —, *Folia Primatol.* **4**, 124 (1966).
6. R. D. Martin, in preparation.
7. M. X. Zarrow, V. H. Denenberg, C. O. Anderson, *Science* **150**, 1835 (1965).
8. A. Portmann, *Rev. Suisse Zool.* **72**, 658 (1965).
9. J. A. Jane, C. B. G. Campbell, D. Yashon, *Science* **147**, 153 (1965).
10. W. B. Spatz, *Folia Primatol.* **4**, 26 (1966); M. C. McKenna, *ibid.* **4**, 1 (1966).
11. R. K. Winklemann, in *Evolutionary and Genetic Biology of the Primates*, J. Buettner-Janusch, Ed. (Academic Press, New York, 1963), p. 229.
12. J. Tigges, *Folia Primatol.* **4**, 103 (1966).
13. L. Van Valen, *Evolution* **18**, 484 (1964); *ibid.* **19**, 137 (1965).
14. W. L. S. Straus, *Quart. Rev. Biol.* **24**, 200 (1949).
15. I thank Professor K. Lorenz and Dr. I. Eibl-Eibesfeldt for assistance and hospitality, and Frl. N. Fischer for invaluable technical assistance. Supported by Deutscher Akademische Austauschdienst German Exchange Scholarship, 1964-1966.

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4 April 1966

conditioned before heart rate (2); and Dykman, Mack, and Ackerman and Obrist found that heart rate and "non-specific motor responses" were acquired at roughly the same rate, and both were conditioned before flexion (3). For heart rate and bar pressing, the two responses that are our concern in this report, Stebbins and Smith (4) have shown that changes in heart rate do occur during suppression of bar pressing, but they have not presented data on the speed of acquisition and on the form (the changes over time) of the two types of response. We now present data on the form and speed of acquisition of the two responses in order to answer the questions posed above.

The subjects were seven naïve, male, hooded rats about 120 days of age. An eighth rat was discarded because of a fault in its implanted electrode recording system. The apparatus consisted of four Skinner boxes controlled automatically by standard Grason-Stadler operant conditioning units.

Two conditioned stimuli (CS) of 70-db intensity were employed. One stimulus was a continuous white noise, and the other was the same white noise interrupted four times per second. The unconditioned stimulus (UCS) was an electric shock of 0.5-second duration and 1.3-ma intensity. A delayed conditioning procedure with a 3-minute CS-UCS interval was employed; that is, the CS lasted for 3 minutes and terminated at UCS onset.

Heart rate was recorded from perimetrically 7.5 cm long ran from the electrodes (5). Insulated wires approximately 7.5 cm long ran from the electrodes to an Amphenol "Subminax" connector. The electrodes were inserted through an incision made on the scalp while the rat was under Nembutal anesthesia. They were pushed through this incision under the skin to a position on the ribcage, one on each side of the body. The connector was firmly cemented to the skull. During recording, the connector was attached to a cable which led to a mercury swivel system and then to a Grass polygraph (model 5).

Two days after the operation all animals were placed on a 24-hour feeding schedule and their weight was reduced to approximately 75 percent of the weight they maintained when they had free access to food. Following "magazine training," they were given 2-hour bar-pressing sessions daily, for 8 consec-

Heart Rate: Changes during Conditioned Suppression in Rats

Abstract. Heart rate of rats was recorded in the Estes-Skinner conditioned emotional response situation. Response to the conditioned stimulus was a decrease in rate. The change in heart rate was conditioned more slowly than suppression of bar-pressing; it was of shorter duration and was more variable than suppression.

Since a number of responses are conditioned at the same time in classical conditioning, the following question arises. To what extent are the classically conditioned responses (CR's) affected differently, and to what extent are they affected similarly by the same classical conditioning procedure? There is surprisingly little evidence from an-

imal research on the simultaneous measurement of classically conditioned responses, and what evidence does exist is not clear-cut. In studies on the simultaneous recording of heart rate and leg flexion, for example, Gantt found that heart-rate was conditioned before leg flexion (1); Jaworska, Kowalska, and Soltysik found that flexion was

