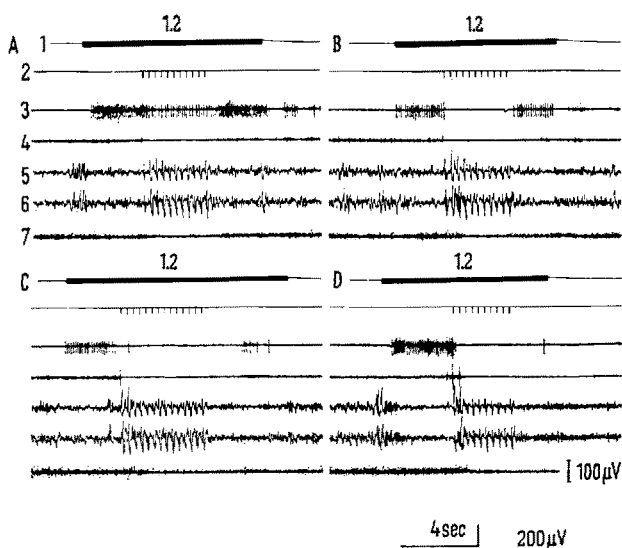


the tonus and the decrease of the monosynaptic response of the antigravity muscles are not accompanied by reciprocal effects on the antagonistic flexor muscles. The usual patterns of reciprocal innervation appear only when group III cutaneous afferents are co-stimulated



Abolition of the monosynaptic reflex by low frequency stimulation of group II cutaneous afferents. Unrestrained, unanaesthetized cat. Experiment made 3 days after the implantation of the electrodes. (1) Stimulation of the left medial gastrocnemius nerve at 100/sec, 0.05 msec pulse duration, 1.2 times the threshold for the monosynaptic reflex. The nerve was crushed and ligated distally to the stimulating electrode. (2) Stimulation of the left superficial radial nerve at 3/sec, 0.05 msec pulse duration, 0.4 V. (3) Left lateral gastrocnemius muscle. (4) Left tibialis anterior muscle. (5) Left fronto-temporal; (6) Right fronto-temporal. (7) Posterior cervical muscles. – Reduction (A) and abolition (B, C, D) of the monosynaptic reflex by low frequency stimulation of the lower threshold cutaneous afferents. This effect may outlast the stimulus (C, D). – Note also the decrease of the tonus of the posterior cervical muscles and of the tibialis anterior (flexor muscle). These effects are accompanied by induced EEG synchronization. Calibration of 100 μ V is referred to channels 3, 4 and 7.

The Effect of DOPA on Spinal Reflexes from the FRA (Flexor Reflex Afferents)

Recent biochemical and histochemical investigations make it likely that there are descending pathways with noradrenergic synaptic terminals in the spinal cord¹. In acute spinal cats L-DOPA (L-3, 4-dihydroxyphenylalanine, precursor of the catecholamines dopamine, noradrenaline and adrenaline) gives a pronounced increase of the flexor reflex evoked by pinching the skin. An electrophysiological analysis has now been made of the effect of L-DOPA on transmission from the FRA (flexor reflex afferents) to α -motoneurons, ascending pathways and primary afferents. It has been a constant finding that the DRP (dorsal root potentials), which are caused by primary depolarization in the FRA², are markedly reduced after intravenous administration of L-DOPA (67 mg/kg). The Figure shows this for the effects from high threshold

(5) When not only the MR but also the PR is elicited by stimulating the medial gastrocnemius nerve with intensities supra-threshold for the FRAs, low rate stimulation of cutaneous group II fibres inhibits both reflexes. Only when cutaneous group III fibres are co-stimulated is the flexor response elicited by exciting the high threshold muscular afferents enhanced, while the MR is still decreased. This flexor response is accompanied by an increased activity in the cervical EMG (orienting reaction) and by EEG desynchronization.

(6) When low rate stimulation of group II cutaneous afferents is applied during the stage which precedes the appearance of an episode of deep sleep (as shown by the spontaneously occurring gradual reduction of the cervical EMG), the EMG and behavioural patterns of deep sleep are precipitated. In these instances, low rate stimulation of group II cutaneous fibres does not produce EEG synchronization, but only flattening of the EEG and EMG silence.

