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INNERVATION OF LOCOMOTOR MOVEMENTS BY THE LUMBOSACRAL CORD IN BIRDS AND MAMMALS

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In earlier experiments (1960) I was able to demonstrate that in pigeons the lumbosacral cord has a high degree of autonomy, and when isolated from the rest of the central nervous system can autonomously co-ordinate walking movements of the hind limbs. A pigeon with the spinal cord transected in the lower thoracic region under normal circumstances can neither stand nor walk; but when it is placed in a special apparatus (a kind of carriage) so that it is in a normal attitude with the feet resting on the floor it can make genuine walking movements when the hind part of the body is stimulated. It was found essential that the legs be more or less extended and the soles of the feet resting on the floor.

The question arose whether in mammals with isolated lumbosacral cord it was possible to elicit walking movements of the hind limbs which were completely autonomous, i.e. without the fore limbs being involved in the locomotion as well.

In order to test this it was necessary to place a mammal, in these experiments a cat, in a special apparatus, as was done with the pigeons, i.e. so that the front limbs were immobile and no walking movements thereof could cause alternating stretching of the hind limbs.

For these experiments an apparatus was constructed on the same principle as that used in the experiments with pigeons. It was a sort of carriage on which the animal could be fixed. The hind limbs, in moderate extensor tonus, rested with the soles on the ground, while the front limbs rested on a board which constituted part of the apparatus, and thus could not take part in locomotion. In this way any stretching of the hind limbs by the front part of the animal was rendered impossible.

Spinal transections were made at the level of the eleventh thoracic vertebra. In one animal the transection was made at the level of the eighth thoracic vertebra, but no difference in response was observed.

In this connexion I must emphasize that such experiments can only be carried out with very tame, quiet animals. Restless, aggressive cats are unsuitable.

Out of five spinal cats investigated with this apparatus, one made walking movements with the hind limbs while walking with the fore limbs. The other four cats, after transection of the spinal cord some weeks or months previously, did not show any walking movements of the hind limbs when they moved forward on the front limbs. It was possible, however, in the latter cats to elicit alternating movements of the hind limbs by stimulation of a limb and by holding the animal up in the air by the neck (Freusberg's phenomenon, 1874).

None of the cats, when attached to the apparatus described, with the hind limbs resting with the soles on the ground, showed walking movements of the hind limbs as long as the apparatus was standing still.

When various places on the skin of the posterior part of the body were stimulated with forceps, when the sole of one foot was pinched or a hind limb bent or stretched, no walking movements occurred but only withdrawal of the stimulated part of the body, or defence movements. In pigeons all these manipulations caused a walking movement (flight reaction).

When the apparatus on which the cat was fixed was drawn forward, so that the hind limbs in a medium extensor tonus rested with the soles on the ground, there occurred marked alternating walking movements in both hind limbs, and these continued as long as the apparatus was moved forward. When the apparatus was stopped the walking movements of the hind limbs ceased immediately (Pl. 1, fig. 1).

When the cat, fixed on the apparatus, was drawn forward by the neck the hind limbs also performed walking movements, whereas the front limbs were unable to make walking movements (Pl. 1, fig. 2).

The rhythm of the walking movements of the hind limbs of the spinal cat could not be influenced by application of stimuli to the skin, in contrast to the spinal pigeons, which always responded with an acceleration of the rhythm to stimuli applied to the skin, especially to the anal region.

In the spinal cats the rhythm of the walking movements of the hind limbs depended only on the rhythm of locomotion of the anterior part of the animal or on the speed with which the carriage to which the animal was attached was moved forward.

From the above observation it may be concluded that in the spinal cat the locomotor centres in the lumbosacral cord need a continuous supply of stimuli from the periphery for their function. These peripheral stimuli are mostly conducted from the proprioceptors to the spinal cord. This had already been observed by Sherrington (1910 and 1914) in his investigations of alternating movements in spinal cats. Through these peripheral stimuli the activity in the locomotor centres in the lumbosacral cord can be evoked and maintained. These centres are automatic to this extent that after elimination of the higher centres by the transection they can co-ordinate the walking movements. However, the spinal cat differs from the spinal pigeon in that in the former the walking movements, once evoked, cannot be maintained completely autonomously; a continuous supply of alternating rhythmic stimuli from the periphery is required. These stimuli are produced by a certain stretching of the hind limbs which is in turn produced by locomotory movements of the anterior part of the body which cause alternating contractions of the flexor and extensor muscles. In the spinal cat we find a sort of mutual activity between the locomotor centres in the spinal cord and the periphery.

