PHYSIOLOGY

THE ROLE OF THE CEREBRAL HEMISPHERES IN THE COMPENSATION OF MOTOR FUNCTIONS FOLLOWING BILATERAL HEMISECTION OF THE SPINAL CORD*

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I. M. Sechenov [7] demonstrated far-reaching changes in the reflexes of the lower extremities of the frog following transverse hemisection of the spinal cord. He assumed that under these conditions impulses may traverse the healthy portion of the spinal cord, from the muscles of the lower extremity to the cerebrum and vice versa by-passing the injured area.

In the dog, E. A. Asratyan [1, 2] found that restoration of disturbed static and motor functions resulting from various types of injuries of the spinal cord, peripheral motor or receptor organs or nerves could only take place in the presence of an intact cerebral cortex. Besides, it was shown in E. A. Asratyan's laboratory that in the pigeon more or less prompt and complete sensory-motor compensation took place following transverse hemisection in the thoracic, lumbar [6] and cervical [4] segments of the spinal cord, its prolonged insignificant teasing [8] or deafferentation of the lower extremity. Extirpation of both cerebral hemispheres caused a reversal to the status obtaining immediately following injury of the spinal cord. But in contrast to mammals the re-established functions in birds remained, to a significant degree, even following the extirpation of the cerebral hemispheres.

It was of interest to clarify the extent of restoration of motor functions following transverse bilateral section at various levels of the spinal cord and the role of the cerebrum.

These questions were studied in experiments on pigeons which underwent a one-stage hemisection of the cervical spine at the level of segment 7-8 and on the contralateral side in the region of segment 24. Reflex response to electrical and mechanical stimulation, the rheobase and chronaxie of motor nerves of the lower extremities were studied pre- and post-operatively, as was the degree of compensation of lost functions. Clinical observations were carried out on the extent of lost and restored motor functions. The cerebral hemispheres were removed following restoration of function in order to determine their role in the compensatory processes. The study was carried out on 11 pigeons.

The pigeons withstood the operation well. They could take food unaided 2-3 hours after operation. All pigeons sustained severe impairment of motor function. For 3 days the majority were lying on a side or could not assume a more or less definite posture. The wing on the side of the sectioned cervical cord was extended. The extended wing was often under the body and did not react to mechanical stimulation. The other wing responded to such stimulation by weak withdrawal. The leg on the side of the hemisected cervical cord reacted vigorously, while the one on the side of the hemisected lumbar cord responded very weakly.

*The experimental part was carried out at the suggestion and under the supervision of E. A. Asratyan in the division of physiology of the central nervous system of the V. M. Bechterev Institute for the Study of the Brain during 1939-1940.

In 14-15 days the birds assumed a definite lying posture; thus as a rule the leg on the side of the injured cervical segment 7-8 was stretched out unusually far to the front whereas the extremity on the side of the injured segment 24 remained stretched out to the rear (Fig. 1).

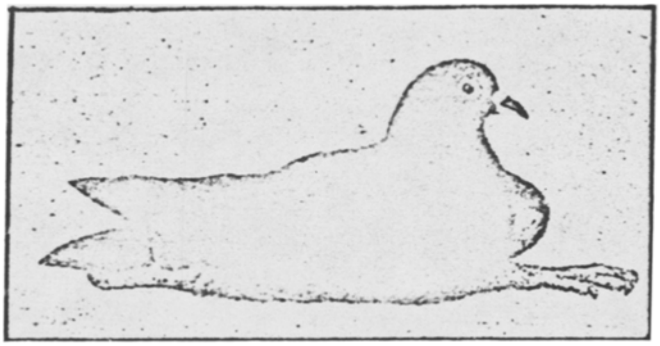

Fig. 1. Pigeon No. 10, 15 days after spinal cord operation. The leg on the side of the injured spinal cord segment 7-8 is stretched out forward while the leg on the side of the injured segment 24 remains to the rear. The left wing still remains extended.

Although after 18 days the pigeons remained lying, they attempted to move by flapping their wings against the floor. After 19-20 days the pigeons began to stand up unsteadily and even take 2-3 steps, raising the wings and swaying from side to side like birds after removal of the cerebellum. With that, the birds could raise the leg on the side of the lumbar hemisection considerably higher and step on it firmer than with the other leg. At the approach of the experimenter several birds took wing but fell flat immediately. All birds could bend forward with effort to peck seeds or drink water.