utive days, under a 2.5-minute variable-interval (VI) food-reinforcement schedule. (On this schedule the first bar press after a predetermined interval of time was followed by food. The duration of the interval varied in a fixed, irregular order, with a mean of 2.5 minutes.) The 9th day consisted of a "pre-test" session during which the CS's were presented four times each. Acquisition of conditioned suppression began on the day following this session and was continued for 6 days. In this part of the experiment, one CS (the CS+) was paired with shock four times during each daily session. The VI schedule of food reinforcement continued through the presentations of the CS+. Following the 6th day of acquisition, all animals were switched to a discrimination procedure. On each discrimination training day, the CS+ was paired with shock on four trials, and the second CS (the CS-) was presented alone on four trials. For four rats, the CS+ was the continuous white noise, and the CS-, the interrupted noise. For three rats, the stimuli were reversed. The sequence of CS+ and CS- trials was CS+, CS-, CS-, CS+, CS-, CS+, CS+, CS- on odd days and the reverse on even days.

Data on pre-test, acquisition, and dis-

crimination for both heart rate and bar pressing are presented in Fig. 1. Since the data for the 5th day of discrimination were essentially similar to those for the 1st and 2nd days, data for the 3rd and 4th days of discrimination are not presented. The mean number of presses and the mean heart rate are shown minute by minute for each of the 3 minutes preceding onset of CS and the 3 minutes during CS. Each point represents the average for the four trials which occurred during a single day's session, except for the pre-test day where each point represents the average for the last two trials.

On the pre-test day, there was no difference in either bar pressing or heart rate between the 3-minute pre-CS and the 3-minute CS periods.

In order to compare the speeds of conditioning of heart rate and suppression of bar pressing, the method of allowances (6) was employed to determine the first day on which the response rate during the CS+ was significantly different from the rate during the pre-CS+ period. The acquisition criterion was the first day on which at least one of the three measurements taken during the CS+ could be recognized as being different from all three of the pre-CS+ measurements. This

criterion was reached on day 2 of training for suppression, and on day 6 for heart rate. Thus, suppression was conditioned more rapidly than heart rate.

It may be, of course, that the difference in speed of conditioning could be attributed to our having chosen an inappropriate measure of the change in heart rate during the CS (that is, a measure that was not sensitive to the conditioning procedure). One possibility is that the significant change in heart rate was of short duration and occurred immediately after CS onset. If there was any subsequent reflex compensatory change, then a 1-minute average might have obscured the effect. In order to check this conjecture, the data for two 10-second periods following CS onset were examined. No significant differences between the CS+ and pre-CS+ rates occurred during the first 6 days of acquisition (although the second 10-second period after the onset of CS+ was close to significance on acquisition day 6. Another possibility is that the relevant heart-rate measurement might have been the magnitude of the change in heart rate without consideration of the direction of this change. In order to study the magnitude of the heart-rate change independent of direction, the following measure was employed. The heart rate during each minute of the CS was subtracted from the average pre-CS heart rate. The absolute value of this difference gave a measure independent of direction of change, while the algebraic value gave a measure in which direction of change was considered. Separate comparisons were made between the pre-test day and each training day. (The method of allowances as described above was employed in making these and subsequent comparisons. Analyses of variance gave essentially the same results). For both algebraic and absolute heart-rate values, the first significant difference between the pre-test day and a training day occurred on day 6. When bar-pressing data were analyzed in this manner, the first significant difference occurred on day 2 for both the absolute and algebraic measures. Again, heart-rate conditioning was slower than suppression conditioning. The difference does not seem to have been an artifact of the measurement procedure.

