THE EFFECT OF EARLY PARTIAL DECORTICATION ON VISUAL AND AUDITORY CONDITIONED REFLEXES IN CHICKENS

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The possibibility of complete functional,and even morphological,restoration of portions of the cortex removed at an early age from dogs and cats [5, 3, 8] raises the problem of to what extent the same process may take place in animals in which the brain is less highly organized than in mammals. Birds are an interesting group to study.

The cerebral cortex of birds consists chiefly of the well developed corpus striatum. The cerebral cortex is very poorly developed, and represented only by its evolutionarily old portions and occupies a small strip covering the corpus striatum. Numerous experiments with complete excision of the cerebral hemispheres in adult birds have shown that the animals lose the power of detailed perception of the surroundings [1, 2, 4, 9, 10]. However, if only the cortical layer is removed, leaving the corpus striatum on both sides intact, then pigeons retain previously elaborated conditioned reflexes [2].

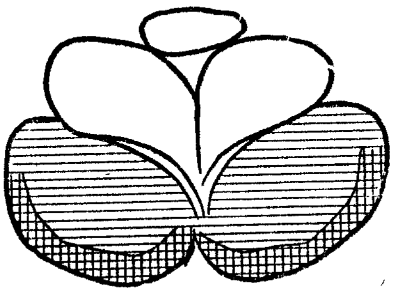

Fig. 1. Diagram of portions of cerebral cortex removed. Frontal section at boundary of middle and hind thirds; region removed in the first group shown by horizontal shading, that in the second group by vertical shading.

The present work has been carried out to investigate the possibility of restoration of the visual and auditory systems, and also to what extent morphological regeneration of the removed portions of the hemispheres may take place in young chickens.

METHOD

The experiments were carried out on "Russian White" chicks aged 6-12 days. The animals were divided into two groups. In the first group consisting of 17 birds, the posterior halves of the cerebral hemispheres, including the cortical rudiments in this region and part of the corpora striata, were removed through holes trephined on both sides of the skull. In the second group consisting of 6 birds, only the cortical rudiments lying in the superficial portion of the hemisphere over the ventricles were removed (Fig. 1). In addition, the same operations were carried out on 5 adult birds.

After 3-4 months from the time of operation, the conditioned reflexes in 28 of the operated and 14 of the control birds were studied. Conditioned reflexes were established to the opening of the feeding trough, to the light stimulus from a 75 watt 120 volt lamp, and to 500 c/s sound stimulation from a generator, all these stimuli being reinforced by feeding.

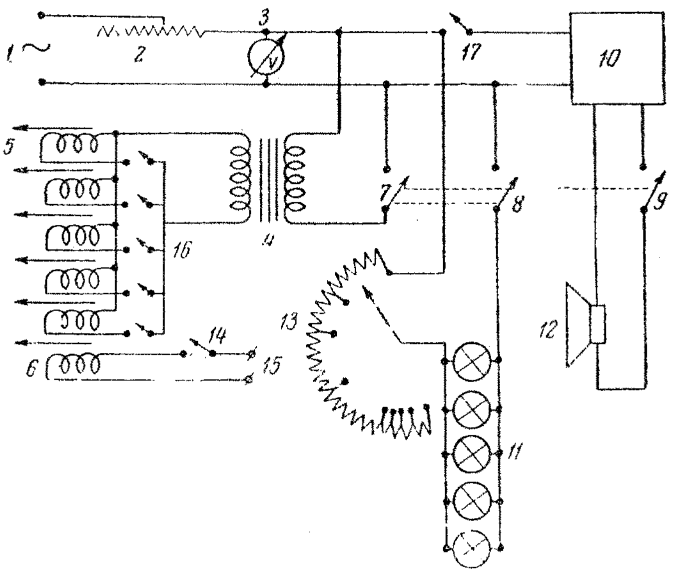

Fig. 2. Diagram of the apparatus for studying visual and auditory reflexes in chicks. 1) Main supply, 2) rheostat , 3) voltmeter, 4) step-down transformer, 5) time marker, 6) time marker, 7) common switch for markers, 8) switch for light signal, 9) switch for sound stimulation, 10) sound generator, 11) light signal lamps, 12) loudspeaker, 13) rheostat for controlling light intensity, 14) switch for time marker, 15) source of current pulses for time marker, 16) contacts of lid feeding trough, 17) switch for sound generator.

TABLE 1

Figures Showing the Formation of Conditioned Reflexes in Control and Experimental Chicks with Excised Posterior Halves of the Cerebral Hemispheres.

