

NERVE FIBRE INTERACTION IN THE ROOTS

By RAGNAR GRANIT.

To the clinician the root region is of particular interest on account of the symptoms developing during root compression. In accordance with the observations of Granit, Leksell and Skoglund (1944) compression may lead to nerve fibre interaction contrary to the law of isolated conduction. It is likely that the isolation, maintained by the normal fibre membranes, breaks down under the stress of the pressure. This means that its internal electrical 'battery' the poles of which are kept apart and isolated by the membrane separating inside and outside of the nerve fibre, may have a chance of distributing its currents within the compressed region. Where such currents from one fibre enter another fibre an anode will be formed; where they leave it on their way to the other pole of the battery there will be a cathode. In accordance with Pflüger's law there will be excitation at the cathode and depression at the anode. In this manner internal currents within the compressed region of a root may set up changes of excitability which are reflected by abnormal motor and sensory responses, to be expected, particularly, when impulses are passing through the critical zone.

Now it was found by Rexed (1947) that the demarcation potential (which is the potential of the 'battery' and maintains the demarcation current between the intact and cut region of a nerve fibre) is a function of fibre size. In parallel measurements he showed that fibre size and demarcation potential increased simultaneously. In the roots where the number of large fibres is greatest

the demarcation potential too reaches its maximum value. One may therefore expect damaged fibres in the root region to be particularly prone to set up currents capable of altering the excitability in this region. Rexed (1947) has recently shown that arachnoidal proliferations with cyst formation in the spinal nerve roots can damage a large number of fibres at their entry into the intervertebral foramina.

It has long been known that local cooling of nervous tissue renders the cooled region electronegative relative to a normal portion of the nerve. In this laboratory thermostimulation has been studied systematically for some time (Bernhard and Granit, 1946; Granit and Skoglund, 1945, C. von Euler, 1947; Granit and Lundberg, 1947). It therefore seemed natural, when planning an experiment on interaction between two roots in the decerebrated cat, to place one root into a thermode, cool it and in this manner force it to generate a battery in which currents run from the normal warm nerve to the cooled part of the root within the thermode. Generally the ventral L 7 was placed in the 1 cm long, well isolated and lacquered metal thermode through which water was circulated; electrodes were applied to the ventral S 1 for a stimulating shock, repeated at intervals of 1—1.2 sec. Sometimes electrodes and thermode were placed on the divided L 7. A muscle, the *tibialis ant.* or the *gastrocnemius*, was attached to the isometric Brown-Schuster myograph. The leg was rigidly fixed.

Description of Experiments.

In fig. 1 is shown a type of response to cooling which is common enough but unwonted in this particular experiment. The heavy horizontal line in the middle is the myograph to which *m. tib. ant.* is attached. The muscle is being stimulated every second by a shock to L 7 causing the small contractions visible on the record. The vertical lines in the upper part have superimposed upon them the ordinary muscle spikes (action potentials) picked up by silver pins stuck into the muscle and led to amplifier and oscillograph in the usual manner. Thus every shock elicits a brief muscle contraction accompanied by a spike.

In this experiments L 6 is on the thermode. A thermo-couple

records its temperature. It is connected to a galvanometer the mirror of which is illuminated by two lights in such a fashion that either light will form a record on the film when the temperature changes between its extremes. These are the thin horizontal lines in fig. 1.

We are now ready to study the effect of cooling the root. It is, of course, severed from the spinal cord, as are the roots used in all these experiments. When the temperature (fig. 1) drops from 37

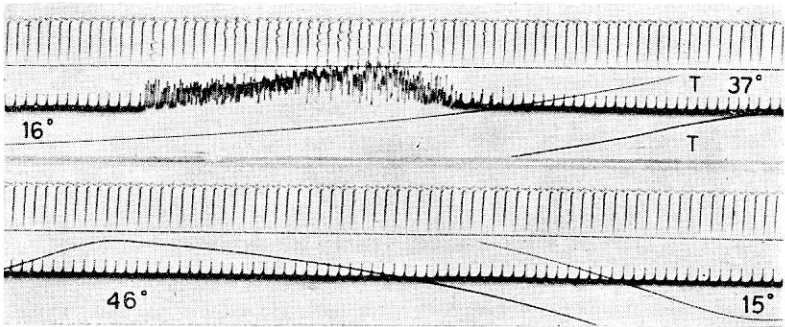


Fig. 1. Thermode on the ventral L 6, stimulating electrodes on L 7. *M. tib. ant.* on myograph. Slanting lines marking temperature of thermode. Upper part of figure shows movement of sweep circuit started by shock to L 7. In this experiment muscle spike recorded by sweep circuit. Heavy line in the middle of the film illustrates myograph zero on which superimposed twitch by shock to L 7. Convulsive contractions elicited during first phase of cooling.

