Long-duration signals. Figure 1b shows a positive, long-duration signal recorded in an explant using a microelectrode. Intermediate-duration positive signals (50–500 msec) are superimposed on it.

Intermediate range (10–500 msec) signals. These usually occur in repetitive patterned sequences[4]. Figure 1 shows a sequence of pulses recorded simultaneously from a gross electrode (Figure 1a) underlying the explant and a microelectrode lying outside neurons within the explant (Figure 1b). A series of such simultaneous pairs of grouped pulses were recorded in this way. Each of the pair of sequences had approximately the same duration and started at the same time after the same silent interval. There was a pulse in the microelectrode recording for nearly all pulses in the gross electrode recording. Thus the gross and microelectrode activity are sufficiently similar to have been initiated at a common source. Equally similar sequences can be recorded with microelectrodes in the tissue and in the film of fluid external to the tissue. Entry of the microelectrode into the tissue was accompanied by a 7 mV negative DC shift, which varied (as much as 2 mV) between different sites in the tissue.

The sites and extents of electrically active areas within an explant can be studied (a) by placing an explant on the cut end of a microcable containing twenty 0.08 mm diameter, individually insulated platinum electrodes and observing activity from varying pairs out of the twenty, or (b) by observing the several foci of activity detectable using microelectrodes at different sites in the film of fluid at the periphery of an explant.

Signals observed with technique (a) are in the microvolt range, while those with technique (b) are in the millivolt range, but are otherwise the same. There are discrete small foci of activity within the tissue. A 200–300 μ movement of the microelectrode tip away from a focus (in technique (b)) may result in the activity's being no longer detectable, and restoration of the position of the microelectrode tip causes a return of activity. Several foci may be present in one explant, each with similar but not identical telencephalic patterns of signals. The spread of the potential from a single focus is narrowly directional.

Short duration (1-2 msec) signals. Typical negative 'extracellular' 1–2 msec potentials (Figure 3a) occur in groups whose duration and intergroup intervals are similar to those detected with gross electrodes and microelectrodes in the film of fluid around the explant. The grouped 1–2 msec signals vary in amplitude; thus they must originate in several neurons.

Figure 3b shows one of a series of fast (1–2 msec) 20 mV positive spikes (AC amplification) recorded intracellularly from a non-motile cell whose granules stain selectively with methylene blue and which had the form of a neuron (Figure 2). These spikes were preceded by a 30 mV negative DC shift when the cell membrane was penetrated. The membrane potential and the spikes are smaller than those reported from other animals in vivo, but these measurements are less in other chick embryo tissues than in the same tissues in other animals (e.g. resting potential and action potential from chick auricular muscle fiber are 29.1 and 39.2 mV, and for cat 60.4 and 65.2 mV[11]). The measurements are made during the first 72 h after explantation, so that potassium released from damaged cells may alter the potassium/sodium ratio and reduce signal amplitude.

The neuron-like cells within the active foci are electrically active, and it is likely that the sequences of signals detected by all of the above means are associated with their activity[12].

Résumé. A l'aide de micro-électrodes, des potentiels rythmiques spontanés ont été enregistrés dans du tissu télencéphalique d'embryons de poulets âgès de 14 jours, in vitro. Ces potentiels sont semblables à ceux précédemment décrits en utilisant des électrodes de 80 μ en platine. La possibilité pour ces potentiels d'être produits par les neurones de l'explant est discuté.

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February 14, 1966.

[11] *Handbook of Biological Data,* National Academy of Sciences (W. B. Saunders Co., 1961), Section 235, p. 293.

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Studies on Modality Segregation and Second-Order Neurones in the Dorsal Funiculus

The dorsal funiculus of the spinal cord has been considered as composed exclusively of primary afferents ascending to the dorsal column nuclei, or terminating within the cord. This conception has been based on anatomical work, and it has been shown that the ascending fibres are arranged in a segmental way[1]. From electrophysiological studies on the gracile nucleus[2,3] it can be concluded that fibres activated from rapidly adapting hair receptors, slowly adapting receptors sensitive to touch or pressure of the skin, and vibration receptors ascend in the funiculus. There is also evidence that group I muscle afferents from the forelimb ascend in the dorsal funiculus[4,5]. This investigation has demonstrated a differential distribution of primary afferents activated from different receptors, and also the unexpected existence of a secondary tract in the dorsal funiculus.

[1] P. Glees, R. B. Livingston, and J. Soler, Archs Neurol. Psychiat. *187*, 190 (1951).
[2] G. Gordon and M. G. M. Jukes, J. Physiol. *173*, 263 (1964).
[3] E. R. Perl, D. G. Whitlock, and J. R. Gentry, J. Neurophysiol. *25*, *337* (1962).
[4] O. Oscarsson and I. Rosén, J. Physiol. *169*, 924 (1963).
[5] B. Holmqvist, O. Oscarsson, and I. Rosén, Acta physiol. scand. *58*, 216 (1963).

Cats were anaesthetized with pentobarbitone. Muscle and cutaneous nerves in the forelimb were dissected and mounted for stimulation. The skin nerves were in continuity with the periphery. The spinal cord was exposed in the cervical region (C3), and the dorsal funiculus explored with microelectrodes. When a fibre was found, its position in the funiculus was determined and the properties on electrical and adequate stimulation investigated. 175 units were tested thoroughly enough to be classified.