These observations on spinal cats in chronic experiments are not in agreement with the well-known experiments of Graham Brown (1911 and 1916). In acute experiments in anaesthetized cats Brown performed (so he reports) a rapid transection of the spinal cord at the level of the 12th thoracic segment, and immediately after the transection he observed alternating movements of the hind limbs. Since after section of all the dorsal roots which innervate the hind limbs the transection of the spinal cord also caused alternating movements of the hind limbs, Brown concluded that these alter-

nating movements of the hind limbs in the spinal cat are exclusively dependent on the phasic alternations in the spinal cord centres and that these phases are not necessarily dependent on the peripheral stimuli.

The phase distribution in the centres of the spinal cord during locomotion of the hind limbs is regulated, according to Brown, by a central mechanism. A similar conclusion was also drawn by von Holst (1935) on the basis of his experiments with spinal Osteichthyes, but Lissmann (1947) experimenting with Selachii could not confirm his findings. Gray & Lissmann (1940, 1947), from experiments with spinal toads, also arrived at the conclusion that for the normal locomotor rhythm of the hind limbs the peripheral sensory structures, especially the proprioceptors, are necessary.

It seems that the experiments of Brown can be compared to the observation of Tarchanoff (1884), who in his experiments confirmed the long-known fact that ducks and chickens immediately after decapitation can make alternating movements with the legs and wings and so transport themselves over short distances. Undoubtedly these movements are brought about by the strong stimulation of the spinal cord during the transection; they definitely have not the character of normal walking movements. In my opinion the experiments of Brown, which were carried out by the acute method, evoked the same phenomenon. The chronic experiments discussed here, in which the animals were kept alive for many months, have shown that in spinal cats the automatic activity of the locomotor centres in the lumbosacral cord requires a continuous supply of stimuli from the periphery.

There is a great difference between the function of the locomotor centres in the spinal cat and in the spinal pigeon. In the pigeon the automatic activity of the centres of the lumbosacral cord is maintained by stimuli, mostly proprioceptive, which originate in the limbs themselves in the course of walking. This automatic activity of the locomotor centres in the lumbosacral cord in the pigeon can be evoked by exteroceptive stimuli, but in the cat this is not possible. In the cat with isolated lumbosacral cord the occurrence of walking movements of the hind limbs requires a certain stretching of these limbs, which can be caused by locomotory movements of the fore limbs or by movement of the apparatus. In this way the proprioceptors and exteroceptors in the hind limbs are stimulated so that the locomotor centres are brought into activity.

In the cat, a four-legged animal, the locomotor movement of the hind limbs is closely correlated with the movement of the fore limbs. During walking there occurs an interaction between the centres for the front and hind limbs. This was demonstrated by Sherrington (1906) in his well-known experiments with cats in which a high transection of the spinal cord had been carried out. In the cat the walking movement of the hind limbs is closely connected with the walking movement of the fore limbs. This explains why in the cat with isolated lumbosacral cord the hind limbs are unable autonomously to carry out walking movements.

In the pigeon the situation is different; the movements of the legs and the wings have a high degree of autonomy and these limbs can carry out movements independently of each other. This I was able to demonstrate in earlier experiments (1937, 1960).

All the above applies to spinal animals; in normal animals the higher centres evidently are of great importance for induction and maintenance of the locomotor movements in the limbs.

SUMMARY

1. The locomotory movements of the hind limb of the spinal cat have been studied with the animal supported on a wheeled carriage so that the soles of the hind feet rest upon the ground.

2. Locomotory movements of the hind limbs do not occur spontaneously, but only in response to stimulation of proprioceptors and exteroceptors. Such stimulation is provided by locomotory movements of the fore limbs or by forward movement of the carriage. After cessation of these stimulatory movements the locomotory movements of the hind limbs are not maintained.

3. In these respects the spinal cat differs from the spinal pigeon, and it is suggested that the greater autonomy of the lumbosacral cord in the latter is related to its bipedal gait.