Indication of formation of conditioned reflexes	Kind of conditioned reflexes			
	visual		auditory	
	experiment	control	experiment	control
Number of coincidences before the first appearance of the conditioned reflex	2.4	3.9	5.5	1.5
Number of coincidences before consolidation of the reflex	11.4	8.2	6.8	2.3
Stability of the conditioned reflex (% of total number of tests to which positive responses was obtained)	70.7%	80.6%	69.9%	86.4%
Regularity of the conditioned reflex (maximal number of successive positive responses)	12.6	17.0	10.7	15.4
Latent period of the conditioned reflex (in seconds)	5.5	3.0	4.8	2.8

The experiments were carried out in 5 compartments with identical conditioned stimulation (Fig. 2). Simultaneous recordings with inkwriters were made of the application of the light or sound stimuli (conditioned stimuli) and of the opening of the lid of the feeding trough by the birds (conditioned reflex).

TABLE 2

Figures Showing the Development of Differentiations in Control and Experimental Chicks in Whichthe Posterior Portions of the Cerebral Hemispheres were Removed

Differentiated stimuli		Indication of formation of conditioned reflexes (differentiations)	Kind of conditioned reflexes (differentiations)			
			visual		auditory	
light (direct voltage applied to lamp)	sound (frequency in cps		experiment	control	experiment	control
127—60	500—3000	Number of coincidences before the development of a stable differentiation	25.5	16.9	8.4	5.4
		Stability of the differentiations effected (in %)	71.3	76.8	71.2	83.3
		Regularity (maximal number of successive differentiations carried out)	6.5	8.5	6.8	10.9
127—80	500—2000	Number of coincidences before the development of a stable differentiation	4.4	6.6	3.0	2.4
		Stability of the differentiations effected (in %)	67.5	85.0	85.0	86.0
		Regularity (maximal number of successive differentiations carried out)	5.2	7.9	5.9	6.8
127—90	500—1500	Number of coincidences before the development of a stable differentiation	6.5	7.8	1.1	2.3
		Stability of the differentiations effected (in %)	68.8	84.1	66.9	81.9
		Regularity (maximal number of successive differentiations carried out)	4.9	6.5	5.1	7.5
127—100	500—1000	Number of coincidences before the development of a stable differentiation	4.2	8.0	2.1	3.6
		Stability of the differentiations effected (in %)	72.0	81.1	71.9	82.3
		Regularity (maximal number of successive differentiations carried out)	5.0	6.7	5.0	7.1
127—115	500—900	Number of coincidences before the development of a stable differentiation	4.3	4.8	2.5	3.0
		Stability of the differentiations effected (in %)	65.4	82.9	71.0	84.5
		Regularity (maximal number of successive differentiations carried out)	3.8	5.0	3.8	7.1
127—115	500—800	Number of coincidences before the development of a stable differentiation	2.7	6.2	2.2	2.5
		Stability of the differentiations effected (in %)	79.6	81.2	84.1	89.1
		Regularity (maximal number of successive differentiations carried out)	4.5	6.4	5.3	7.0
127—117	500—700	Number of coincidences before the development of a stable differentiation	2.1	2.8	1.2	2.5
		Stability of the differentiations effected (in %)	74.1	83.5	81.9	81.6
		Regularity (maximal number of successive differentiations carried out)	6.9	5.9	6.7	7.3

TABLE 3

Figures Showing Formation of Conditioned Reflexes in Control and Experimental Chicks with Portions of the Hemispheres Removed

Indication of formation of conditioned reflexes (differentiations)	Kind of conditional reflexes			
	visual		auditory	
	experiment	control	experiment	control
Number of coincidences required before the first appearance of a conditioned reflex	—	3.9	1.3	1.5
Number of coincidences before stabilization of reflex	4.9	8.2	1.3	2.3
Stability of the conditioned reflex (positive responses as % of the total)	97.9	80.6	96	86.4
Regularity of the conditioned reflex (maximum number of successive positive responses)	19.2	17.0	16.9	15.4
Latent period of the conditioned reflex (in seconds)	1.9	3.0	2.0	2.8

Initially, for 2 days, all the chicks were taught to open the troughs and to obtain food from them in the illuminated compartment. After this an association was developed between light stimulation and feeding. After forming and consolidating the conditioned reflex until 10 successive positive reactions were obtained, we then proceeded to differentiate the reaction to changes in strength of the light signal (which was given at voltages of 60, 80, 90, 100, 110, 115, and 117 volts). Differentiation of the sound stimuli was made in terms of pitch, using frequencies of 3000, 2000, 1500, 1000, 900, 800, and 700 c/s. Thus, 7 light and 7 sound differentiations were made, beginning with the coarsest and ending with the finest.

At the end of the experiments in which the conditioned reflexes and their differentiation were established, the animals were killed and the brains examined.

RESULTS

Table 1 shows the average times for the formation of the conditioned reflexes, their stability, and consistency, as measured in experiments on the 10 control chicks and in all the operated animals in which the whole of the posterior half of the hemispheres was removed at an early age.