It is concluded that low rate stimulation of group II cutaneous afferents performed in unrestrained, unanaesthetized cats produces a partial inhibition of both spontaneous and reflex muscular activities. This phenomenon is a generalized one and affects both flexor and extensor muscles, as well as monosynaptic and polysynaptic spinal reflexes. The induced pattern of generalized inhibition of the spinal reflex activity is sometimes accompanied by an electrocortical synchronization as previously described²; however, it does not necessarily depend upon it. Under certain circumstances, low rate stimulation of group II cutaneous afferents may also precipitate the pattern of deep sleep.

Riassunto. Nell'animale integro non anestetizzato la stimolazione a bassa frequenza delle fibre cutanee del gruppo II produce una riduzione generalizzata del tono posturale e dei riflessi spinali mono- e polisimpatici, che si accompagna di solito, ma non necessariamente, ad un quadro di sincronizzazione elettroencefalografica². In particolari condizioni sperimentali la stimolazione cutanea suddetta può anche precipitare il quadro di sonno desincronizzato.

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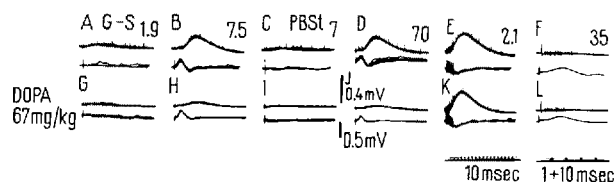
muscle afferents (B, D, H, J). There is no effect on the DRP evoked from group I muscle afferents (E and K). The effect is completely reversible within 1–2 h and effectively antagonized by the adrenergic blocker Phenoxybenzamine. In addition DOPA reduces excitatory and inhibitory actions from the FRA to motoneurons and to ascending pathways, but in the Figure the reduction in the ventral root discharge caused by high threshold muscle afferents is small (F and L).

The finding that DOPA increases the flexor reflex in the acute spinal cat is possibly accounted for by the more

¹ T. MAGNUSSON and E. ROSENGREN, *Exper.* 19, 229 (1963). – A. CARLSSON, B. FALCK, K. TUXE, and N. Å. HILLARF, *Acta physiol. scand.*, in press.

² J. C. ECCLES, P. G. KOSTYUK, and R. F. SCHMIDT, *J. Physiol.* 161, 258 (1962).

effective action on transmission to primary afferents than to flexor motoneurons. If so, the importance of pre-synaptic inhibition of central actions from the FRA is well illustrated.



The dorsal root potentials (DRP) in the upper traces of A-E and G-K were recorded from a dorsal root filament in lower L6. The filament was cut 15 mm from the entry into the cord and placed on two electrodes, one close to the entry zone and the other at the cut end; an upwards deflection signals negativity of the central electrode. Upper traces in F and L are L7 ventral root recordings. Lower traces in all records are from the cord dorsum in L7. Records A-F were taken before and the corresponding lower records G-L after intravenous injection of DOPA (67 mg/kg). The nerve from gastrocnemius-soleus (G-S) was stimulated in A, B, G, H and the nerve from posterior biceps-semitendinosus (PBSt) in C-F and I-L. Stimulus strengths are indicated in multiples of threshold strengths, those in A, G and E, K being just maximal for group I afferents of the G-S and PBSt nerves respectively. F and L were taken at fast speed and the other records at slow speed. All records except F and L consist of superimposed traces. Acute spinal unanaesthetized cat.

There are powerful descending inhibitory pathways controlling transmission from the FRA to motoneurons, ascending pathways and primary afferents³. Attention must be given to the possibility that descending pathways with this function may be noradrenergic and that DOPA acts on spinal reflexes by inducing synthesis and overflow of catecholamines from their synaptic terminals.

Zusammenfassung. DOPA hemmt die Überleitung von Afferenzen des Flexorreflexes zu den primären Afferenzen, Vorderhornzellen und aufsteigenden Bahnen. Es steigert den Flexorreflex, vielleicht dadurch, dass es die Übertragung zu den primären Afferenzen stärker beeinflusst als zu den Vorderhornzellen. Möglicherweise ist eine absteigende Bahn, welche die Übertragung von Flexorreflex-Afferenzen hemmt, noradrenergisch.

