of the upper line corresponds to the upward movement of the gaster; an upward direction corresponds to a downward movement of the gaster. Interruption or subdivision of chirps is clearly shown. The interruptions occurred somewhat more frequently and clearly on the upstroke than on the downstroke.

The sound spectrogram shows that the vibrations of greater intensity (indicated by the pattern darkness) occurred on the upstroke of the gaster. The sound spectrogram also shows the frequencies of the vibrations, and it reveals higher frequencies on the upward stroke. There was a slight lag between the movement of the gaster and the response of the photocell. This is not a serious drawback as the line of the sound spectrogram indicating a single frequency is broad, so precise measurements are not possible.

Another light-sensitive device was used with a dual-beam oscilloscope to provide a more instantaneous response (*5*). By connecting the positive terminal of the solar cell (International Rectifier S1M) to the base of a PNP transistor (GE 2N1144), an increase in light increased resistance from collector to emitter. A 50-kilo-ohm potentiometer controlled the collector-to-base bias, and thus the operating point. The result was a much faster rise-and-fall time than the CdS cell had, and the action reversed. Increased light intensity increased resistance.

The collector-to-emitter resistance was set at 1500 ohm by adjusting the collector-to-base bias potentiometer in total darkness. A Heath VOM (volt-ohm-milliammeter) Model EUW-26 was used for the measurement, and it was left connected to serve as a power supply and series resistance. The collector was connected to the negative terminal of the VOM and to the oscilloscope input. The emitter was connected to the positive VOM terminal and to the oscilloscope ground. The oscilloscope was set at a-c mode, since that setting provided adequate frequency response and eliminated the need for another power supply to provide a bucking voltage.

With the device operating, I attached a worker ant by a slotted plastic strip to a magnetic transducer (*5*) attached directly to a low-noise transistor preamplifier, so that the 0.5-mm beam of light passed across the dorsal surface of the ant's gaster and struck the solar cell. That magnetic transducer-preamplifier combination had an RCA 2N220 transistor to provide about 200 to 500 mv of signal output from a stridulating worker to connect to the upper beam of the oscilloscope, thus reducing the pickup of a-c hum to a minimum. On the oscilloscope screen, any movement of the abdomen was simultaneously shown with the stridulation produced, and the deflection of the lower beam was positively correlated with the up-and-down movements of the gaster. When a chirp was interrupted (Fig. 2), the lower beam showed that the movement of the gaster was not smooth at these points, but actually stopped for the intervals indicated by horizontal movement of the lower beam. Sometimes, on upstrokes the lower beam not only stopped traveling upward but moved slightly downward.

It is evident that vibrations produced by a stridulating ant have several previously unreported features. First, the alternation of high- and low-intensity chirps corresponds to the up-and-down motions of the gaster. Although the ratio between them was only about 3 db—a small difference to the human ear—such a change in intensity might be significant to the vibration receptors of an ant. Second, the high-intensity chirps also include higher frequencies as shown on sound spectrograms; but it is not known whether they are within the range of frequencies detected by the ants. Third, each chirp may be subdivided into pulses, and pauses between the pulses frequently are as great as those between chirps. The staccato reiteration has a pulse repetition rate about four times the rate of 8 to 10 chirps per second or 32 to 40 pulses per second. Since the stridulating ant can control the separation of pulses by the moving of its gaster, it may thus produce stridulations for different messages or functions. The pulse frequency of about 40 per second should be transmitted much farther in soil than the higher frequencies of 1 to 4 khz are, and thus may be detected by the ants more easily than noninterrupted chirps are (*7*).

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Brain Lesions in Birds: Effects on Discrimination Acquisition and Reversal

Abstract. *Bobwhite quail* (Colinus virginianus) *with lesions of the cortex and the dorsal portion of the hyperstriatum (or "wulst") showed a considerable deficit in ability to reverse a learned discrimination between horizontal and vertical stripes. Two birds that had been run on 25 such reversals before ablation showed the same result. Lesioned birds did not, however, differ from controls in the original acquisition of the discrimination. Analysis of performance indicated that the reversal deficit was not due to difficulties in discrimination, interference with motor ability, or lack of motivation. The deficit appeared to be based on perseveration of response to the previous positive stimulus during reversal training.*

No function has as yet been established for the area classified as "cortex" in birds. Rogers (*1*), for example, found that no voluntary motor responses could be elicited by electrical stimulation anywhere in the cortex of the pigeon, nor did he observe differences in general behavior after their cortexes were completely extirpated. Tuge and Shima (*2*) found that cortical ablations had no effect on the establishment of defensive conditioned reflexes in pigeons, and Zeigler (*3*), also working with pigeons, reported no effect of partial cortical lesions on discrimination learning. Further, on purely comparative anatomical grounds, Cobb (*4*) concluded that there was, if anything, an inverse relationship between size of cortex and intelligence in different orders of birds.