It can be seen from Table 1 that the number of coincidences required for the first manifestation of a conditioned reflex are quite different in the case of the visual and auditory stimuli. In all other tests, the experimental animals differ from the controls; they differ in the required reinforcement of the conditioned reflexes, their stability, regularity, and also in the latent period of the motor reactions. Thus, removal of the posterior halves of the cerebral hemispheres in chicks, carried out so as to include the cortex and part of the striatum, leads to some disturbance in the ability of the brains to form new pathways, a disability which is not compensated or restored as the animal develops.

Figures showing the development of differentiations, and their stability and consistency, are shown in Table 2.

It can be seen from Table 2 that in developing differentiations, apart from the first, the rate in the operated animals is not only not lower than in the controls, but may even be higher, though the reflex is less stable and less regular.

Thus, removal of brain substance including portions of the corpora striata causes a marked interference with the action of the visual and auditory stimuli. There is no recovery from this perceptual disturbance, even after long training.

TABLE 4

Figures Showing the Development of Differentiation in Animals with Portions of the Hemispheres Removed, as Compared with Controls

Differentiated stimuli		Quantities indicating formation of conditioned reflexes (differentiations)	Kind of conditioned reflexes (differentiations)			
			visual		auditory	
light (direct voltage applied to lamp)	Sound (tone in cps)		experiment	control	experiment	control
127—60	500—3000	Number of coincidences before the development of a stable differentiation	4.1	16.9	3.6	5.4
		Stability of the differentiations effected (in %)	78.8	76.8	83.2	83.3
		Regularity (maximal number of successive differentiations carried out)	5.0	8.5	4.9	10.9
127—80	500—2000	Number of coincidences before the development of a stable differentiation	2.4	6.6	3.4	2.4
		Stability of the differentiations effected (in %)	86.6	85.0	87.6	86.0
		Regularity (maximal number of successive diffferentiations carried out)	5.6	7.9	5.5	6.8
127—90	500—1500	Number of coincidences before the development of a stable differentiation	1.9	7.8	2.8	2.3
		Stability of the differentiations effected (in %)	90.0	84.1	87.3	81.9
		Regularity (maximal number of successive differentiations carried out)	5.1	6.5	5.0	7.5
127—100	500—1000	Number of coincidences before the development of a stable differentiation	4.8	8.0	3.1	3.1
		Stability of the differentiations effected (in %)	78.5	81.1	84.0	82.3
		Regularity (maximal number of successive differentiations carried out)	4.7	6.7	4.1	7.1
127—110	500—900	Number of coincidences before the development of a stable differentiation	4.1	4.8	2.9	3.0
		Stability of the differentiations effected (in %)	80.1	82.9	86.6	84.5
		Regularity (maximal number of successive differentiations carried out)	5.4	5.0	5.5	7.1

Table 3 shows the results of the average values of the formation, stability, and regularity of the conditioned reflexes developed in chickens in which the cortical rudiments were removed at an early age.

As can be seen from Table 3, the operated chicks perform every bit as well as the controls, and may even surpass them.

Table 4 shows the results of experiments in which a differentiation was made between light stimuli and between sound stimuli. At first large differences were used (127 and 80 volts applied to the lamp, and tones of 500 and 3000 c/s), after which the differentiation was refined.

TABLE 5

Measurement of Conditioned Reflex Activity in Chickens in Whom the Posterior Halves of the Hemispheres had been Removed when Fully Grown

Indication of formation of conditioned reflexes (differentiations)	Kind of conditioned reflexes			
	visual		auditory	
	before operation	after operation	before operation	after operation
Stability of the conditioned reflexes (as % of positive responses)	89.1 75,4 81.1	85.7 77.7 100	94.4 94.6 93.6	100 77.7 100
Stability of the differentiations (as % of total number of tests)	100 100 83.3	87.5 79.1 33.3	97.5 98.0 85.0	100 66.6 16.6
Latent periods of the conditioned reflexes (in seconds)	2.5 6.4 5.0	1.9 3.2 2.7	2.8 3.8 3.9	2.6 3.4 5.3

TABLE 6

Change in Conditioned Reflex Activity of Chickens in Whom the Cortical Structures had been Removed in the Adults

Indication of formation of conditioned reflexes (differentiations)	Kind of conditioned reflexes			
	visual		auditory	
	before operation	after operation	before operation	after operation
Stability of the conditioned reflexes (as % of positive responses)	83.5 89.3	54.0 100	69.0 94.1	47.2 100
Stability of the differentiations (as % of total tests)	100 100	100 100	93.7 68.7	100 100
Latent periods of conditioned reflexes (in seconds)	3.0 1.7	5,0 2.2	4.0 1.3	2.8 2.7

It can be seen that the operated animals perform as well as the controls, and in some cases even better. Thus, removal at an early age of the superficial portions of the hemispheres with their cortical rudiments causes no noticeable disturbance of conditioned reflex activity, such as occurs in the 8-12 month animals.

