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1. J. Olds and P. Milner, *J. Comp. Physiol. Psychol.* 47, 419 (1954).
2. J. Olds, *Science* 127, 315 (1958).
3. Similar utilizations of operant conditioning techniques have been reported by Blough for determining visual thresholds in the pigeon and by Weiss and Laties for measuring tolerance of pain in the rat: D. S. Blough, *Science* 121, 703 (1955); B. Weiss and V. G. Laties, *ibid.* 128, 1575 (1958).
4. Appreciation is expressed to E. R. Hart for helpful suggestions on problems of stimulation and recording.
5. J. C. Lilly *et al.*, *Science* 121, 468 (1955). The pulse-pair generator was manufactured by the Grass Instrument Co.
6. All placements specified were verified histologically.
7. The amount of rest between sequences of brain-stimulation, both during and between experimental sessions, appears to be a critical factor. Rat F-49, for example, on continuous tegmental self-regulation, typically maintained the preferred level of 13 to 15 ma for about 30 minutes, and then increased the current to the top step, keeping it there by working only the "up" lever. This current-maximizing behavior was practically eliminated by introducing the 5-minute on-off procedure and spacing experimental sessions 2 to 3 days apart. Keeping in mind the discussion at the end of the present paper, and assuming with Olds (2) that positive and negative cell groups are reciprocally inhibitory, one may conclude that these effects may reflect temporary increases in the thresholds of negatively reinforcing structures that are brought about by the intensive self-stimulation of the positive site and which dissipate in time when rest is permitted.
8. J. Olds, *J. Comp. Physiol. Psychol.* **49**, 281 (1956).
9. Continuous monitoring of the stimulating circuit by means of a cathode-ray oscilloscope and comparison resistances indicated that current increases were actually supplied to the brain and were not the result of artifacts such as polarization of the electrodes.
10. Findings related to these have been reported by W. W. Roberts, *J. Comp. Physiol. Psychol.* 51, 400 (1958) and by G. H. Bower and N. E. Miller, *ibid.* 51, 669 (1958).

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Simple Method for Determining Potential Evapotranspiration from Temperature Data

Abstract. A value for the total amount of water that, theoretically, could be lost from soil and vegetation through evaporation and transpiration, if sufficient soil moisture were always available, may be obtained readily by multiplying a given time-period factor by the sum of time-unit means of positive centigrade temperatures divided by the number of time units in the period.

Potential evapotranspiration from areas of natural vegetation may be determined from temperature records alone by the use of the following formula:

$$\text{Potential evapotranspiration (in mm)} = \left[58.93\left(\frac{\text{Unit period of time}}{\text{No. of units of time in 1 yr}}\right)\right] \times \left[\text{Comparative plant growth mean temperature (°C)}\right]$$

Solved values for the first bracket for periods of time normally used for determining potential evapotranspiration are as follows: 1 year, 58.93; month of 31 days, 5.00; month of 30 days, 4.84; month of 28 days, 4.52; and 1 day, 0.16. For leap years, monthly values would be: 31 days, 4.99; 30 days, 4.83; and 29 days, 4.67.

For tropical and subtropical regions (except at high elevations) for all periods, and for other regions for periods when temperatures do not drop below 0°C, mean temperatures, as usually recorded or published, are represented by the value within the second bracket. For periods of time which include recorded temperatures below 0°C, the comparative plant growth mean temperature must be obtained in a different manner. The latter mean temperature was utilized as one factor for determining plant formations or life zones in a chart published in 1947 (*1*), and is considered to be the mean temperature of greatest significance to vegetation, and to be directly comparable in terms of plant life with the mean at any other point on our planet. The comparative plant growth mean temperature equals the sum of the average positive temperatures in degrees centigrade per unit of time, divided by the total number of these units of time in the period of the mean.

Thus, the mean annual temperature to be utilized in the formula equals the sum of the mean monthly temperatures above 0°C divided by 12. The monthly mean equals the sum of the daily means above 0°C, divided by the number of days in that particular month. The daily mean equals the sum of the hourly means above 0°C, divided by 24. At stations where mean daily temperatures are determined as one-half the sum of the maximum and minimum temperatures, such means are satisfactory except for days when the minima are below 0°C; on such days half of the maximum temperature, if it is positive, may be used as the daily mean.

Determination of potential evapotranspiration from temperature values alone, without need for data on precipitation or other climatic factors, is possible because of the two following considerations.

1) The potential evapotranspiration rate at a given temperature decreases proportionately along the gradient of increasing precipitation from arid to wet areas, so that the product of the evapotranspiration rate and the mean annual precipitation is the same all along the gradient. This is reflected in the regularity of the pattern of changes in physiognomy between the single climatic plant associations of each of the formations along the precipitation gradient.

2) Local variations in edaphic and atmospheric factors sufficient to cause an appreciable change in either evaporation or transpiration, or in both, are counterbalanced by the different physiognomies of the natural vegetation, developed in the past through evolutionary processes, which bring the actual evapotranspiration into equilibrium with the potential evapotranspiration rate and the moisture available. These variations are reflected in the diversity of aspect and lack of regularity of the pattern of changes of the physiognomies of the (usually several) edaphic, atmospheric, and hydric associations of the same plant formations along the moisture gradient.

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1. L. R. Holdridge, *Science* 105, 367 (1947).

