DISTURBANCE AND RESTORATION OF MOTOR FUNCTIONS IN DUCKS AFTER HEMISECTION OF THE SPINAL CORD

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The development of compensatory adaptations in birds after injury to the central nervous system has been studied mainly in pigeons [2-7]. It is, therefore, interesting to examine the adaptive phenomena in ducks, in which walking is the principal method of progression. We have investigated the character of the motor disturbances (standing and walking) and the extent to which they recover in ducks after hemisection of the spinal cord, and we have examined the importance of the prosencephalon in the development of the compensatory adaptations after this injury.

EXPERIMENTAL METHOD

Chronic experiments were carried out on 29 Peking ducks. Hemisection of the spinal cord was first carried out at the level of the 6th cervical vertebra, and in two subsequent stages the hemispheres of the prosencephalon were removed. Each subsequent operation was carried out after restoration of the disturbances of function due to the previous operation was as complete as possible.

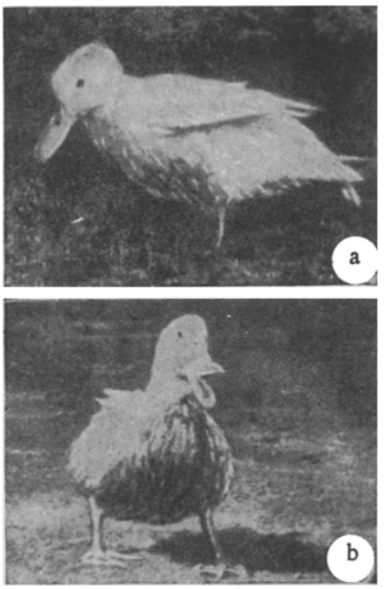
In every case the operations were performed under urethane anesthesia (1 g/kg body weight), the drug being injected intramuscularly. Pilot experiments on ducks showed that hemisection of the spinal cord caused death of the bird from respiratory arrest. We, therefore, used artificial respiration during the operation, starting it before natural breathing had ceased.

In order to assess the disturbances of posture and movement and the degree of recovery from them the birds were inspected and photographed, and the threshold of excitability of the flexor reflex to an induction current* and the skin temperature of the limbs were determined before and after the operation.

EXPERIMENTAL RESULTS

Hemisection of the spinal cord caused considerable disturbances of function in ducks. After the operation, on the side of the section the respiratory movements of the thorax ceased and the limbs were paralyzed. The wings were slightly depressed, especially on the side of hemisection, and the birds sat leaning towards the side of hemisection (Fig. 1, a). The threshold of excitability of the flexor reflex of the limb on the side of hemisection of the spinal cord was 1.0-2.5 cm higher than that of the opposite limb. The skin temperature of the ipsilateral limb was 1-4° higher than that of the contralateral. Compensation of these disturbances took place gradually. On the 3rd-4th day the ducks tried to stand on their legs, but succeeded in performing only haphazard movements which often caused them to turn over on to their backs. After about 1 week, the birds were able to stand with considerable difficulty, but the movements of the sound limb were much stronger and of a much wider range than the movements of the affected limb. On standing, most of the body weight was taken by the sound limb. The position of the wings was nearly normal. Some of the birds attempted to walk at this period after the operation, but sat down after taking 1 or 2 steps. All the ducks could swim well and quickly in a pond, but the side of the body corresponding to the hemisection sank deeper into the water. Two weeks after the operation most of the ducks could walk, leaning forward and towards the side of the affected limb. If their balance was impaired the ducks used their wings for support when walking. At this time the respiratory movements of the thorax were restored on the side of the hemisection. One month after the operation the

* The threshold of excitability of the flexor reflex was measured by the number of centimeters between the coils of a Dubois-Reymond induction apparatus (5000 turns, supplied by a 2V battery.)