The hyperstriatum, a complex area of the avian telencephalon which is part of a great elaboration (as compared with reptiles and mammals) of the corpus striatum in birds (*5*), is now being studied. Zeigler (*3*) found that massive hyperstriate destruction (combined in all cases with partial corticoid lesions) produced marked deficits in visual discrimination learning and retention in pigeons. His data did not permit a detailed analysis of the nature of the deficit in performance, but it was not due to gross visual disturbance, as he reported no apparent deficits in accuracy of pecking. Shima (*6*) showed that depression induced by application of KCl to the hyperstriatum abolished a learned key-pecking response in the pigeon. The response then returned as the bird recovered from the depression.

We used a more "sensitive" behavioral task than had been used previously, and the lesions were limited to only one portion of the rather large and complexly differentiated hyperstriate area. This portion is the dorsal region, the *hyperstriatum accessorum* and the *hyperstriatum dorsale*, which forms a distinct saggital elevation on the surface of the hemispheres which is often referred to as "wulst." The task used was discrimination followed by multiple successive reversals of the discrimination. Performance on reversals of the discrimination may reflect a qualitatively different process than that reflected by performance during the acquisition of a discrimination (*7*).

The subjects were eight adult male Bobwhite quail from the Georgia Quail Farm in Savannah. The apparatus consisted of a modified Skinner box with a food cup mounted at the base of one wall. Centered above the food cup, at birds' eye level, were two windows 3.8 by 3.8 cm through which the stimuli were projected. A Grason-Stadler visual display projector was mounted in each window behind a Lehigh Valley pecking key of transparent plexiglass. The feeding apparatus was a hollow copper tube which allowed a supply of food to fall from a funnel to the food cup when a solenoid switch was operated.

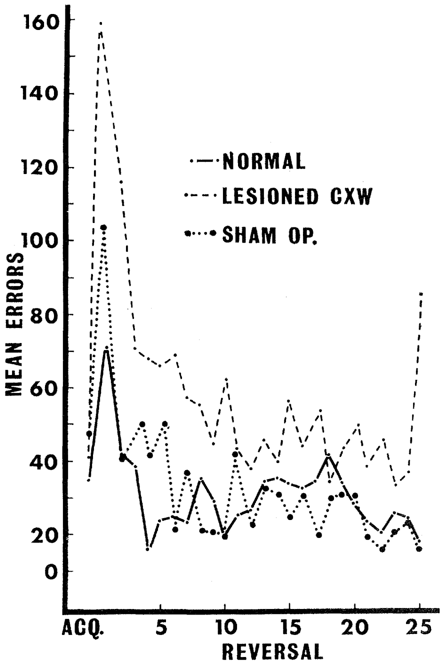

Fig. 1. Mean errors to criterion for acquisition of a response and for each of 25 successive reversals of the response.

Each stimulus was a set of three white stripes on a black field; one set was horizontal, the other vertical. Both horizontal and vertical sets appeared at each simultaneous presentation in random spatial arrangement. The apparatus automatically: (i) presented stimuli in different positions with a random arrangement of intertrial intervals of 60, 90, and 120 seconds; (ii) terminated the presentation of stimuli after all responses; (iii) reinforced each correct response with 0.2 g of food; and (iv) recorded on an Esterline-Angus multiple-event recorder the onset, duration, and termination of stimuli, and noted the occurrence and correctness of each response and each intertrial peck.