Two pigeons began to fly after 27 days with disproportionate motion of the wings. As a rule they landed on the floor but could not alight on a pole. Other pigeons regained these functions on the 29th to 30th days. After 30-33 days they were still unable to alight on a pole but were able to stand and walked with legs wide apart. This defect did not disappear after 5 months (Fig. 2). Subsequently the ability to fly was restored more or less satisfactorily; only 3 pigeons could not fly after 10 months, although when tossed up they did not fall flat as in the beginning but were able to sit down.

All pigeons showed vegetative disturbances (fall out of flight and small feathers, etc). With the passage of time (a month or more) these disturbances increased in severity; after $4^{1/2}$ to 5 months the small feathers returned to normal although the flight feathers were still absent.

Post-operative investigation of the motor nerves of the extremities showed an increase of $2\text{-}2^1/_2$ v in the rheobase bilaterally, but it was on an average 0.8 v higher on the side of the hemisection carried out in the neck. Subsequently the chronaxie of the motor nerve was found increased on the side of the hemisection in the lumbar region.

Later the rheobase of the motor nerve of the wing homolateral with the cervical hemisection was somewhat increased while that on the side of the lumbar hemisection diminished. The chronaxial changes were almost parallel to those of the rheobase.

During the first post-operative days mechanical stimulation elicited no reflex response on the side of the lumbar hemisection and only weak ones on the side of the cervical lesion. Reflexes reappeared, on an average, 17 days post-operatively and were normal after the 36th day. Reflex response was slow and incomplete where re-establishment of general motor function was retarded.* Under these circumstances the chronaxie returned to the pre-operative level, although the motor function remained impaired.

*With impaired nutrition or narcotic condition of the animal re-establishment of function was significantly delayed.

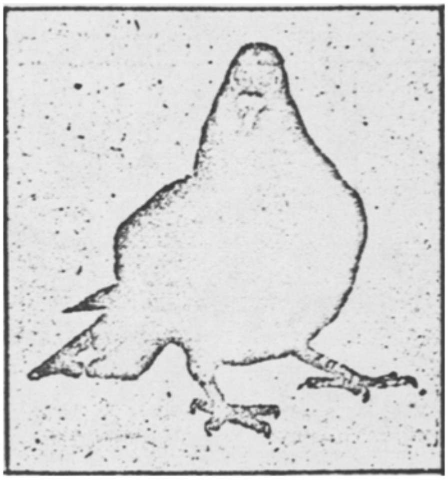

Fig. 2. Pigeon No. 10 five months after spinal cord operation. The bird stands with spread legs, body bent backward, wing with several feathers missing, turned contralaterally to lumbar hemisection.

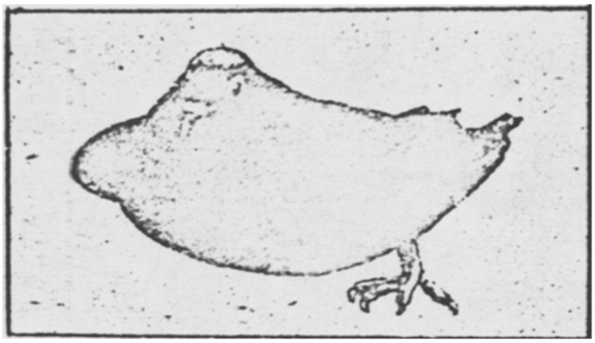

Fig. 3. Pigeon No. 10 five days after removal of the cerebral hemisphere contralateral to the lumbar spinal cord hemisection. The leg on this side is somewhat to the rear of the body, the wing on the other side lowered. This was the picture found following spinal section but with the position of the extremities reversed.

In 4 of 11 pigeons a two-stage removal of the cerebral hemispheres was carried out. As in the spinal cord section, following removal of one of the cerebral hemispheres the pigeons continued to lie on the side of the cervical cord section for 3-5 days, but the position of the extremities was the reverse of that noted following cord section (Figs. 1 and 3). Five to 9 days post-operatively the pigeons began to stand up with the legs widespread.

Walking with a wide defect was resumed after 9-10 days: in the beginning the homolateral leg of the cervical hemisection was raised and brought forward, hitting the floor strongly; the other leg was brought up passively (as seen in man in spinal caries or analogous to that noted in the dog by Pavlov following removal of the anterior portions of the cerebral hemispheres). Precisely thus did the pigeons walk following spinal operation, unilateral lower cervical cord section and the removal of the contralateral cerebral hemisphere.