The two CR's also differed with respect to the temporal pattern of re-

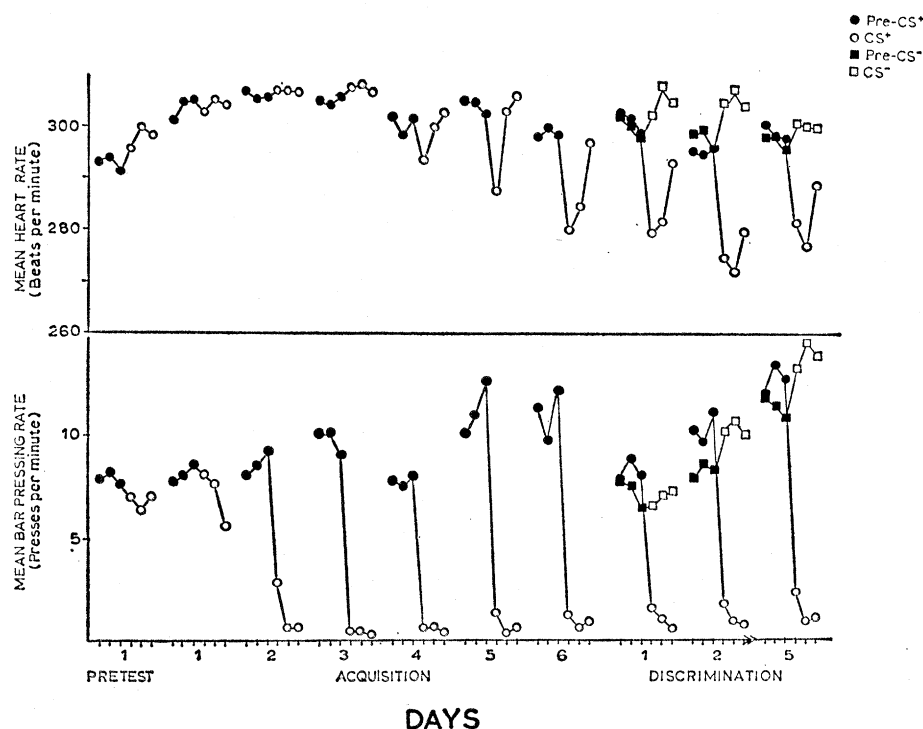


Fig. 1. Mean heart rate and mean bar-pressing rate as functions of conditioning days. Solid symbols show the mean rate for each of three consecutive 1-minute periods before CS onset. Open symbols show the mean rate for each of three consecutive 1-minute periods during presentation of the CS. Circles represent data for the CS+; squares, for the CS-.

sponse during the CS+ within a given trial. Heart rate showed a significant deceleration during the first 2 minutes of the CS+ and an acceleration toward the original pre-CS+ level during the 3rd minute. Bar pressing, on the other hand, showed a significant deceleration during all 3 minutes of the CS+ period.

Also, there were more individual differences in the direction of the heart-rate change to the CS+ than in the direction of the bar-pressing change. On acquisition day 6, for example, only five rats showed a heart-rate deceleration during both of the first 2 minutes of the CS+. Bar-pressing rate during the CS+ decelerated for all rats.

Our data on direction of the heart-rate change during the CS+ do not agree with those of Stebbins and Smith (4). These authors reported that the heart rate accelerated during the CS+; we found the predominant change to be a deceleration. While such differences in direction of change have been reported before, our knowledge of the variables controlling direction is still too meager to identify the factors which could account for this difference (7).

The response to the shock (UCR) was invariably an increase in heart rate; the response to the CS+ was predominantly a decrease. Thus, the direction of the heart-rate CR does not seem to be determined simply by the direction of the UCR. Almost from the first publication of Pavlov's work in English there have been doubts about his conclusion that the CR is simply a copy (a partial copy in some cases) of the UCR (8). These doubts are further substantiated by the data of the present experiment.

A significant difference between CS+ and CS- was found on the 1st day of discrimination for both heart rate and suppression. Furthermore, there was no significant generalization to the CS- on its first presentation. Thus, the discrimination occurred too rapidly to produce data that would have permitted a comparison of the development of the discrimination for heart rate and suppression. These data do, however, provide a control for the effects of unpaired presentations of shock and CS; if our results were produced by pseudoconditioning or sensitization, discrimination should not have taken place.

Our results support the view that conditioned responses can be relatively

independent in the way they are affected by the same classical conditioning procedure. In fact, it would seem that the effects of a classical conditioning procedure are more easily seen in the CS's modulation of ongoing operant behavior than in its modulation of autonomic responses such as heart rate. This conclusion can, of course, be criticized. One might be tempted to suggest that heart-rate changes were simply artifacts of changes in bar-pressing rate. That is, that the heart decelerated when bar pressing decreased during the CS+ and accelerated, or decelerated less, if bar pressing continued. This interpretation does not seem likely since the conditioned heart-rate response appeared only toward the end of the experiment—long after suppression had reached asymptote. If this heart-rate response were a simple function of bar-pressing rate, the relationship should have become apparent as soon as the bar-pressing rate during the CS had stabilized.