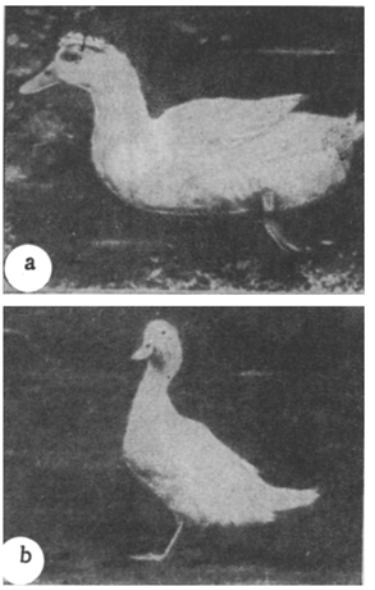


Fig. 1 Fig. 2

Fig. 1. Duck No. 1 one day (a) and one month (b) after right hemisection of the spinal cord.

Fig. 2. Duck No. 7 three days (a) and 15 days (b) after removal of the left hemisphere of the prosencephalon (hemisection on the right side).

ducks stood with their feet wide apart and could walk for not more than 25 m (Fig. 1, b). No difference could be found at this period between the thresholds of excitability of the flexor reflex of the affected and sound limbs, or between their skin temperatures. Approximately 3 months after hemisection of the spinal cord recovery of the disturbed functions of standing and walking reached its upper limit and the ducks walked well and for long periods, although defects of movement persisted on the side of the hemisection. In cold weather there was a marked temperature difference (as much as 7°) between the two limbs. Besides these disturbances, the ducks undergoing operation had dry feathers and brittle claws. Similar dystrophic changes have been observed after removal of one hemisphere of the prosencephalon in chicks and pigeons [1]. Hence, the locomtor disturbances caused in ducks by hemisection of the spinal cord were gradually but incompletely compensated.

In order to discover the role of the prosencephalon in the development of these compensatory adaptations, in eight ducks one hemisphere was removed between 4 and 15 months after hemisection; in 4 birds the contralateral hemisphere was removed (first group), and in the other 4 birds the ipsilateral (second group).

The operation was followed by decompensation of the previously restored functions in all the ducks; they could neither stand nor walk. After removal of the contralateral hemisphere of the prosencephalon both limbs were semiflexed and displaced in a dorsal direction (Fig. 2, a). The threshold of excitability of the flexor reflex and the skin temperature were slightly raised in the limb on the side of the hemisection of the spinal cord. In the ducks of the second group the limb on the side of the hemisection was more severely affected: the limb was held pointing backward and in a dorsal direction; active movements were preserved in the other limb. A slight increase in the threshold of excitability of the flexor reflex was observed in the limb opposite to the extirpated hemisphere; the skin temperature was greatly increased in the limb on the side of the hemisection of the spinal cord (by up to 10°). Ten days after the operation the ducks in which the contralateral hemisphere had been removed could stand with their legs widely separated, and they could walk by throwing forward slightly the limb on the side of the extirpated hemisphere (Fig. 2, b). At this same period the ducks from which the ipsilateral hemisphere had been removed were also able to stand, and from time to time they made one or two steps and then sat or fell down. Most weight was taken by the sound limb.

At the end of the 3rd week after operation all these defects during standing and walking persisted. The ducks from which the contralateral hemisphere was removed could not walk further than 10 m; those from which the ipsilateral hemisphere was removed could walk only a few steps because of the more severe impairment of the function of the limb on the side of the operation. The difference between the thresholds of excitability of the flexor reflex

and between the skin temperature of the limbs in all the ducks disappeared within 2-3 weeks after removal of one hemisphere of the prosencephalon. The ducks of the first group achieved maximal possible compensation of the functions disturbed a second time and could stand and walk from 1 to 1.5 months after the operation, while this process took 1.5 to 2 months in the second group; recovery was more complete in the first group, and at this period they could walk for a long time, limping slightly with the limb on the side of the hemisection; the ducks of the second group could walk only a little way and they often trod on one foot with the other. As before, the feathers and claws were brittle. It is interesting to note that one duck began to molt 2 months after the removal of the contralateral hemisphere. After molting its feathers grew more slowly than in normal ducks; the wing feathers grew more slowly on the side of the hemisection than on the contralateral side.