After a period of adaptation to apparatus and adjustment to a limited feeding schedule of 15 g per day of Purina game bird chow, training began. Each daily training session was 2 hours long; a maximum number of 83 stimuli were presented in each session. There were less if the bird was unresponsive, since the apparatus was programed to project the stimuli until the bird pecked the key. At the end of each training session, the bird returned through a guillotine door to his home cage, adjacent to the testing box, and received the difference between the amount of food earned during the training session and 15 g.

In acquisition training, half the subjects were trained to respond to the horizontal stripes, while the other half were reinforced for pecks in response to the vertical. When a bird had reached the criterion of three successive training sessions at 90 percent correct choice or better, the next session was a reversed aquisition condition. For example, if horizontal was positive in acquisition training, vertical became positive in the first reversal training session. The criterion for successful learning in reversal training sessions was 16 or more correct responses in the last 20 of each session. The training day after the one in which the subject met this criterion, another reversal training session was programmed. Thus, if a bird met criterion on day 6 when horizontal was positive, on day 7 vertical was positive. This procedure was continued until 25 reversal training sessions had been run for each bird.

The birds were divided into three groups. Group N was a normal control group of four birds not operated on in any way. Group CXW was a group in which the intended lesion was complete bilateral removal of "wulst" and cortical tissue. It consisted of two birds, lesioned before any training, and two of the normal birds, who had been given 25 reversal training sessions before being operated on. Two sham-operated birds were also studied. These birds had not been used in any experiments before the operations.

The birds were lesioned by the aspiration method with a 0.06-cm glass cannula. The anaesthetic was 0.8 ml of *Sedax* injected into the body cavity; ether was also used as necessary. After surgery, the birds were placed in isolated living quarters and allowed a minimum of 10 days after the operation before training was begun.

At the end of training, the birds were killed, the brains were cross-sectioned at 50 μ, and stained with Cresyl fast violet, and the locus and extent of the lesions were reconstructed.

Mean errors to criterion for acquisition training and for each of the 25 reversals of the response are shown in Fig. 1. There is little indication of any difference in performance between the normal and sham-operated birds. For the CXW group, however, there was a marked deficit in reversal performance, but there was no deficit in acquisition performance. A repeated measures analysis of variance over blocks of five reversals indicated that the CXW birds differed significantly ($F = 6.18$, df 1, 7, $P < .05$) from the controls. There was also an overall significant decrease in number of errors across blocks ($F =$ 10.94, $P < .01$) and a significant interaction of the blocks and the lesions ($F = 5.58$, $P < .01$). This interaction is clearly reflected in the improvement of the CXW birds after the reversal training; this improvement decreased the difference between the results of the CXW birds and those of the controls.

Mean error scores for each individual bird showed complete separation of the CXW and normal birds in the first five reversals and minimal overlap over the whole series. Every lesioned bird showed a deficit in reversal training. This deficit was not a deficit in ability to discriminate between stimuli, nor was there any deficit indicated in frequency or latency of pecking. Examination of the individual performance records clearly indicated that the lesions produced marked perseveration of response to the previously correct stimulus when reinforcement contingencies were reversed. CXW birds responded consistently below chance for extended periods at the beginning of each reversal training session, frequently doing so for more than 100 trials in succession. By the second reversal training session, all normal birds had eliminated such extended perseverative runs, but the lesioned birds had not. The performance of the CXW birds that were trained before the operation indicated that there were no savings from their previous extensive training; indeed, their performance showed "negative savings," as it was considerably poorer the second time—as poor as

