

reported in the Table), the simple laparotomy induced a decrease of 14.3% in the weight of preputial glands.

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#### Zusammenfassung

An weiblichen intakten, adrenal- oder ovariektomierten und sowohl adrenal-, als auch ovariektomierten Ratten wurden 2 h nach Injektion von 5-Hydroxytryptamin die Gewichtsveränderungen und der Ascorbinsäuregehalt der Nebennieren und der Präputialdrüsen untersucht. Eine Abnahme des Ascorbinsäuregehaltes der Nebennieren und der Präputialdrüsen wurde festgestellt und eine Gewichtszunahme der Präputialdrüsen selber beobachtet. Die Ergebnisse stimmen mit den bekannten Befunden über eine ACTH-freisetzende Tätigkeit des 5-Hydroxytryptamins überein.

### Identification of a Third Subdivision of the Dorsal Spino-Cerebellar Tract

Ascending tracts in the dorso-lateral funiculus (Flechsig's fasciculus) have been analyzed by recording the mass discharge from the dissected fasciculus and by intracellular recording from single fibres. Four types of ascending pathways have been differentiated<sup>1</sup>.

A. Neurones monosynaptically activated by impulses in muscle spindle afferents (Ia and II).

B. Neurones monosynaptically activated by impulses in Golgi tendon organ afferents.

C. Neurones activated by impulses in group II and III muscle afferents, and also by impulses in skin and joint afferents. These excitatory actions are drawn from an extremely wide ipsilateral receptive field. On adequate stimulation, a discharge can be evoked by muscle stretch and also from large areas of skin (usually by pressure and pinching, but sometimes also by bending of hairs).

D. Neurones activated exclusively by ipsilateral low threshold cutaneous afferents from a very restricted receptive field, the discharge being adequately elicited by bending of hairs.

There was reason to assume that type A and B constitute the dorsal spino-cerebellar tract, because, on stimulation of group I muscle afferents, a potential can be recorded from the anterior cerebellar vermis, which corresponds to the discharge in these neurones<sup>1</sup>. Stimulation of group II and III muscle afferents, on the other hand, did not evoke a potential change in the cerebellar cortex; hence it could not be assumed that the axons of type C terminated in the cerebellar cortex.

In the present experiments, a more direct approach has been used for identification of axons belonging to the dorsal spino-cerebellar tract by investigating whether they can be activated antidromically from the cerebellar cortex.

<sup>1</sup> Y. LAPORTE, A. LUNDBERG, and O. OSCARSSON, *Acta physiol. scand.* 36, 175, 187 (1956).—Y. LAPORTE and A. LUNDBERG, *Acta physiol. scand.* 36, 203 (1956).—A. LUNDBERG and O. OSCARSSON, *Acta physiol. scand.* 38, 53 (1956).—B. HOLMQUIST, A. LUNDBERG, and O. OSCARSSON, *Acta physiol. scand.* 38, 75 (1956).—O. OSCARSSON, *Arch. ital. Biol.* 96, 199 (1958).

Of 67 neurones belonging to type A and B, 50 could be activated antidromically from the anterior vermis. Those 17 axons which could not be activated antidromically may have terminated in the most rostral part of the vermis, not exposed for stimulation. None of 47 axons tested could be activated by stimulation of the dorso-lateral funiculus in the proximal L V segment, as would be expected since Clarke's column does not extend caudally below the L IV segment.

63 neurones belonging to type C were identified; 36 of them could be activated antidromically from the anterior cerebellar vermis. Stimulation of the dorso-lateral funiculus in upper L V failed to activate the axon of any type C neurone with connection to cerebellum. Hence it can be concluded that neurones of type C constitute a third subdivision of the dorsal spino-cerebellar tract.

However, it is noteworthy that the proportion of neurones not activated antidromically from the cerebellum is larger with type C than with A and B (43 resp. 25%). There is, indeed, evidence of another ascending system of type C because of 22 neurones, which could not be activated from cerebellum, 11 were activated on stimulation of the dorso-lateral funiculus in L V and consequently have their cell bodies below the caudal end of Clarke's column. No experiments have been made to find the termination of these axons.

None of the units of type D could be activated antidromically from the cerebellum, and with all of these neurones the axons could be stimulated in L V.