Vegetative functions were damaged again, following removal of the cerebral hemispheres: thus there was a falling out of the small feathers (more intensive than after the spinal cord operation) and ulcerations appeared on the extremities. Locomotor function began to be restored 20-26 days after removal of one cerebral hemisphere, but disturbances in gait and vegetative functions persisted after 4-4½ months (Fig. 4).

Following removal of the remaining cerebral hemisphere the disturbances in locomotor and vegetative functions became intensified. During the first week the pigeons remained lying motionless. Their condition improved somewhat after 7-10 days when they attempted to stand up with the help of the wings, but having stood up they immediately fell on their heads. There was an increased falling out of the small feathers. After 11 days the birds often assumed the position shown in Fig. 5. The condition of the pigeons became worse daily and in spite of increased nutrition they began to lose weight. After 16 days they did not make any attempts at standing up and shifted from place to place in a lying position with the aid of wings.

After 45 days there was a greater weight loss and the birds swallowed poorly. There was no further improvment in compensatory functions (even after 5 months) and the birds succumbed.

Post-mortem showed that the striatal system was completely removed. No pathologic changes were noted where hemisection was carried out in the spinal cord.

One stage removal of the cerebral hemispheres was carried out in 5 pigeons. Experiments showed that in pigeons the motor functions lost following spinal cord hemisection were not secondarily re-established after a

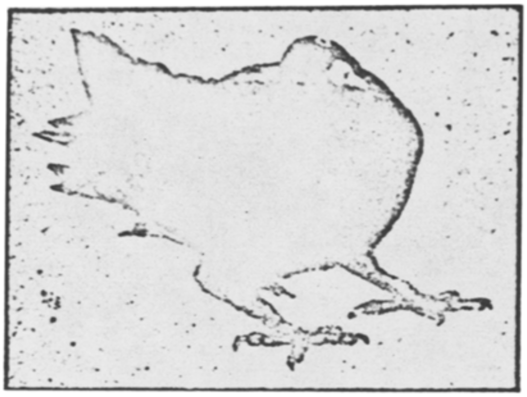

Fig. 4. Pigeon No. 10 four months after removal of one cerebral hemisphere. Several flight and small feathers are missing and the bird stands with spread legs, head inclined contralaterally to removed cerebral hemisphere.

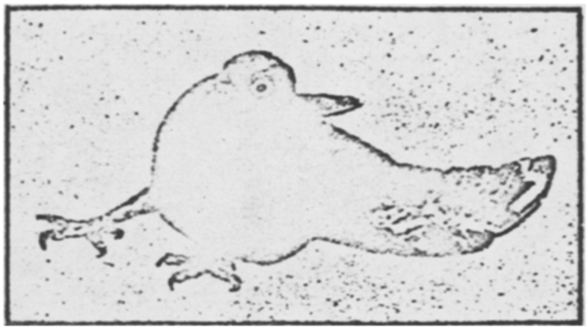

Fig. 5. Pigeon No. 10 eleven days after removal of the remaining hemisphere. The locomotor and vegetative disturbances noted in Fig. 4 are intensified.

one-stage removal of both cerebral hemispheres. A gradual worsening in the general condition and particularly an impairment in the vegetative functions, resulted in the death of two birds 25-28 days post-operatively, while the others lived for $5^{1}/_{2}$ months without showing any signs of re-establishment of motor functions.

Thus, removal of the forebrain brought forth a complete recurrence of defects of motor functions that were noted following spinal cord operation.

As is evident from the data given, bilateral hemisection at various levels of the spinal cord results in severe disturbances in motor and vegetative functions with subsequent significant restitution. Decompensation of motor functions occurs following two-stage removal of the forebrain with insignificant secondary re-establishment. More intensive impairment of the motor and vegetative functions occurred in pigeons subjected to a one-stage removal of the forebrain subsequent to a bilateral hemisection at various levels of the spinal cord. Under these conditions secondary compensation of function did not take place even after $5^{1}/_{2}$ months.

Thus, it is evident that the cerebral hemispheres play a significant role in the compensation of motor functions. Following bilateral hemisection in various regions of the spinal cord, a one-stage removal of the cerebral hemispheres, the central nervous system is not able to assure reflex-compensation of lost functions, while with the same operation but with insignificant prior damage to the spinal cord (transverse hemisection in one place in the thoracic or lumbar region [6], the cervical region [4], a transverse section through any lateral quarter of the cervical region [5] or prolonged insignificant teasing) significant secondary restitution of function follows. It may therefore be concluded that in the formation of compensatory reflex mechanism in birds, not only the forebrain participates (basically according to the conditioned-reflex principle), but also the lower parts of the central nervous system (reflex principle).

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