The possibility that some sea water may be entering the eye across the cornea cannot be categorically rejected, since the aqueous humor is slightly hyperosmotic with respect to the sea water in which these fish were maintained. The composition of the fluid does not resemble sea water, however, and this would seem to indicate that any inward movement across the cornea would have to be essentially a movement of pure water and not of ions. For example, the concentration of magnesium ion is essentially the same in plasma and aqueous (3 mmole/kg), a value 20 times smaller than that for sea water (61 mmole/kg). A second possible explanation of these data could be based on the hypothesis that some constituent is reabsorbed from the aqueous humor, perhaps across the iris.

In the absence of evidence supporting either of the above two interpretations, the following tentative speculation is introduced: (i) in the dogfish, water is apparently moving from the plasma into the aqueous humor against an osmotic gradient; (ii) the additional work needed for this process is reflected in the unusually high bicarbonate ion concentration in dogfish aqueous humor; and (iii) carbonic anhydrase is instrumental in this process (*9*).

RUSSELL F. DOOLITTLE*
CYNTHIA THOMAS†
WILLIAM STONE, JR.
Marine Biological Laboratories,
Woods Hole, Massachusetts, and
Ophthalmic Plastics Laboratory,
Massachusetts Eye and Ear Infirmary,
Boston

References and Notes

1. M. E. Langham, *Physiol. Revs.* **38**, 215 (1958).
2. R. W. Berliner and J. Orloff, *Pharmacol. Revs.* **8**, 137 (1956).
3. H. Davson, *Physiology of the Ocular and Cerebrospinal Fluids* (Little, Brown, Boston, 1956).
4. H. W. Smith, *Biol. Revs. Cambridge Phil. Soc.* **11**, 49 (1936).
5. The dogfish used in the analyses were *Mustelus canis*. Aqueous samples were taken from the pupillary region; blood samples, from the caudal vein.
6. G. Walls, "The Vertebrate Eye and Its Adaptive Radiations," *Bull Cranbrook Inst. Sci. No. 19* (1942).
7. T. H. Maren reported this effect in the spiny dogfish *(Squalus acanthias)* [*Federation Proc.* **17**, 391 (1958)]. We are indebted to him for his help in suggesting dosages and sampling times which enabled us to obtain similar results in our own fish. It should be noted, however, that Maren reports a somewhat lower distribution ratio (in untreated fish) for bicarbonate in the spiny dogfish.
8. The sea water in our tank had an osmolarity of 910 ± 5 milliosmoles.
9. This project was supported by the Office of Naval Research and by the Boston Lions Club Eye Research Fund. We wish to thank Alfred Marshak for suggesting certain aspects of this work, and Jin Kinoshita and Oliver Cope for the use of certain critical pieces of apparatus.

* Present address: Department of Biological Chemistry, Harvard Medical School, Boston, Mass.

† Present address: Division of Medical Sciences, Boston University, Boston, Mass.

23 February 1960

Control of Vocal Responding in Chickens

Abstract. Schedules of reinforcement were shown to control the rate of chirping by chickens in the same way as other motor responses in subhumans. Under a discrimination procedure, chickens responded selectively to the visual stimulus associated with food reinforcement for chirping. Control experiments demonstrated that food influenced the rate of responding because it was presented dependent on the chick's vocalizing and not because it had an innate eliciting or "emotionalizing" power.

The appropriate conditioning procedures for modifying subhuman vocalizing have, until recently, been little studied and poorly understood (*1*). It has not been clear whether respondent or operant conditioning techniques (*2*), or both, are suitable for the control of this behavior (*3*). The studies reported here (*4*) show that the rate of chirping by a hungry chicken can be controlled by schedules of presentation of food. The temporal patterns of vocal responding thus obtained are similar to those found with other operants under schedules of reinforcement, for example, key pecking in the pigeon and bar pressing in the rat, and a wide variety of human motor responses.

The subjects for these experiments were two Bantam chickens which were run individually at 80 percent of their ad libitum body weight (*5*) in sessions that lasted from 30 minutes to 6 hours. The experimental space consisted of an 8-in., cubical, sound-insulated compartment. An opening in one wall provided access to a food tray whose presentation was scheduled automatically. A microphone mounted in the ceiling of the compartment controlled a voice-operated relay which reacted to about 95 percent of the audible chirp responses by sending pulses to programming and recording equipment.

The rate of vocal responding was observed under two experimental and five control conditions. Figure 1 summarizes the data obtained from one bird; a second bird gave similar results. The first two studies were controls in which the rate of chirping was observed under conditions of no presentation of food ("operant level") and continuous presentation of food ("free-feeding") (*6*). The stabilized rate of responding under each of these two control conditions is shown in Fig. 1. Because chirping decelerated in the early stages of the operant-level session, it may be inferred that an average rate lower than 24 responses per minute would have been obtained for this condition if the session had been extended beyond its half-hour duration. The average rate during a 1-hour free-feeding session was 27 responses per minute. The chickens chirped both while pecking at the grain in the tray and while not eating.