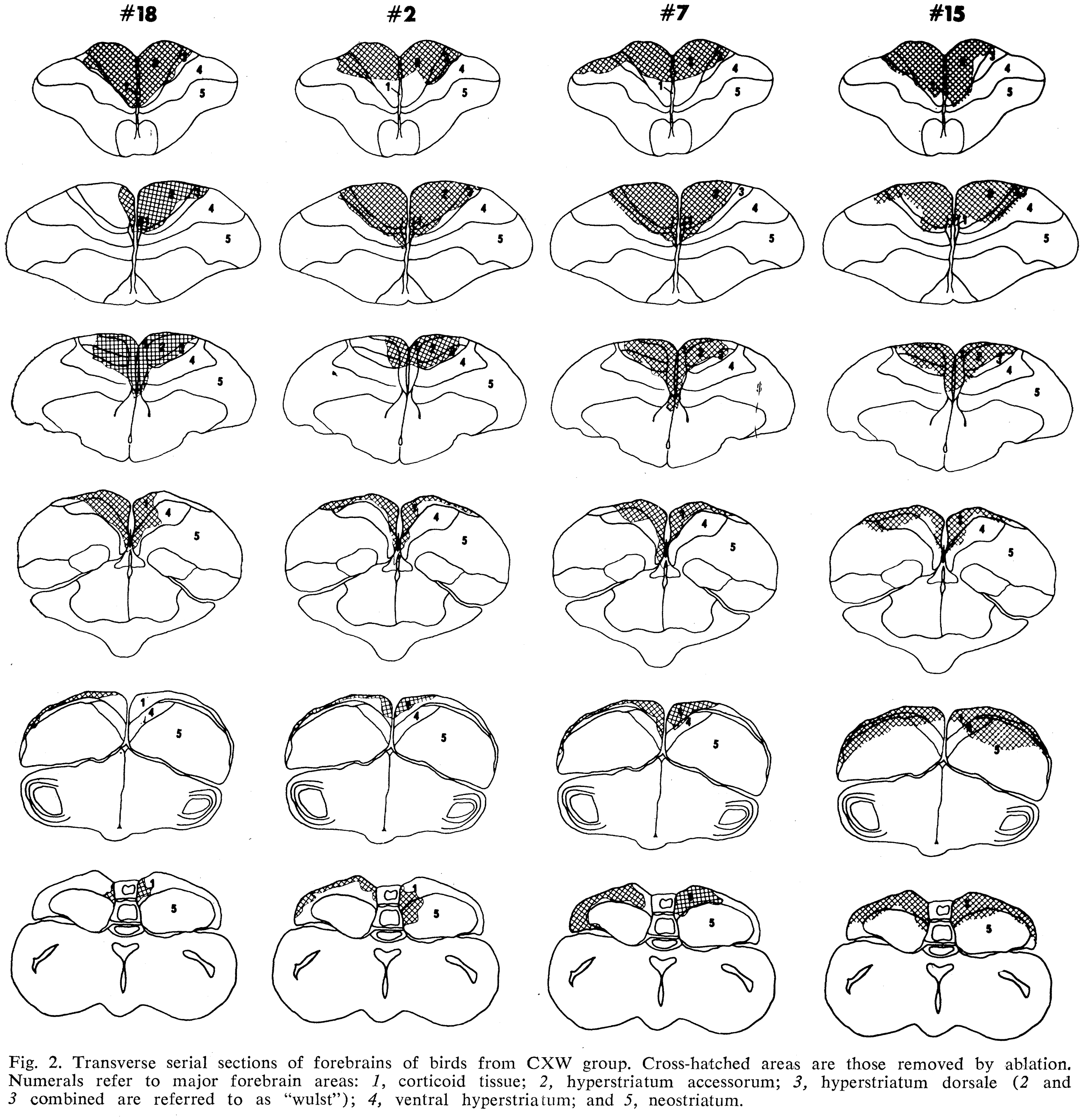

Fig. 2. Transverse serial sections of forebrains of birds from CXW group. Cross-hatched areas are those removed by ablation. Numerals refer to major forebrain areas: *1*, corticoid tissue; *2*, hyperstriatum accessorum; *3*, hyperstriatum dorsale (*2* and *3* combined are referred to as "wulst"); *4*, ventral hyperstriatum; and *5*, neostriatum.

that of the lesioned birds that had not been trained.

The CXW birds improved as the reversal training continued. Two birds (Nos. 2 and 18) equalled the performance by the control by the tenth reversal training session and thereafter, whereas the other two were still inferior down to the 25th reversal training. Since one each of the pair of birds in each subset was pretrained and one was not, the differences must be either attributed to individual variability or attributed to differences in the lesions actually produced.

The extent of the lesions actually produced in the CXW group are indicated in Fig. 2. Six serial transverse sections are shown for each bird; these sections were drawn from tracings of enlarged photomicrographs upon which the extent of the lesion has been indicated by cross-hatching. There has been massive bilateral damage to the cortex and wulst in all of these birds. Other areas were minimally damaged. Little wulst was spared in any of the birds, but the extent of cortical destruction in the caudal pole varies considerably. Bird No. 18 retained the most cortex with the caudal portion largely untouched; bird No. 2 retained more than half of the cortical tissue in this area, and birds Nos. 7 and 15 lost almost all of the cortex. Since birds Nos. 2 and 18 were the better performers in that they reached control levels by the 10th reversal training session, there is at least some ground for speculating that difference between the "temporary" and "permanent" deficits in performance was related to the extent of cortical damage. Thus we have some behavioral evidence suggesting that the cortex plays a functional role in birds.