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#### Zusammenfassung

Aktionspotentiale einzelner Fasern des Funiculus dorso-lateralis des Rückenmarks wurden registriert und dabei nach Axonen gesucht, die antidrom von der Kleinhirnrinde erregt werden konnten. Es gelang die Identifizierung einer dritten Unterabteilung der dorsalen spino-cerebellaren Bahn. Diese Neurone werden sowohl durch Muskelafferente der Gruppen II und III als auch durch Haut- und Gelenkafferente erregt. Zwei andere aufsteigende Bahnen, deren Zellkörper unterhalb des caudalen Endes der Clarkschen Säule liegen und deren Axonen sich in dem Funiculus dorsolateralis befinden, erreichen die Kleinhirnrinde nicht.

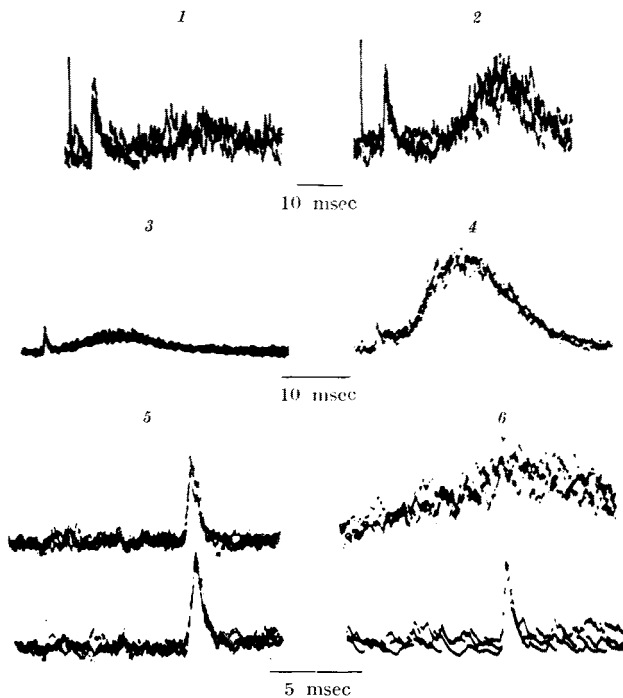
### The Relationship Between the Flexion Reflex and Certain Ascending Spinal Pathways

In spinal cats, impulses in group II and III muscle afferents, in skin and in high threshold joint afferents give rise to the flexion reflex with excitation to flexor and inhibition to extensor motoneurons<sup>1</sup>. In decerebrate cats, these actions are markedly depressed or even absent because the interneurons mediating them are tonically inhibited from suprasegmental centres<sup>2</sup>.

<sup>1</sup> D. P. C. LLOYD, *J. Neurophysiol.* 6, 293 (1943).—L. G. BROCK, J. C. ECCLES, and W. KALL, *Proc. Roy. Soc. London (B)* 138, 453 (1951).—R. M. ECCLES and A. LUNDBERG, to be published.

<sup>2</sup> R. M. ECCLES and A. LUNDBERG, *Exper.* 14, 197 (1958).

The present investigation was developed also in relationship to the problem of the functional significance of ascending pathways influenced by these afferents. Four such pathways (*A-D*) are known at present: *A* and *B* have their axons in the dorsal part of the lateral funicle and the receptive field is ipsilateral<sup>3</sup>. Pathway *A* is a subdivision of the dorsal spino-cerebellar tract, whereas the axons of pathway *B* have their cellbodies below the caudal end of Clarke's column. The termination of the axons of pathway *B* is unknown.



Comparison of discharge in ascending spinal tracts in decerebrate cats before (left column) and after (right column) section of the spinal cord. Records 1 and 2 show the discharge in the dissected Flechsig's fasciculus on stimulation of the ipsilateral hamstring nerve. Records 3 and 4 were obtained from the dissected spinal half (except the dorsal column) on stimulation of the contralateral hamstring nerve. Observe that the early components of the discharge, due to activity in group I activated neurones of the DSCT (1 and 2) and of the VSCT (3 and 4) have not changed after section of the cord.