In a third experiment the presentation of food was contingent on responding; a fixed-ratio 20 schedule of reinforcement was employed (*7*). Under this schedule, the food tray, containing meal, was presented for 4 seconds after every 20 chirps. An extremely high rate of responding was generated by this procedure; the average rate observed in a 1-hour sample after 10 hours of conditioning was 115 responses per minute. A typical sample of the performance obtained with the fixed-ratio 20 schedule is shown in Fig. 2, in which cumulative chirp responses are plotted as a function of time. The diagonal marks on the curve indicate the presentation of food. The interreinforcement time under this schedule averaged about 16 seconds.

In the fourth experiment, a control, food was presented with the same frequency and duration as obtained under

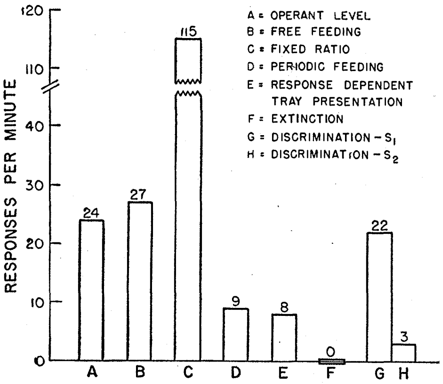

Fig. 1. Rates of chirping obtained under control and experimental conditions with one Bantam chicken.

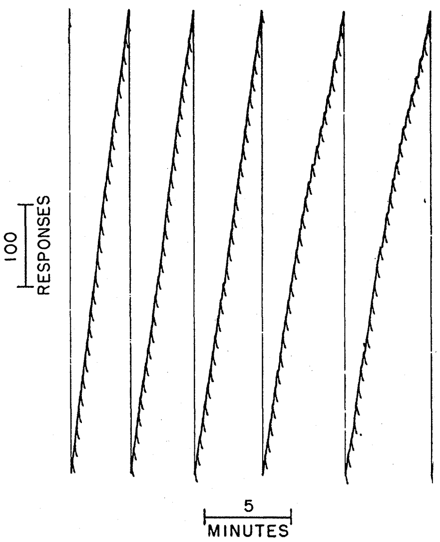

Fig. 2. Cumulative response curve for the chirp response of one chicken under a fixed-ratio 20 schedule of reinforcement.

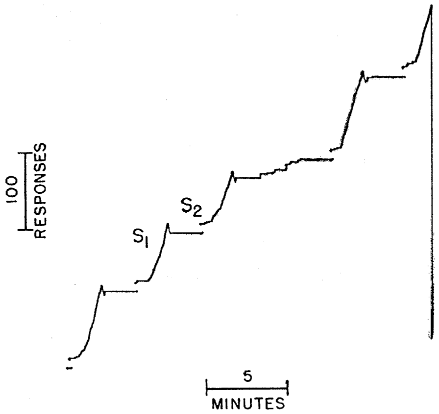

Fig. 3. Cumulative response curve for the chirp response of one chicken under a discrimination procedure.

the fixed-ratio schedule: 4 seconds of access to the food tray every 16 seconds. However, this periodic feeding was provided independent of responding. Figure 1 shows that the rate under periodic feeding (bar *D*) was less than 10 percent of the rate observed under fixed-ratio (20) (bar *C*). Apparently, it is the response requirement rather than the food presentation alone that is responsible for the high rate of responding under fixed-ratio schedule.

A fifth experiment demonstrated that the high rate of vocalizing obtained under fixed-ratio reinforcement was not simply the result of the stimulus change provided by response-dependent tray presentation. The procedure for this control condition was the same as that for the fixed-ratio condition, a 4-second tray presentation after every 20 responses, except that the food tray was now empty. The average rate of responding in the fifth hour under this condition is shown in Fig. 1, bar *E*. When a formerly neutral stimulus is paired repeatedly with a primary reinforcer it acquires a temporary control over responding which dissipates if the stimulus continues to be presented without further pairing (*8*). In the vocalizing experiments reported here, the food tray and the food were presented concurrently on thousands of occasions. The effect on the rate of chirping of discontinuing this pairing was slight initially. By the second experimental hour, however, presentation of the empty tray had, for the most part, lost its control over the rate of chirping (see Fig. 1). The terminal effect of the presentation of the empty tray may be compared to the effect of simple extinction—the sixth experimental condition—in which neither food nor tray is ever presented. Under the extinction procedure, the response rate fell to zero within a half hour.

