AUTOMATIC ACTIVITY OF THE LOCOMOTOR CENTRES
OF THE LUMBAR CORD IN LIZARDS

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My previous experiments with salamanders (Triton cristatus; ten Cate, 1927) and
tortoises (Testudo graeca; ten Cate, 1937) have shown that, after transection of the
spinal cord in the thoracic region, locomotor movements of the hind limbs can be
observed under favourable conditions while the front limbs remain motionless. These
alternating movements are well co-ordinated but last only a short time; the front
limbs then also begin to move.

To confirm these observations, made by chance, experiments were performed by a
new method in which, after severing the thoracic cord in the lizards Lacerta lepida and
L. viridis, the locomotor movements of the hind limbs could be studied after the front
limbs had been immobilized.

In decapitated lizards (L. viridis) Steiner (1886) made ‘slices’ of the body using
sharp scissors, starting at the front and working backwards. When he reached the hind
part of the body he observed movements of the hind limbs and of the tail which
resembled locomotor movements. These locomotor movements, which lasted a short
time, were provoked by the violent excitation of the spinal cord as a result of the
transection. Similar alternating movements of the hind limbs were described by
Graham Brown (1916) in spinal cats and by Tarchanoff (1895) in spinal ducks.

The literature indicates, and I have been able to convince myself repeatedly, that in
quadruped animals during progression the alternating movements of the hind limbs
are closely integrated with the locomotor movements of the front limbs. This was first
shown by Sherrington (1914) in spinal cats and by Gray & Lissmann (1940, 1947) in
toads.

It is also well known that animals with a transected thoracic cord usually show
locomotor movements of the hind limbs when they walk forward with their front
limbs. In animals with an isolated lumbar cord the occurrence of walking movements
in the hind limbs requires a certain degree of stretching of these limbs, which is
caused by the locomotor movements of the front limbs. By stretching the limbs
proprioceptors and exteroceptors become stimulated and alternating walking move-
ments are then induced by reflex action. The rhythm of the front limbs is taken up by
the hind limbs.

To establish that the isolated lumbar cord can elicit walking movements completely
autonomously it is necessary to eliminate the movements of the front limbs.

METHOD

To eliminate the influence of the movements of the front limbs and thus to establish
the automatism of the locomotor centres of the hind limbs in the lumbar cord an
apparatus was constructed on the same principle as that used in the experiments with spinal pigeons in my previous experiments (ten Cate, 1960). It was a sort of carriage on which the lizard could be fixed so that the front limbs were immobile while the hind limbs rested with their soles on the ground.

Transection of the cord was made under ether narcosis at the level between the thoracic and lumbar cord or a little higher. After the operation the animals were observed for some months and different reflexes were examined. The experiments with the apparatus were carried out at intervals of some days.

EXPERIMENTS WITH SPINAL LIZARDS

The flexor reflex could be provoked in both hind limbs a few hours after the operation. Irritation of the tail was followed by winding movements, which were at first very slow but later become more rapid. Only some days after the operation could the cross reflex be elicited in spinal lizards when the soles of the hind limbs were stimulated. Somewhat later, usually in the second week, alternating movements could be provoked by excitation of the limbs or of the tail.

At the same time the hind limbs began to make alternating movements when the spinal animal walked with its front limbs. The rhythm of the movements of the hind limbs was at first very slow, but gradually became quicker. Later the rhythm in both pairs of limbs was the same as long as the animal was moving. When the movements of the front limbs stopped the movements of the hind limbs ceased also.

In experiments with the apparatus the hind limbs at first remained motionless when the apparatus was moved forward. After a few days the hind limbs began to produce alternating movements when the apparatus was moved. The rhythm of these movements was remarkably slow. During this period alternating movements of the hind limbs could be elicited by excitation of the skin of the hind part of the body. About 2 weeks later excitation of the exteroceptors of the hind limbs or of the tail provoked locomotion of these limbs even when the apparatus was standing still. By these alternating movements of the hind limbs, the rhythm of which was a little slower than normal, the apparatus could be moved forward a little.