Records 5 and 6 show the VSCT discharge recorded from the right dissected spinal half on stimulation of the left hamstring nerve. The unconditioned discharges are shown in lower traces; the upper traces were obtained after a conditioning volley in the left gastrocnemius nerve (interval between conditioning and testing volleys 12 msec).

The axons of pathway *C* are located in the ventral quadrant of the cord and the cell bodies in the lower lumbar segments. The receptive field is bilateral, the axons do reach the brain stem but their termination is unknown<sup>4</sup>.

The neurones of pathway *A*, *B* and *C* receive excitatory action from group II and III muscle afferents, from skin, and from high threshold joint afferents. The receptive field is extremely wide and includes antagonist muscles and large areas of skin. The neurones usually respond to a single volley in a peripheral nerve with a train of impulses, and, on adequate stimulation, there is a long-lasting after-discharge, such as would be expected with actions mediated through a chain of interneurones.

<sup>3</sup> Y. LAPORTE, A. LUNDBERG, and O. OSCARSSON, *Acta physiol. Scand.* 36, 188 (1956).—A. LUNDBERG and O. OSCARSSON, *Exper.* 15, 195 (1959).

<sup>4</sup> O. OSCARSSON, *Arch. ital. Biol.* 96, 199 (1958).

Pathway *D* is the ventral spino-cerebellar tract (VSCT). Its neurones are monosynaptically excited by Golgi tendon organ afferents, but, in addition, in the majority of VSCT neurones impulses in the afferents giving rise to the flexion reflex evoke, through polysynaptic pathways, inhibition. Also in this case, the receptive field is very wide<sup>5</sup>.

The description above refers to spinal cats and, in the present investigation, transmission to these tracts have been compared in decerebrate and spinal cats (Figure). Records 1 and 2 were obtained from the dissected dorsal part of the lateral funicle and show the discharge in pathway *A + B* before (record 1) and after (record 2) section of the spinal cord. The large release indicates that transmission to pathway *A* and *B* is tonically inhibited from suprasegmental centres in the non-spinal state. An equally large release is found in the corresponding records 3 and 4, showing the discharge in pathway *C* as recorded from the dissected right spinal half on stimulation of the left hamstring nerve. A release of inhibitory action on to VSCT neurones after cord section is illustrated in records 5 and 6. The VSCT discharge, evoked on stimulation of Ib afferents in the hamstring nerve, was recorded from the dissected spinal half (unconditioned discharge in lower traces of records 5 and 6). The upper traces were obtained after a conditioning volley had been evoked in the gastrocnemius nerve. The large release of inhibitory action after section of the remaining intact half of the cord shows that the interneurones mediating this action are tonically inhibited in the non-spinal state.

Further experiments have revealed that the control of these four ascending pathways is similarly organized as the suprasegmental inhibitory control of the flexion reflex. In both instances, the control is unaffected by stimulation of the anterior lobe of cerebellum leading to complete collapse of decerebrate rigidity or by ablation of cerebellum. It does not decrease after bilateral destruction of the vestibular nuclei but disappears after a lesion at obex. The descending tracts responsible for this control are in all cases located in the dorsal part of the lateral funicles, and from either side a bilateral effect is exerted.

As regards the functional significance of these four pathways, it should be noted that they can neither be classified as exteroceptive nor as proprioceptive. Their connection with primary afferents rather associates them with the flexion reflex. The similarity in supraspinal control of these pathways and of the flexion reflex suggests that they may convey information regarding the state of the flexion reflex, as decided both by the receptor activity and the degree of supraspinal control of the flexion reflex interneurones. Such information may be of general importance in the reflex taxis of the animal, or it may be more specifically utilized by supraspinal centres in regulation of this reflex.

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#### Zusammenfassung

Vier aufsteigende Rückenmarksbahnen werden bei spinalen Katzen durch somatische Afferenzen, die den Flexorreflex auslösen, beeinflusst. Genau wie beim Flexorreflex ist die Übertragung auf diese Bahnen bei dezerebrierten Katzen stark gehemmt. Die Regulierung der supraspinalen Hemmung der Bahnen und des Flexorreflexes scheint in gleicher Weise organisiert zu sein.

<sup>5</sup> O. OSCARSSON, *Acta physiol. Scand.* 42, Suppl. 146 (1957).