See text.

to 14° the cooled region sets up a discharge which elicits convulsive contractions in the muscle. Additional spikes appear in the vertical oscillograph record along the upper edge of the film. The contraction is restricted to the falling phase of the temperature curve. During this phase the test contraction from the other root is wholly covered by the direct excitatory effect from the cooled root. When it again appears, at the later stage of cooling, it is seen to be of practically the same size as before cooling. There is therefore no effect of the cooled root upon the impulse set up by the test shock to the adjacent root.

Warming the root to 46° (fig. 1, lowermost record) is seen to

have no effect whatever, neither direct (from the warmed root) nor indirect upon the test shock set up in the other root (C. v. Euler, 1947; Granit and Lundberg, 1947).

The direct effect of cooling is a complication which it is desirable to avoid. In some cats it is minute and does not interfere with the recording of the test contraction set up from the electrically stimulated root. In all animals the direct effect disappears during repeated cooling whereas the 'cold potential' is far more resistant,

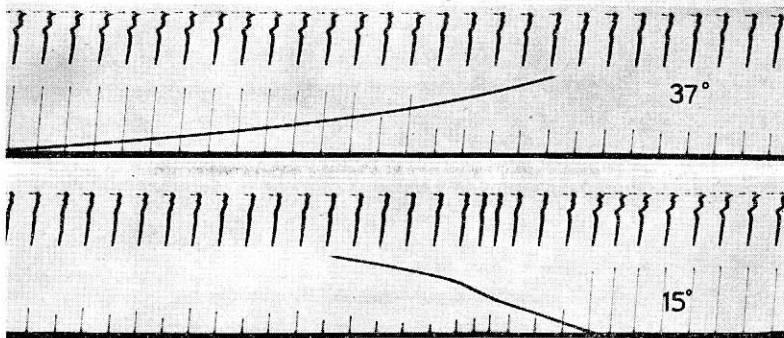


Fig. 2. As fig. 1, but thermode and electrode on each half of divided L7. See text.

and, if good from the beginning, remains practically constant at a time when the autorhythmic mechanism has ceased to respond to it. The failure of the 'cold potential' to set up a discharge is probably due to a rise in accommodation. Thus, sooner or later, it will become possible to perform the experiment without the added complication of a heavy direct discharge from the cooled root but there is nearly always a small rise of muscle tension. In some cats the experiment can be done immediately.

Fig. 2 illustrates an experiment in which the ventral root L7 had been divided into two portions. The one was placed in the thermode, the other one on the stimulating electrodes. There was no direct effect on *m. tib. ant.*, as seen from the steady baseline of the myograph at the bottom edge of the film. The tension on the muscle was negligible. The test contraction at 37° is about 300 gr. In response to the cooling of one portion of the root the

effect of the shock to the other portion is greatly facilitated. The test contraction increases to about 850 gr (the recording device did not here give full proportionality). The effect disappears immediately upon warming the root. The muscle spike increases and diminishes with the muscle contraction.

If the facilitating effect, described above, originates in the root region it should appear already in the nerve. In order to elucidate