These observations show that the locomotor centres in the isolated lumbar cord can co-ordinate the walking movements of the hind limbs more or less autonomously.

In experiments with mechanical excitation of the hind part of the body in spinal lizards it is necessary to take into account the particular irritability of this part in the spinal animal. When the stimulus is a little too strong irregular movements can easily occur in the limbs and also in the tail-defence reflex. Only when the amount of the excitation applied is exactly correct can regular alternating movements be elicited, which have the character of normal walking movements.

DISCUSSION

By this method of eliminating the movements of the front limbs by fixing the spinal lizard to the apparatus, the automatic function of the locomotor centres of the lumbar cord could be exactly studied. It could be established that excitation of the skin of the hind limbs or of the tail in spinal lizards could produce locomotor movements of these
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limbs. These movements are alternating, at a rhythm which is a little slower than that of the normal walk. The rhythm of the walking movements of the hind limbs of the spinal lizard could not be influenced by application of stimuli to the skin. Once evoked the alternating movements of the hind limbs can be maintained for a short time completely autonomously.

These observations show that the motor centres of the lumbar cord can be stimulated from the periphery and that they cannot only co-ordinate the movements of the limbs but also—and this is of importance—maintain them for a some length of time without the application of stimulation from outside. Purely by reflex action the motor centres of the lumbar cord can maintain the alternating walking movements of the hind limbs as a result of the combined action of the motor centres and the proprioceptors of the muscles and joints and the stretching of the skin.

In the experiments with the apparatus the locomotor movements of the hind limbs of the spinal lizard were always slower than under ordinary conditions when the spinal animal was able to walk with the front limbs as well. It may be concluded that under normal conditions the rhythm of the alternating movements of the hind limbs is initiated by the nervous centres of the front limbs which transmit impulses to the centres of the hind limbs.

These experiments with lizards confirm my earlier observations on spinal salamanders and spinal tortoises, previously mentioned. The experiments with spinal lizards placed in the apparatus show a certain resemblance to the results of experiments with spinal pigeons placed in a similar apparatus. In both cases the locomotor movements of the hind limbs could be elicited by irritation of the skin of the hind part of the body. In experiments with the apparatus the rhythm of the walking movements in birds was the same as under normal conditions and could be accelerated by the application of stimuli. In lizards the rhythm was a little slower than normal and could not be altered by stimulation of the skin.

After severing of the thoracic cord, the walking movements of the hind limbs, once initiated, continued for some time, both in lizards and in birds. In lizards and birds the automatic activity of the centres in the lumbar cord can be maintained by stimuli, mostly proprioceptive, which originate in the hind limbs themselves in the course of walking. From experiments carried out by the same method in spinal cats (1962), it appears that the locomotor centres of the hind limbs are more integrated with the centres of the front limbs than in birds and in lizards. There is a difference between the innervation of the hind limbs in lizards and in mammals.

SUMMARY

1. The motor centres of the isolated lumbar cord of lizards can co-ordinate the alternating movements of the hind limbs and also maintain them completely autonomously for a short time.
2. The rhythm of the alternating movements of the hind limbs studied in spinal lizards placed on a carriage is slower than when walking with both pairs of limbs.
3. Stimuli applied to the skin of the hind part of the body have no influence on the rhythm of walking in spinal lizards, in contrast to birds.
4. When walking with both pairs of limbs under normal conditions the rhythm
of locomotion is initiated by the motor centres of the front limbs and is transmitted to
the centres of the hind limbs.

REFERENCES


EXPLANATION OF PLATE

Walking movements of the hind limbs of the spinal lizard (*Lacerta lepida*) fixed on the apparatus. Fig. 1. Hind limb in flexion. Fig. 2. Hind limb in extension.
Fig. 1

Fig. 2

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