It follows from the experimental findings that the removal of one hemisphere of the prosencephalon in these ducks caused disturbances of the locomotor functions, not merely by decompensation of the functions of one limb (on the side of hemisection), but also by deranging the functions of the other limb. When four ducks had reached the upper limit of recovery of standing and walking after removal of one hemisphere of the prosencephalon, the other was removed. Two of the ducks were kept under observation for a long period: one for 30 and the other for 42 days.

Removal of the second hemisphere again caused decompensation of the twice restored functions of standing and walking.

Although the general condition of the ducks was very poor for the first 2-3 days, on the 7th-8th day they attempted to stand, and after 3 weeks they were able to stand and walk. They walked slowly for short distances, frequently falling sideways, towards the side of hemisection of the spinal cord.

For control purposes, one hemisphere was removed from 4 ducks without previous hemisection of the spinal cord. The operation caused disturbance of the movements of both limbs, the contralateral limb being affected rather more severely. However, after 2 weeks the ducks were walking normally again. Two months later the second hemisphere was removed from these four ducks, and one remained under observation for 60 days. After removal of the second hemisphere this duck could neither stand nor walk, but within a week it began to stand, and then to walk, limping with the limb contralateral to the hemisphere last removed. Two weeks later it was walking almost normally, and even cleaned its beak with the leg most severely affected after the second operation.

Whether subjected to preliminary hemisection of the spinal cord or not, all the ducks deprived of their prosencephalon were unable to seek and take food unaided. It was also noted that if they encountered difficulty in walking, the ducks from which the hemispheres had been removed never used their wings for support.

It may therefore be concluded that the prosencephalon in ducks takes part in the development of compensatory adaptations after hemisection of the spinal cord. Nevertheless, this participation is not of primary importance, for after removal of the entire prosencephalon the ability to compensate for the disturbances of locomotor functions is not completely lost. This conclusion is in agreement with results obtained by other researchers working with pigeons and chicks. Although ducks progress mainly by walking (and not by flying), this function is, nevertheless, weakly represented in the prosencephalon; apparently it is mainly effected by the lower divisions of the central nervous system. The prosencephalon becomes primarily responsible for the restoration of disturbed functions in later stages of phylogenesis – at the level of the higher mammals.

SUMMARY

Experiments were staged in chronic conditions on 29 ducks. At first, hemisection of the spinal cord was done at the level of the sixth cervical vertebra, and then two-stage excision of the hemispheres of the forebrain was performed. Each of the subsequent operations was carried out after the highest possible restoration level of disturbed functions (caused by the previous operation) was reached. Urethane anesthesia (1.0 gm/kg of body weight) was used.

Locomotor functional disturbances caused by the spinal cord hemisection in ducks are compensated, although only partially, in about 3 months. Excision of one of the hemispheres of the forebrain led to decompensation of the motor functions restored earlier. Removal of one of the forebrain hemispheres in ducks caused locomotor functional disturbances not only as a result of functional decompensation of one extremity (at the side of hemisection), but also due to disturbed function of the second extremity. The highest possible restoration level of the secondarily disturbed standing and walking functions occurred somewhat earlier and was somewhat more complete after the removal of the contralateral hemisphere of the forebrain (in 1-1.5 months) than following the excision of the homolateral hemisphere (in 1.5-2 months). Removal of the second forebrain hemisphere again provoked decompensation of the twice restored standing and walking functions; the latter were restored three weeks after the last operation.

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All abbreviations of periodicals in the above bibliography are letter-by-letter transliterations of the abbreviations as given in the original Russian journal. *Some or all of this periodical literature may well be available in English translation.* A complete list of the cover-to-cover English translations appears at the back of this issue.