REFERENCES

BROWN, T. GRAHAM (1911). The intrinsic factors in the act of progression in the mammals. *Proc. Roy. Soc.* **84**, 308.

BROWN, T. GRAHAM (1916). Die Reflexfunctionen des Zentralnervensystems mit besonderer Berücksichtigung der rhythmischen Tätigkeiten beim Säugetier. *Ergebn. Physiol.* **15**, 480.

TEN CATE, J. (1960). Locomotor movements in the spinal pigeon. *J. Exp. Biol.* **37**, 609.

TEN CATE, J., STOMMEL, J. A. & WALTER, W. G. (1937). Flügelreflexe bei Rückenmarkstauben. *Arch. néerl. Physiol.* **22**, 332.

FREUSBERG, A. (1874). Reflexbewegungen beim Hunde. *Pflüg. Arch. ges. Physiol.* **9**, 358.

GRAY, J. (1947). Further observations on the effect of deafferentation on the locomotory activity of Amphibian limbs. *J. Exp. Biol.* **23**, 121.

GRAY, J. & LISSMANN, H. W. (1940). Ambulatory reflexes in spinal Amphibians. *J. Exp. Biol.* **17**, 227.

HOLST, E. VON (1935). Erregungsbildung und Erregungsleitung im Fischrückenmark. *Pflüg. Arch. ges. Physiol.* **235**, 345.

LISSMANN, H. W. (1947). The neurological basis of the locomotory rhythm in the spinal dogfish. *J. Exp. Biol.* **23**, 143, 162.

SHERRINGTON, CH. (1910). Flexion reflex of the limb, crossed extension reflex and reflex stepping and standing. *J. Physiol.* **40**, 28.

SHERRINGTON, CH. (1914). Further observation on the production of reflex stepping by combination of reflex excitation with reflex inhibition. *J. Physiol.* **47**, 196.

TARCHANOFF, J. (1884). Ueber automatische Bewegungen bei enthaupteten Enten. *Pflüg. Arch. ges. Physiol.* **33**, 619.

EXPLANATION OF PLATE

Fig. 1. Walking movements of the hind limbs of the spinal cat fixed on the apparatus. The cat is drawn forward by the neck.

Fig. 2. The spinal cat fixed on the apparatus shows walking movements of the hind limbs when the apparatus is moved forward. At the same time the animal is scratching her head with the left fore leg.

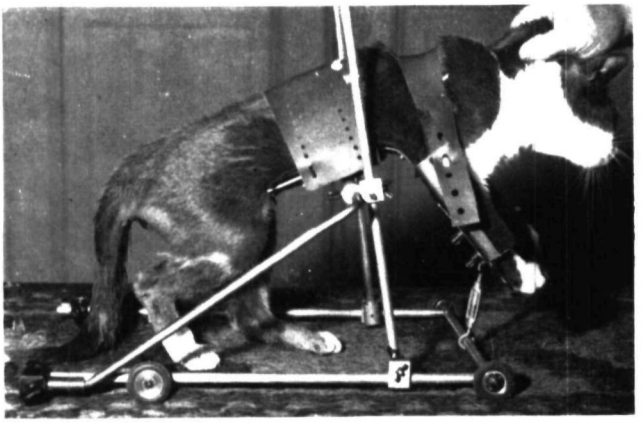

Fig. 1

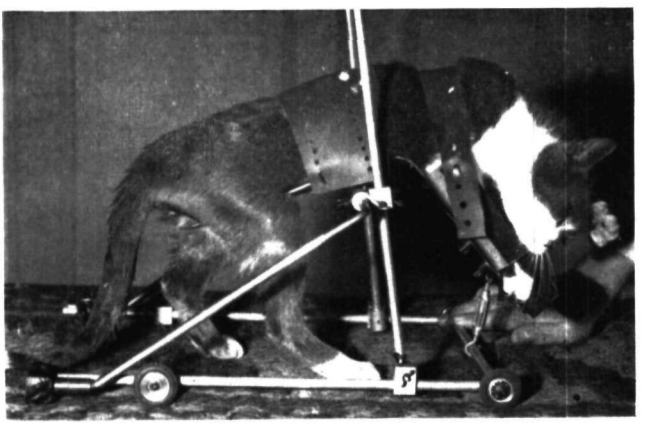

Fig. 2