As demonstrated in Figure 1, it was shown that fibres with different properties ascend in different parts of the funiculus. The superficial layer consists almost exclusively of fibres activated from quickly adapting receptors stimulated by the bending of hairs (Figure 1, A). The intermediate part of the funiculus is largely occupied by group I muscle afferents (Figure 1, C). A few high threshold muscle afferents were found in the same region or slightly deeper (not illustrated). Primary afferents carrying impulses from the slowly adapting touch-pressure sensitive organs occur mainly in the deep part of the funiculus, though a few fibres of this type were found near the surface (Figure 1, B).

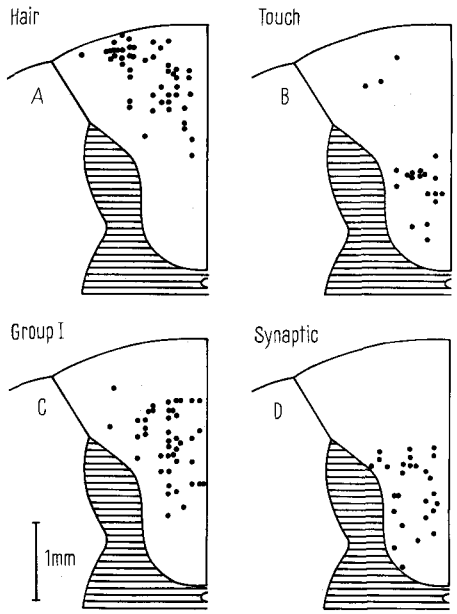

Fig. 1. Position in dorsal funiculus of fibres from quickly adapting hair receptors (A), of fibres from slowly adapting touch-pressure receptors (B), of group I muscle afferents (C), and of synaptically activated fibres (D). Diagrams represent left half of dorsal funiculus at third cervical segment.

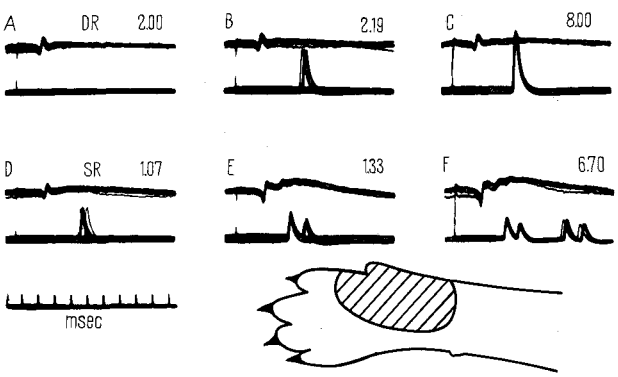

Fig. 2. Microelectrode recording from synaptic unit (lower sweep) and triphasic recording of ingoing volley from surface of dorsal funiculus at sixth cervical segment (upper sweep). A–C, stimulation of muscle nerve (deep radial), and D–F, stimulation of skin nerve (superficial radial) at indicated strengths (expressed in multiples of threshold strength). Diagram shows extension of cutaneous receptive field. Variability in spike size is due to movements of spinal cord.

27 of the units encountered were synaptically activated. They occurred intermingled with the touch-pressure units in the deep part of the funiculus (Figure 1, D). These neurons were recognized by their inability to follow high stimulation frequencies, usually failing at about 150 c/sec. As illustrated in Figure 2 they were activated both from skin and muscle nerves. The synaptically activated units were never activated from group I muscle afferents, the threshold always being well above the group I maximum (Figure 2). However, the synaptic fibres were activated from low as well as high threshold cutaneous afferents. The latency of the response evoked from skin nerves was always short, indicating a monosynaptic linkage. On stimulation of muscle nerves the latency was sometimes longer, suggesting two or more synapses.

When tested adequately, the synaptic units gave a fast adapting response on the bending of hairs, and a slowly adapting response on slight touch of the skin. These observations suggest contribution from both hair receptors and touch-pressure receptors. Strong, slowly adapting discharges were evoked by pinching the skin. Cooling the skin produced a discharge of considerable duration. Whether this was due to the temperature sensitivity of the touch-pressure receptors[6] or to contribution from special temperature receptors is unknown. The receptive area of the synaptic fibres was relatively small (2–5 cm^2) but always larger than that of the primary afferents.

The synaptic fibres activated from the forelimb nerves enter the dorsal column in the lowermost cervical segments (unpublished observations), and their occurrence in the third cervical segment suggests that they reach the dorsal column nuclei. The convergence from cutaneous and high threshold muscle afferents indicates that the path is one of the many ascending tracts activated from the so-called flexor reflex afferents[7]. In contrast with other tracts of this type, the dorsal funiculus path has small receptive fields indicating a good spatial discrimination.

Zusammenfassung. Der dorsale Funiculus der Katze wurde elektrophysiologisch untersucht und es wurde nachgewiesen, dass primäre Afferenzen welche verschiedene Sinnesmodalitäten vermitteln, in verschiedenen Teilen des Funiculus verlaufen. Eine bisher unbekannte Gruppe von synaptisch aktivierten Nervenfasern wird diskutiert.

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[6] C. C. HUNT and A. K. MCINTYRE, J. Physiol. *153*, 88 (1960).

[7] A. LUNDBERG, *Physiology of Spinal Neurons* (Eds, J. C. ECCLES and J. P. SCHADÉ; Elsevier Publishing Company, Amsterdam-New York); Progr. in Brain Res. *12*, 135 (1964).