Removal of Portions of the Hemispheres in Adult Chickens

The experiments on these birds were arranged so that at first conditioned reflexes and differentiations were elaborated, after which portions of the hemispheres were extirpated. After recovering from the operation, tests were made of the state of the positive and differentiated conditioned reflexes.

In 3 adult birds, the posterior halves of the hemispheres including portions of the corpora striata had been removed. The results of the conditioned reflex study are shown in Table 5.

From Table 5 it can be seen that after the operation not only was there no reduction in the stability of the conditioned reflexes already elaborated, but that in most cases they became even more stable when the reflex was reinforced; there was a noticeable reduction in the latent period of the reactions. However, removal of the posterior portions of the hemispheres, including the corpora striata, caused a profound disturbance of the negative conditioned reflexes. This was shown by a marked reduction in the stability of previously elaborated differentiations.

The superficial layers of the hemispheres including the cortical rudiments were removed from 2 adult birds in whom conditioned reflexes and differentiations had been elaborated. The results obtained in these experiments are shown in Table 6, from which it can be seen that removal of the cortex caused a deterioration in one case and an improvement in the other of the stability of the positive conditioned reflexes. In most cases the latent periods were increased. However, the stability of the differentiations was not only not reduced by the operation, but, as can be seen from the example of the differentiated response to the auditory stimuli, it was actually increased. It is not possible to draw any further conclusions from the results on this group of adult operated birds, because of the scatter in the results and the small number of animals concerned.

As a result of these observations it was established that conditioned reflex activity was maintained in chickens in which the occipital portions of the cortex were removed at an early age, and that perceptual function was damaged in birds in which, in addition, there was damage to the corpora striata. This result confirms the importance of the corpora striata in forming circuits in a brain in which the cortex is phylogenetically immature [4, 6, 7]. It is not unexpected that the disturbance of the conditioned reflex activity is such that responses to positively conditioned stimuli are as a rule preserved, but there is a reduced ability to differentiate between stimuli. This may indicate that simple temporary connections may be formed in the portions of the corpora striata remaining, and that the whole striatal system (or, in any case, of its posterior portions) may participate in the more complex analytical acts.

Morphological studies of the brain of the operated animals showed that extirpation at an early age which includes the corpora striata in most cases causes irreversible damage, but that when only part of the occipital cortex is removed, no visible damage can be discerned after 6-7 months.

It has been shown that in mammals, regeneration of portions of the cerebral hemispheres removed at an early age may take place [3, 5, 8]; this occurs only in birds for the cortical region, and does not apply to the corpora striata which form the main mass of the cerebral hemispheres.

SUMMARY

Removal of the cerebral hemispheres, including the corpora striata, in young chicks has a marked effect on their subsequent conditioned reflex activity. The stability and regularity of the conditioned reflexes is reduced, and differentiation of the visual and of the auditory conditioned signals deteriorates. Removal of the rudimentary cortical areas in young chicks has little effect on their subsequent reflex activity, and does not affect accurate visual or auditory differentiation. Disturbances of visual and auditory analysis caused by injury to the corpora striata are found also in adult hens, but do not occur when only the rudimentary cortical areas are destroyed. Cortical areas removed from young chicks regenerate, while there is no recovery from damage to the corpora striata.

LITERATURE CITED

[1] B. I. Bayandurov, The Trophic Function of the Brain*. Medgiz, 1949.

[2] I. S. Beritov, Pflugers Arch., 1926, Bd. 213, S.370.

[3] N. N. Dzidzishvili, in book: Reports of the 2nd Trans-Caucasian Congress of Physiology, Biochemistry, and Pharmacology*. Izd. AN Georgian SSR. Tbilisi, 1956.

[4] A. I. Karamyan, The Evolutionary Function of the Cerebellum and Cerebral Hemispheres*. Moscow, 1956.

[5] A. B. Kogan and T. V. Ivannikova, Byull. éksptl. biol. i med., volume 39, No. 3, pp. 6-9 (1955).

*Original Russian pagination. See C. B. Translation.

[6] L. A. Milyutina, in book: Research Reports of the 2nd Moscow State Medical Institute* ,Moscow, 1958, p. 69.

[7] V. V. Petelina, in book: Problems of the Comparative Physiology of Higher Nervous Activity* , edited by D. Biryukov, Institute of Evolutionary Morphology, AMN SSSR, Leningrad, 1958.

[8] A. V. Polezhaev, A. I. Matveeva and N. A. Zakharova, Reports of the AN SSSR,* volume 113, p. 472 (1957).

[9] M. Schrader, Pflugers Arch., 1889, Bd. 240, S. 503.

[10] P. Flourens, Recherches expér. sur les fonctions du systeme nerveux. Paris, 1842.

* In Russian.