The effects produced by the cortex-wulst lesions represent some form of restricted learning deficit free from sensory, motor, or motivational artifacts. Not only the lack of deficit in acquisition, but the fact that the operated birds consistently and persistently responded to the wrong stimulus during the early stages of each reversal training session is evidence that they did not lack ability to discriminate the stimuli nor lack motivation. Further, the effect on reversal of the response but not on acquisition of it supports the notion, expounded by Bitterman (*7*) on the basis of comparative behavioral data, that ability to acquire a response and ability to reverse it reflect qualitatively different processes.

Zeigler (*8*) found that in pigeons wulst lesions also produced a reversal deficit, but they did not produce a deficit in acquisition of a visual discrimination. The effect of ablation in this area on reversal but not on discrimination learning per se appears to be a valid and repeatable phenomenon, found across species and variations in training procedures. The avian cortex-wulst region appears to be a well localized, anatomically distinct, relatively pure integrative area over which we can range with lesions of varying extent and locus apparently without producing serious motor, sensory, or motivational deficits. This fact, plus the opportunity for comparing avian hyperstriatal structure and function with mammalian cortical structure and function, suggests that the avian brain might be a fruitful locus for learning more about the neural bases of learning.

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Prenatal Auditory Imprinting in Chickens

Abstract. *A batch of eggs was exposed to a patterned sound continuously from day 12 to day 18 of incubation, while a control group was hatched in the quiet. In a postnatal test all chicks tended to creep toward a stationary sound source, but the experimental group showed a preference for the sound heard during incubation. In a second test the experimental chicks followed a moving model longer when it emitted the familiar sound than when it emitted a novel sound or no sound at all.*

Although the imprinting process has been known for over 60 years, its auditory aspects have received only recent attention. A young animal is usually exposed to some parental substitute shortly after birth and then later tested for recognition of the tone and following responses toward the substitute. Gottlieb (*1*) found the recognition and following to be enhanced by the addition of sound to the model, but this may not involve true auditory imprinting since the sound could have served only to call visual attention to the substitute. Others (*2*) have found evidence for immediate prenatal auditory sensitivity in chicks, as well as for later postnatal discriminative capacity, but it has left open the question whether prenatal stimulation can be the basis of postnatal behavior. We investigated the possibility that prenatal auditory stimulation might contribute to immediate postnatal recognition and attraction through a process of auditory imprinting.

The auditory system in embryonic birds develops quite early; by about day 4 the brain is already sufficiently developed that the acoustic ganglia and nerves are clearly discernible (*3*). However, structural development does not imply functional development. To determine the earliest stage at which there is direct evidence for auditory sensitivity, a batch of chicken eggs was incubated and one was examined each day from day 4 to day 18. The embryo (or fetus) was removed from the sac and exposed to bursts of 1000-hz tone at approximately 85 db. The first observable movement and twitching occurred on day 12 and was obtained consistently thereafter.

Two groups of domestic White Rock chicken (*Gallus gallus*) eggs were incubated. The experimental group ($n = 15$) was exposed prenatally to a patterned sound, while the control group ($n = 20$) was raised in a quiet, sound-attenuated incubator. Within 6 hours after they had hatched, every chick in both groups was tested for recognition and responsiveness to two stimuli: the tone pattern presented prenatally to the experimental group, and a novel test sound. The experimental sound was a series of 1-second beeps of 200-hz tone separated by 1 second of quiet. The novel stimulus was the same pattern of 2000-hz beeps. For the experimental group the sound was approximately 85 db at the shelf on which the eggs rested and was presented from day 12 to day 18. Day 12 was the earliest at which we found evidence for auditory sensitivity, and the sound was stopped on day 18 to avoid any possibility of its presence during the para- or postnatal periods.

Testing was done on a circular table 90 cm in diameter. Concentric circles