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Departments of Physiology and Pharmacology, University of Göteborg (Sweden), August 8, 1963.

³ R. M. ECCLES and A. LUNDBERG, *J. Physiol.* 147, 565 (1959). – B. HOLMQVIST, A. LUNDBERG, and O. OSCARSSON, *Arch. ital. Biol.* 98, 60 (1960). – D. CARPENTER, I. ENGBERG, H. FUNKENSTEIN, and A. LUNDBERG, *Acta physiol. scand.*, in press.

Some Responses of the Superior Colliculus of the Cat and their Control by the Visual Cortex

That the superior colliculus may have functions other than visual is suggested by anatomical data concerning afferent pathways¹⁻³ indicating the existence of somesthetic and acoustic afferents, in addition to the optic fibres.

On the other hand, projections from the striate cortex to the superior colliculus have been described¹ and confirmed by stimulation experiments^{4,5}. Since the visual cortex can be activated by non-visual as well as visual stimuli⁶⁻¹¹, the cortico-collicular projections may represent an additional pathway to the colliculus of visual and non-visual impulses.

The results presented below show that in the cat, under chloralose anaesthesia, responses are evoked in the superior colliculus by visual, somesthetic and acoustic stimuli, and that the cortico-collicular pathway plays a different role according to the type of response. More precisely, three types of responses may be distinguished: (1) Visual responses that are recorded throughout the whole colliculus. In our experimental conditions, the latency of these responses is 25 ± 5 msec. (2) Long-latency somesthetic and acoustic responses that are recorded in the superficial layers of the colliculus. Stimulation of any of the four legs is effective in evoking a response in the colliculus. For the anterior legs, the latency is about 60 msec. The acoustic response to a click has a latency of about 70 msec. (3) Short-latency somesthetic and acoustic responses (8-10 msec) that are recorded in the deeper layers of the colliculus.

The peripheral stimuli which evoke collicular responses also evoke cortical responses in the striate area. As ALTMAN and MALIS¹² have already observed, the latency of

the cortical visual potential is always shorter than that of the collicular potential; the difference appears to be constant – 5 to 10 msec – regardless of the absolute values of the latencies. We were able to repeat this observation and extend it to the long-latency somesthetic and acoustic responses. The long-latency collicular responses are consistently preceded by responses of the visual cortex, i.e. the latency of the non-visual responses is 5 to 10 msec shorter for the cortex than for the colliculus.

We next investigated the role of the visual cortex in the three types of responses. Surgical ablation of striate and peristriate areas suppresses the long-latency somesthetic

¹ J. ALTMAN, *J. comp. Neurol.* 119, 77 (1962).

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³ F. D. ANDERSON and C. M. BERRY, *J. comp. Neurol.* 111, 195 (1959).

⁴ W. T. NIEMER and J. JIMENEZ-CASTELLANOS, *J. comp. Neurol.* 93, 101 (1950).

⁵ S. SHANZER and S. DUMONT-TYC, *J. Physiol. (Paris)* 53, 473 (1961).

⁶ F. BREMER, in *Some Problems in Neurophysiology* (University of London 1953), p. 79.

⁷ R. JUNG, H. H. KORNHUBER, and J. S. DA FONSECA, in *International Colloquium on Specific and Unspecific Mechanisms of Sensory-Motor Integration*, Pisa (1961), (Elsevier Publ. Co., in press).

⁸ R. F. THOMPSON and R. M. SINDBERG, *J. Neurophysiol.* 23, 87 (1960).

⁹ A. FORBES and R. S. MORISON, *J. Neurophysiol.* 2, 112 (1939).

¹⁰ D. P. PURPURA, *J. Neurophysiol.* 18, 246 (1955).

¹¹ P. BUSER and P. BORENSTEIN, *Electroenceph. clin. Neurophysiol.*, Suppl. 6, 89 (1957).

¹² J. ALTMAN and L. I. MALIS, *Exper. Neurol.* 5, 233 (1962).