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Decrease in Threshold without Depolarization in Cyanide-Treated Muscle

Abstract. When smooth muscle of *Mytilus* is treated with relatively weak solutions of sodium cyanide, a transitory hyperpolarization or no change in polarization precedes final depolarization. Thresholds for thermal, chemical, and electrical stimulation are all decreased during this period. Strength-duration curves indicate a reversible decrease in threshold of about 50 percent during this period.

As an outgrowth of investigations into the nature of the mechanism of the cooling stimulus in smooth muscle of *Mytilus* (*1*), we decided to examine the relationship between inhibition of respiration by metabolic poisons and the effects of these

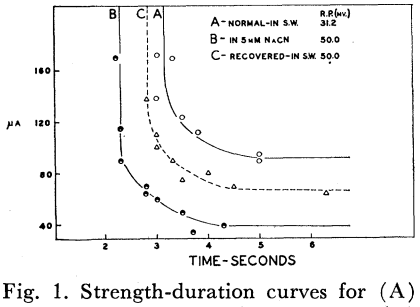

Fig. 1. Strength-duration curves for (A) normal *Mytilus* muscle in sea water; (B) the same muscle after treatment for 1 hour in 5m*M* NaCN; and (C) the same muscle subsequently allowed to recover for 1.5 hours in sea water (intensity of threshold square wave pulses in microamperes versus duration in seconds). The rheobase is decreased after treatment with cyanide, and this effect is partially reversible in sea water. The resting potential, which usually returned to the normal value after recovery in sea water, did not do so in this particular muscle, perhaps because of relatively long treatment with cyanide.

poisons on the threshold to cooling (2).

Resting potentials, recorded between the depolarized and experimental end of the muscle, were amplified and led to one channel of a dual-channel rectilinear galvanometric recorder, as in previous studies. Changes in tension were detected by a sensitive isometric transducer (3) in a bridge circuit, amplified, and led to the second channel of the recorder. The same electrodes were used for stimulating and for recording potentials.

We realized, of course, that prolonged treatment with sufficiently high concentrations of metabolic inhibitor would depress the resting potential irreversibly. Also, since it had been found in studies of this muscle that any agent which resulted in subthreshold depression of the resting potential enhanced the effect of cooling, it was obvious that one should expect that an interference with respiration would *ipso facto* decrease the threshold to cooling stimulation or to a chemical stimulus such as the application of potassium ion. This was indeed found to be the case.

However, we noticed that, in treatment with sodium cyanide, the eventual depression of the resting potential was preceded by a period in which either no change in potential occurred or an initial marked but transitory *rise in* resting potential developed if 1 or 2.5 or even 5 m*M* solutions of NaCN in sea water were used. This raised the question of the significance of the change to muscle excitability.

In 1952 Ling (4) carried out a similar study. He investigated the effects of metabolic inhibitors upon the resting potentials of frog muscle and found that 5 m*M* NaCN, which did not in itself produce a significant fall in resting potential in frog muscle, greatly hastened the fall in resting potential caused by 5 m*M* iodoacetate if the cyanide and the iodoacetate were simultaneously applied. Following this lead in our studies of invertebrate muscle, we found that during the initial treatment with cyanide, the threshold amount of cooling necessary for contraction of *Mytilus* muscle was also decreased. It was also possible to potentiate the stimulating effects of the potassium ion by means of this procedure, which does not, in the concentrations used, decrease the membrane potential but, rather, usually enhances it.

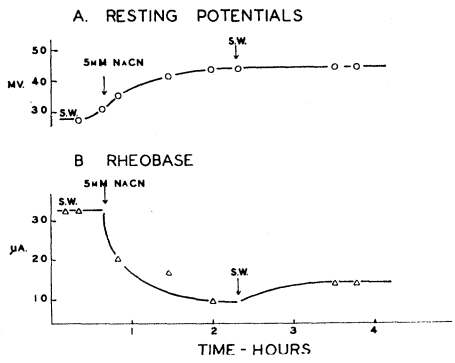

Fig. 2. Resting potentials, in millivolts (A), and rheobase, in microamperes (B), versus time, in hours, for *Mytilus* muscle treated with 5m*M* NaCN and allowed to recover in sea water. In this muscle, the time course of development of hyperpolarization mirrors the decrease in rheobase.

The phenomenon of a decrease in threshold unaccompanied by depolarization was felt to be of sufficient interest to merit further study. Consequently, in order to investigate changes in excitability quantitatively, the classical strength-duration curves were determined, first on normal muscle in sea water and then on the muscle during treatment with NaCN. Resting potential values were recorded concurrently.

It is clear that on treatment with NaCN, a decrease in threshold (5), unaccompanied by membrane depolarization, occurs, and that this effect is partially or completely reversible (depending upon the duration of treatment with cyanide) when the muscle is returned to sea water (Fig. 1). In Fig. 2, determinations of the rheobase and subsequently recorded resting potentials in another muscle are plotted against time. A correlation between degree of hyperpolarization and decrease in threshold evident in this experiment was encountered in many cases.

Hodgkin and Keynes (6) found that cyanide reduces the rate of sodium efflux in cephalopod axons, but this is not the case in frog muscle (7).

In *Mytilus* muscle, the situation is doubtless a complex one and may well involve changes in the concentrations of ions inside and outside the fibers, and changes in charge as well as changes in membrane permeability. One might attempt to explain the hyperpolarization in terms of movements of ions or water.

It is true that depolarization is normally the first step in excitation. However, the use of cyanide or some other agent may possibly affect a link in the chain of events further along than depolarization, and thus activate the contractile process (8).

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2. This work was supported in part by grant B-799(C3) made to one of us (R.G.) by the National Institutes of Health.
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24 August 1959