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.

LAURENCE J. STETTNER
WILLIAM J. SCHULTZ

Department of Psychology,
Wayne State University,
Detroit, Michigan 48202

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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

Table 1. Average distance that the chicks moved toward a stationary sound source. In the experimental group one chick did not respond under either stimulus; in the control group, four did not respond to the 200-hz stimulus and four (two of them nonresponders under the first stimulus) did not respond to the 2000-hz stimulus. The averages, however, were computed for the total number of chicks tested.

Group	Number tested	Distance (cm) moved when stimulus:	
		200 hz	2000 hz
Experimental	15	25.22	11.84
Control	20	13.72	13.46

were painted on the table beginning at the center and extending for 60 cm; these circles facilitated measurement of the chicks' movement from the center. On the remaining 15-cm periphery two small speakers were mounted at angles of 0° and 180°. Shortly after it hatched, each chick was placed in the center of the test board, and either the experimental or novel sound was turned on for 45 seconds. Only one speaker was active at a time. At the end of 45 seconds the distance the chick had moved toward the speaker was measured, the chick was returned to center, and the other tone was given. The order of presentation of the two sounds and the order of use of the two speakers were counterbalanced. The sound was approximately 65 db at the center of the table. The results are given in Table 1.

The difference between the distances moved in response to the two test tones in the imprinted group is highly significant ($t = 3.37$, 14 df, $P < .01$). There is no appreciable difference between the responses of the control group to the two frequencies. Although both sounds were clearly attractive, the chicks responded differentially to a sound presented during the prenatal period.

In a second experiment chicks in the experimental group were tested for following behavior. At the end of the discrimination test each chick was returned to the center of the table and a child's pull-toy model chicken was moved in front of it by hand from one edge of the table to the other at a rate of about 1.2 m/min. Every chick was tested under each of three conditions: two passes with the model quiet, two passes with a small speaker on its back emitting the novel sound, and two passes emitting the experimental sound. The order of presentation of the conditions was counterbalanced from chick to chick. When the model reached the edge of the table, the trial was terminated. The chick was considered to be following as long as it was within 10 cm of the model. The average amount of time that the chick spent following the model out of a maximum of about 30 seconds was: no sound, 5.35 seconds, novel sound, 10.07 seconds, and experimental sound, 15.21 seconds. An analysis of variance of these scores showed a significant difference ($F=10.15$, 2/26 df, $P < .005$). The 5 percent least significant difference between the means is 4.71, indicating that each of the three conditions differs significantly from the others.

Newly hatched chicks seem to find any sound attractive, but a sound heard during the prenatal period proved more attractive than a novel one in two tests. In the second test the imprinted chicks even occasionally tried to jump on the toy model to get to the speaker. The results of these tests do not seem attributable to a natural preference for lower-frequency stimulation, since chicks in the control group found both the 200-hz and 2000-hz patterns equally attractive. Thus, young chicks are able to respond differentially to a sound heard prenatally. One possible explanation of the results of the following test could be that the sound merely called attention to the model, so that the following was primarily a response to a visual form. But since the model was passed directly in front of the chick several times it is unlikely that the chick could not see it. These studies indicate that the auditory system functions considerably prior to hatching, and perhaps more important, that auditory events during the prenatal period can influence immediate postnatal preferences and behavior. To the extent that the term "imprinting" implies the ability to use this earlier exposure to stimuli as a basis for later behavior such as recognition, attraction, or following, we believe that the experiment demonstrated prenatal auditory imprinting.

J. BROWN GRIER
Department of Psychology,
Northern Illinois University, DeKalb
S. ALLEN COUNTER
WILLIAM M. SHEARER
Department of Speech,
Northern Illinois University, DeKalb

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Brain Monoamine Oxidase in Mice after Exposure to Aggression and Defeat

Abstract. *Effects on the monoamine oxidase activity of the hypothalamus, amygdala, and frontal cortex of untrained mice exposed to repeated defeat by trained fighters for two 5-minute periods a day for 0, 1, 2, 4, 8, 14, or 20 days were studied. Activity in the hypothalamus increased significantly during the first 2 days of fighting, while the activity in the amygdala and frontal cortex remained essentially unchanged. After 8 days, activity in all three brain areas declined. After 14 days of fighting the monoamine oxidase activity returned to normal, but another decrease was observed in the three areas after 20 days of fighting.*

Changes in the concentration of serotonin in the brain directly affect behavior (*1*). Norepinephrine is also directly involved with behavior (*2*). In addition, norepinephrine is related to the behavioral alterations observed when an animal is attacking or being attacked (*3*). Both serotonin and norepinephrine are involved in the learning ability of mice (*4*). These observations were made after the concentrations of amine in the brain were changed by the administration of drugs or by electrical stimulation of the brain. No experiments, however, have been reported which show the effects of the manipulation of behavior on concentrations of amine in the brain.

Before the role of serotonin and norepinephrine in behavior can be clarified, it is necessary to study the enzyme systems involved in their metabolism. We studied monoamine oxidase, the enzyme that is responsible for the eventual oxidative deamination of monoamines, to determine the effect on this enzyme of repeated exposure to fighting aggression in mice. Mono-