In the final study, food was made contingent on responding during one stimulus and on not responding during a second stimulus. When a red light was on in the subject's compartment, food presentation was contingent on the first chirp after 2 minutes had elapsed. Following one reinforcement on this fixed-interval schedule (*7*), a green light was turned on and food presentation was then contingent on a pause in responding of at least 2 minutes. These conditions alternated. Each of the birds learned the stimulus discrimination within an hour. High rates of responding were observed during the stimulus that was paired with fixed-interval reinforcement (S_1) and low rates of responding were observed during the stimulus that was paired with reinforcement for not responding (S_2). When cumulative chirps in S_1 are plotted as a function of time, a pattern of responding is obtained that is typical of operant performance under fixed-interval schedules of reinforcement: the interval begins with a pause and the rate increases as the time of reinforcement approaches. Figure 3 shows a sample of the cumulative response record obtained during a stable discrimination performance (average rates for this session appear in Fig. 1, bars *G* and *H*). The average rate of responding during the fourth hour of training on the discrimination procedure was 22 responses per minute in S_1, and three responses per minute in S_2; the modal rate of responding in S_2 was zero.

HARLAN LANE
Psychology Department, Harvard University, Cambridge, Massachusetts

References and Notes

1. Some anecdotal information has been available, however. See, for example, O. H. Mowrer, *Learning Theory and Personality Dynamics* (Ronald Press, New York, 1950), pp. 688–726.
2. Although the respondent-operant distinction is a behavioral one, it overlaps considerably with the distinction, in physiological terms, between autonomic and skeletal responses.
3. Skinner has suggested that "vocal behavior below the human level is especially refractory" to operant conditioning: B. F. Skinner, *Verbal Behavior* (Appleton-Century-Crofts, New York, 1957).
4. This research was supported in part by a grant from the National Science Foundation, and was carried out during the tenure of a predoctoral fellowship from the National Institute of Mental Health, U.S. Public Health Service.
5. The chicks were 5 weeks old at the start of this research. After 5 months there was a marked change in topography and decline in rate of chirping in the home cage and the experiments were discontinued. Because the chicks were growing during this 5-month interval, continued maintenance of 80 percent of their ad libitum body weight, as initially determined, would have resulted in starvation. Therefore, every month the birds were given free access to food in their home cage for 2 days and a revised "running weight" was computed.
6. Wirthmore Feeds, Inc., kindly contributed the chick starter for these experiments.
7. C. B. Ferster and B. F. Skinner, *Schedules of Reinforcement* (Appleton-Century-Crofts, New York, 1957).
8. W. K. Estes, *J. Comp. and Physiol. Psychol.* **42**, 286 (1949).

9 February 1960

Descending Projections to Spinal Motor and Sensory Cell Groups in the Monkey: Cortex versus Subcortex

Abstract. In rhesus monkeys, corticospinal fibers have been found to terminate in motor, sensory, and internuncial cell groups. The present study reveals that the subcorticospinal fibers terminate primarily on internuncial neurons. Possible mechanisms involved in transmission of cortical and subcortical influences on motor and sensory cell groups are discussed.

Previous neuroanatomical studies in the rhesus monkey (*1*) revealed that pre- and postcentral corticobulbar and corticospinal projections terminate in motor, internuncial, and sensory cell groups (Fig. 1*A*). The motor and internuncial cell groups receive precentral fibers primarily. The sensory cell groups of the spinal trigeminal complex and the spinal posterior horn receive postcentral fibers primarily, while the nuclei cuneatus and gracilis receive both pre- and postcentral fibers. The precentral fibers to motor and internuncial neurons subserve motor functions and in all likelihood represent "direct" and "indirect" corticomotoneuronal pathways (see *2*). The pre- and postcentral projections to the sensory nuclei, on the other hand, probably represent cortical sensory feedbacks. This hypothesis is supported by physiological demonstrations of a cortical influence on these sensory nuclei (*3*). Since the brain stem likewise influences the sensory nuclei (*3*, *4*), the cortical influence on these nuclei was first thought to be mediated through the reticular formation (*3*). However, in cats, a direct cortical pyramidal influence upon the nuclei cuneatus and gracilis (*5*) has been demonstrated physiologically, in striking agreement with the anatomical observations (*6*).

In view of the physiological findings of subcortical influences on sensory nuclei, subcorticospinal pathways were studied anatomically.

In nine rhesus monkeys, lesions were made in the medulla oblongata (level of hypoglossal nucleus). The sum of these lesions interrupted all the longitudinal bundles throughout the medullary *tegmentum*, leaving the pyramidal tract and its immediate vicinity untouched. The descending fiber degeneration was studied, by use of the Nauta-Gygax technique (*7*). As planned, this study revealed the terminal distribution of the descending fibers. Therefore, contrary to the classical approach, the descending fibers will be grouped strictly according to their termination. The origin of these fibers will be studied later.

Descending fibers were encountered throughout the tegmentum below the lesions. Among these fibers two types