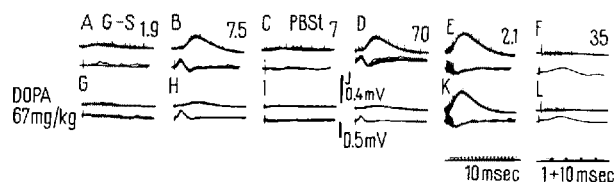


effective action on transmission to primary afferents than to flexor motoneurons. If so, the importance of pre-synaptic inhibition of central actions from the FRA is well illustrated.



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.

N. E. ANDÉN, A. LUNDBERG,
E. ROSENGREN, and L. VYKICKÝ

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).

² C. U. A. KAPPERS, G. C. HUBER, and E. C. CROSBY, in *Comparative Anatomy of the Nervous System of Vertebrates, Including Man* (Hafner, New York 1960), p. 979.

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).

and acoustic responses, whereas the short-latency somesthetic and acoustic responses, as well as the visual ones, persist.

The topical application of potassium chloride (3M) on the striate area is known to suppress the evoked potentials of this area. With this treatment, similar results to those of ablation are obtained, so far as somesthetic and acoustic responses are concerned. There is in this case a complete disappearance of the long-latency responses, whereas the short-latency responses are not modified (Figure). Furthermore, the amplitude of the visual response of the colliculus diminishes progressively as the cortical visual potential fades out, until it reaches a new stable value (Figure).

The cortical application of strychnine (1%) produces opposite results: the short-latency acoustic and somesthetic responses are again not modified; but the long-latency acoustic and somesthetic responses, as well as the visual response (Figure), are now enhanced.

These results indicate that the short-latency responses of the deep layers of the colliculus are independent of the visual cortex, since they are not affected by cortical modifications. On the other hand, the complete disappearance of the long-latency responses, following depression or destruction of the visual cortex, suggests that these responses are normally reverberated from the cortex to the colliculus.

The interpretation of the changes of the visual response is more difficult. The fact that the responses do not disappear after destruction of the visual cortex shows that they can be mediated by a subcortical system. On the other hand, they are under the partial control of the visual cortex, as shown by topical application of strychnine and KCl on the cortex.

BUSER et al.¹³ have observed in various structures, such as the reticular formation, the medial thalamus, the caudate nucleus, the pyramidal tract and the spinal cord,

visual responses very similar to the collicular ones. These visual responses were sensitive to pharmacological agents acting on the visual cortex but resistant to the ablation of the cortex. The authors¹⁴ have suggested the convergence on a subcortical centre of impulses which are mediated directly by a subcortical pathway and indirectly reverberated from the visual cortex. However, there was little anatomical evidence of these connections.

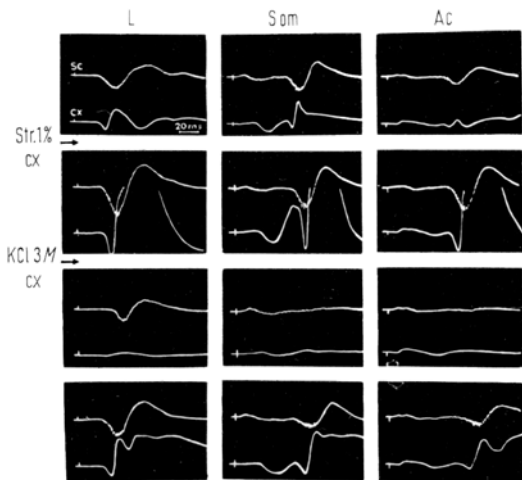
In the case of the visual response of the colliculus, a similar hypothesis can be used and, for the first time, supported by anatomical evidence. The visual response of the colliculus would have two components: one resulting from the activity of the direct retino-collicular pathway, the other corresponding to the reverberation from the visual cortex of impulses relayed by the lateral geniculate. Since BISHOP and CLARE¹⁵ have shown that most of the retino-collicular fibres are of small diameter with very slow conduction rate, this could explain why faster travelling impulses relayed by the lateral geniculate reach the visual cortex before the arrival at the colliculus of the impulses coming directly from the retina¹² and 'catch up' with these impulses in the colliculus. On this basis, one could explain that the two components have the same latency.

Finally, the superior colliculus has numerous projections toward the reticular formation and the thalamus¹⁶. The many observations, showing that the visual responses in these structures are under cortical control¹³, could be explained by assuming that the colliculus is a relay for entry of visual impulses into these non-specific structures¹⁷.

Résumé. A la stimulation périphérique on enregistre dans le colliculus supérieur du chat anesthésié au chloralose, trois types de réponses: réponse à la lumière, réponses somesthésiques et acoustiques de courte latence et réponses somesthésiques et acoustiques de longue latence. Les réponses somesthésiques et acoustiques de longue latence sont sous le contrôle du cortex visuel tandis que les réponses somesthésiques et acoustiques de courte latence ne dépendent pas de cette région corticale. La réponse à la lumière semble correspondre à une décharge complexe, comprenant l'activation de deux systèmes: un système direct rétino-colliculaire et un système indirect rétino-cortico-colliculaire.

DORA JASSIK-GERSCHENFELD and P. ASCHER¹⁸

Instituto de Anatomía General y Embriología, Facultad de Ciencias Médicas, Buenos Aires (Argentina), July 1, 1963.



Upper row traces: Responses of right superior colliculus (superficial layers) recorded with a bipolar concentric electrode (upper beam) and right visual cortex (lower beam) to different peripheral stimuli (L: light; Som: contralateral forelimb; Ac: acoustic). Second row traces: The same responses after topical application of strychnine 1% on the visual cortex. Third row traces: Modification of the responses after topical application of a 3M solution of KCl on the visual cortex. Lower row traces: Recuperation of the original responses after 30 min (see text).

¹³ P. BUSER et al., in *International Colloquium on Specific and Unspecific Mechanisms of Sensory-Motor Integration*, Pisa (1961), (Elsevier Publ. Co., in press).

¹⁴ P. ASCHER, D. JASSIK-GERSCHENFELD, and P. BUSER, *Electroenceph. clin. Neurophysiol.* 15, 246 (1963).

¹⁵ G. H. BISHOP and M. H. CLARE, *J. comp. Neurol.* 103, 269 (1955).

¹⁶ J. ALTMAN and M. B. CARPENTER, *J. comp. Neurol.* 116, 157 (1961).

¹⁷ Paper supported by a grant from the Air Force Office of Scientific Research and from the Consejo Nacional de Investigaciones Científicas y Técnicas, Buenos Aires (Argentina).

¹⁸ On leave of absence from Laboratoire de Neurophysiologie Comparée, Faculté des Sciences, Paris (France).