Another possibility is that the rapid conditioning of suppression was a confounding effect of operant reinforcement. One could argue that heart rate was controlled only by classical conditioning, whereas suppression of bar pressing was controlled not only by classical conditioning but also by the operant punishment of bar pressing. This argument, of course, holds only if one assumes that bar pressing can be punished by shock onset while heart rate cannot. While punishment of bar pressing may have affected the course of suppression, it does not seem likely that it can account for all of the present results since suppression is known to occur rapidly even when conditioning trials are given in a different apparatus with no bar present (9).

It would seem then that the conditioning of the two responses did proceed relatively independently and, further, that the conditioning of suppression was more rapid and stable than the conditioning of heart rate. If this conclusion is correct, then the results of this experiment pose a problem for research in which a single CR is employed as an index of some internal state (conditioned fear, anticipatory goal response, association, or expectation). For example, suppression of bar pressing alone (10) or heart rate alone (11) have been employed as indexes of fear during avoidance conditioning. But, since the conditioning

procedure affects these CR's in different ways, one's description of the development of fear during avoidance conditioning would differ considerably depending on which CR was employed.

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References and Notes

1. W. H. Gantt, *Physiol. Rev.* **40**, 266-291 (1960).
2. K. Jaworska, M. Kowalska, S. Soltysik, *Acta Biol. Exp.* **22**, 23-34 (1962).
3. R. A. Dykman, R. L. Mack, P. T. Ackerman, *Psychophysiology* **1**, 209-230 (1965); P. A. Obrist, *Proc. Amer. Psychol. Assoc.* **1965**, 165-166 (1965).
4. W. C. Stebbins and O. A. Smith, Jr., *Science* **144**, 881-83, (1964).
5. L. de Toledo, and A. H. Black, *J. Exp. Anal. Behav.* **8**, 181-82 (1965).
6. F. Mosteller and R. R. Bush, in *Handbook of Social Psychology*, G. Lindzey, Ed. (Addison-Wesley, Cambridge, Mass., 1954), pp. 289-334.
7. A. H. Black, in *Classical Conditioning*, W. F. Prokasy, Ed. (Appleton-Century-Crofts, New York, 1965), pp. 20-47; P. A. Obrist, *Proc. Amer. Psychol. Assoc.* (1965), pp. 165-166; D. Zeaman and R. W. Smith, in *Classical Conditioning*, W. F. Prokasy, Ed. (Appleton-Century-Crofts, New York, 1965), pp. 378-418.
8. L. H. Warner, *J. Genet. Psychol.* **41**, 91-115 (1932); E. R. Hilgard, *Psychol. Rev.* **43**, 366-385 (1936); K. Zener, *Amer. Psychol.* **50**, 384-403 (1937).
9. L. J. Kamin, C. J. Brimer, A. H. Black, *J. Comp. Physiol. Psychol.* **56**, 497-501 (1963); C. J. Brimer and L. J. Kamin, *Can. J. Psychol.* **17**, 188-193 (1963).
10. H. S. Hoffman, and M. Fleshler, *J. Exp. Psychol.* **64**, 288-294 (1962); L. J. Kamin, C. J. Brimer, A. H. Black, *J. Comp. Physiol. Psychol.* **56**, 497-501 (1963).
11. A. H. Black, *Can. J. Psychol.* **13**, 229-242 (1959); J. A. Stern and T. J. Word, *J. Psychosom. Res.* **6**, 167-175 (1962).
12. Research supported by NIH research grant MH-02741 and by research grant APY-42 from the National Research Council of Canada.

31 March 1966

Control of Sensory Fields by Stimulation of Hypothalamus

Abstract. *Stimulation of the cat's hypothalamus, which elicits attack, also establishes sensory fields for two reflexes related to biting. Touching a perioral region leads to head movement, bringing the stimulus to the mouth. Touching the lip-line leads to jaw opening. The size of the fields depends on the intensity of stimulation.*

This report deals with the control of jaw opening, one of the final events in a sequence of responses comprising attack behavior in the cat. Evidence obtained earlier in this laboratory clearly indicated that section of the infraorbital