C. 6. Algebraical summation of excitation and inhibition in single-fibre tonic reflexes

By R. Granit and Barbara Renkin*. *Nobel Institute for Neurophysiology, Stockholm, 60, Sweden*

Sherrington's view that in maintained reflex activity excitation and inhibition are graded to balance out as if they were opposite terms in algebraical summation has been tested by the following experiment, which is based on a simple piece of algebra deduced from known properties of motoneurones (Granit & Rutledge, 1960; Granit, Haase & Rutledge, 1960).

By repetitive electrical stimulation of extensor muscular afferents in the decerebrate preparation a tonic reflex discharge is obtained and

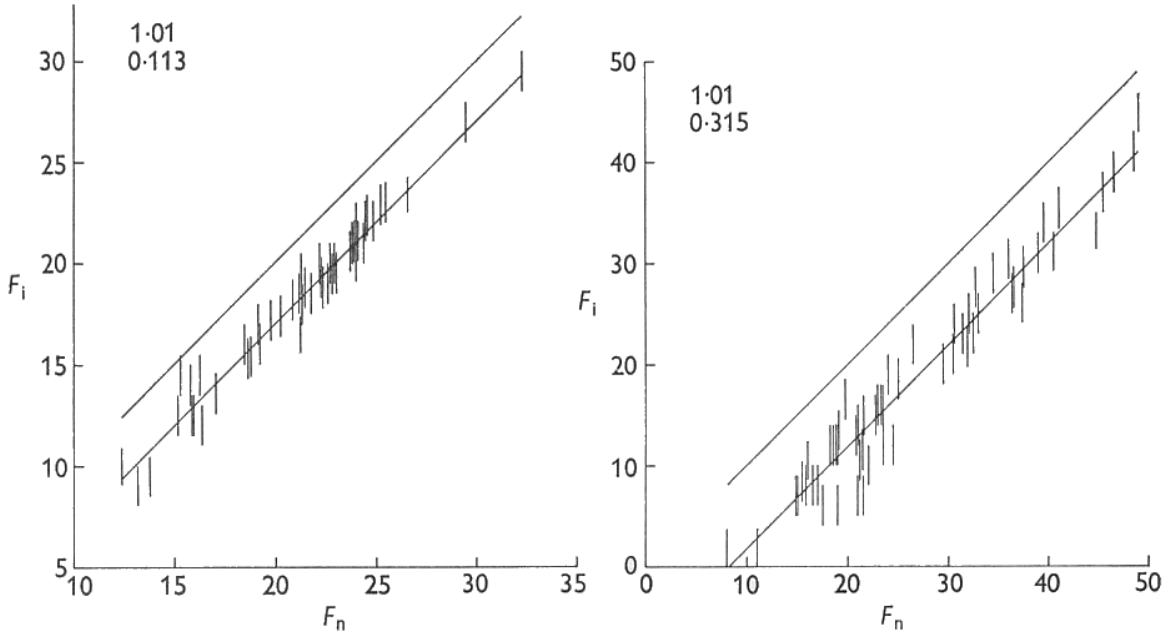

Fig. 1. Two experiments in which constant antidromic tetanus (duration 2 sec) was thrown in at intervals of 7 sec in a discharge from a motoneurone which slowly diminished in rate of firing. Thus a large frequency range F_n was obtained. It is seen that the regression line with regression coefficient 1·01 (left corner) runs parallel to the 45° degree line signifying $F_n = F_i$ or absent recurrent inhibition. Thus $F_n - F_i = \text{const}$. Below regression coefficient, standard error or $s/\sqrt{N}$, in which s is standard deviation and N number of observations.

* Visiting Fellow, Nat. Sci. Found., U.S.A., on leave from National Institutes of Health, Bethesda, Maryland.

recorded in single ventral root fibres. Its normal frequency discharge F_n can by increasing strength or rate of stimulation be varied over a certain range. A constant antidromic stimulation at about 55/sec to the rest of the ventral root is applied in order to induce a constant recurrent inhibition whose effect is to reduce F_n to a lower value F_i. In the previous papers reasons were given for assuming $F_n = k\,(P_{dep} + P_{pol})$ in which k is a proportionality constant, P_{dep} the depolarizing and P_{pol} the (inhibiting) polarizing currents. After adding to this expression the constant recurrent inhibition P'_{pol}, one obtains $F_i = k\,(P_{dep} + P_{pol} + P'_{pol})$ and thus the difference $F_n - F_i = -kP'_{pol} =$ constant.

Testing this deduction by experiment, one obtains results like those of Fig. 1. In all, 470 observations were made on 18 motoneurones. The average result was $F_n - F_i = 5{\cdot}5$ impulses/sec. The mean standard error was 0·24, the weighted mean of the 18 regression coefficients was 0·996 or thus 1·00 as required by the hypothesis (legend, Fig. 1).

When frequency of antidromic stimulation was varied, the effect $F_n - F_i$ was directly proportional to it from some 5–10 up to 30–40 shocks per sec.

Both these results are an exact replica of Hartline's findings with lateral inhibition in the eye of Limulus (cf. Hartline, 1949; Hartline & Ratliff, 1956).

REFERENCES

Granit, R. Haase, J. & Rutledge, L. T. (1960). *J. Physiol.* **154**, 308–328.
Granit, R. & Rutledge, L. T. (1960). *J. Physiol.* **154**, 288–307.
Hartline, H. K. (1949). *Fed. Proc.* **8**, 69.
Hartline, H. K. & Ratliff, F. (1956). *J. gen. Physiol.* **40**, 357–376.