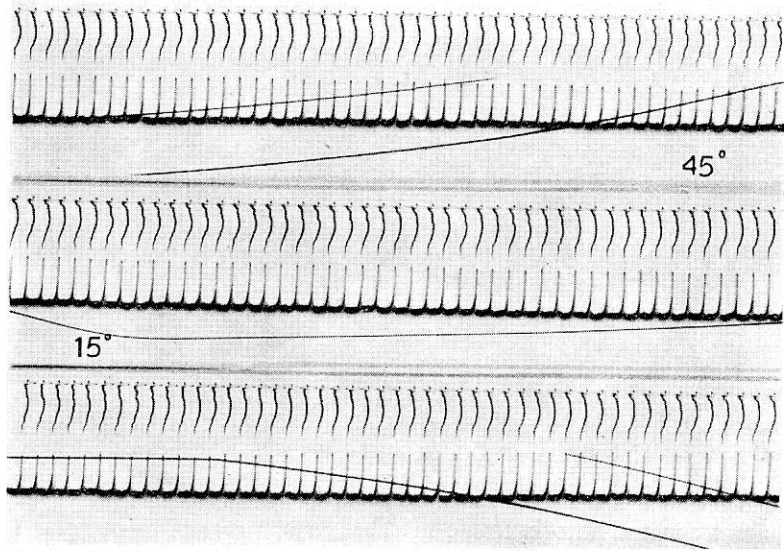


Fig. 3. As fig. 2, but in this case end of the popliteal nerve on the sweep circuit so that spike along upper edge of film is a monophasic nerve spike. Initial temperature 45° . See text.

this question the popliteal nerve was cut in the knee region while the nerve to *tib. ant.* was left intact. In the following experiment stimulating electrodes were placed on one branch of L 7, the thermode on another branch of the same root. The isometric muscle contraction is recorded from the *tib. ant.* muscle, the spike set up by the shock to the root from the cut peripheral end of the popliteal nerve.

Fig. 3 illustrates that the facilitation during cooling not only appears as an increase of the test contraction but also as an in-

crease in the size of the monophasic spike recorded from the nerve. In fact, the increase in the test contraction is modest compared with that of the spike. Both spike and contraction return to their original value upon warming.

In the same experiment the thermode was then removed and replaced by a pair of unpolarisable electrodes through which the root branch was polarised by a constant current. In series with the electrodes was a 50,000 Ω resistance. It proved possible to facilitate or depress the effect of the test shock to the other root branch by appropriate polarisation. The effects were according to Pflüger's law. Both monopolar and bipolar electrodes were used for polarisation. The currents applied were of the order of 0.1—0.4 mA.

Seeing that the thermal effect sometimes is absent, sometimes present, it is of interest to inquire into the relative number of negative and positive cases. Successful experiments were carried out on 20 decerebrate cats. In 15 experiments thermode and electrode were on different roots, mostly L 7 and S 1, in 5 experiments they were on branches of L 7, divided into two equal parts. In 13 of the 20 animals there was interaction of the kind described above, *i. e.* facilitation during cooling. In one there was facilitation upon warming. In 6 the results were wholly negative. The effect of polarisation was tried in a number of experiments. Sometimes it was present, sometimes absent.

The thermal effect, when present, generally is transient and cannot be repeated more than 3 or 4 times.

Comment.

It is clear that in a considerable proportion of the experiments there was interaction between the two roots in the sense that the cooling of one root facilitated the discharge set up by an electrical shock to an adjacent root. It is also clear that the effect of cold can be imitated by electrical polarisation. Despite this it is possible that by some process lacking electrical sign the effect of cold may be transmitted to the region, where the two roots converge, though on the whole an electrical mechanism seems the most probable one.

The phenomenon is of clinical interest and theoretically too it is of some value as a model of what might happen anywhere in the central nervous system in the fork joining confluent paths subjected to electrotonic spread of slow potential changes.

Summary.

Interaction between two adjacent roots occurs in a considerable proportion of experiments in which the effect of the test shock to one root is augmented by local cooling of an adjacent root in a thermode.

REFERENCES

- BERNHARD, C. G. and GRANIT, R.: Nerve as model temperature en-
organ. *J. gen. Physiol.*, 1946, 29, 257—265.
- v. EULER, C.: Selective responses to thermal stimulation of mammalian nerves.
Acta physiol. Scand., 1937, 14, Suppl. 45.
- GRANIT, R., LEKSELL, L. and SKOGLUND, C. R.: Fibre interaction in
injured or compressed region of nerve. *Brain*, 1944, 67, 125—140.
- GRANIT, R. and LUNDBERG, A.: Heat- and cold-sensitive mammalian
nerve fibres. Some somatic reflexes to thermostimulation. *Acta physiol.
Scand.*, 1947.
- GRANIT, R. and SKOGLUND, C. R.: The effect of temperature on the
artificial synapse formed by the cut end of the mammalian nerve. *J.
Neurophysiol.*, 1945, 8, 211—218.
- REXED, B.: Injury potentials along peripheral nerves in relation to histo-
logical structure. *J. Neurophysiol.*, 1947.
- REXED, B.: Arachnoidal proliferations with cyst formation in human spinal
nerve roots at their entry into the intervertebral foramina. *J. Neuro-
surgery*, 1947. In course of publication.