specified crop or animal product grown in a given locality for a representative length of time, subsequent measurements of Cs^{137} should be sufficient to monitor the Sr^{90} concentration as a function of time. This may be illustrated in the case of the U.S. Public Health Service measurements on the Cs^{137} and Sr^{90} content of milk (*13*). The results for 1958 show that the average monthly Cs^{137}/Sr^{90} activity ratio for 10 sampling stations in the United States varied from as low a value as 6.28 ± 1.28 to as much as 15.45 ± 5.62, with an average value of 10.09 ± 2.27; however, the variation about the mean found at any one station does not exceed ±40 percent (Salt Lake City), and average variation per station is ±27 percent for a 6- to 12-month period.

According to the findings in soil, it seems likely that the Sr^{90} concentration in this medium can be determined to within an error of 20 percent by measuring the Cs^{137} content and dividing by 1.6. The need for extending these observations to soils from other localities is obvious. Furthermore, if errors of 20 to 40 percent are tolerable in the estimates of Sr^{90}, relatively inexpensive surveys of wide coverage could be undertaken by monitoring Cs^{137} not only in soil but also in a great variety of material of ecological importance.

PHILIP F. GUSTAFSON
Division of Biological and Medical Research, Argonne National Laboratory, Lemont, Illinois

References and Notes

1. E. C. Anderson and W. F. Libby, *Advances in Biol. and Med. Phys.* **5**, 414 (1957); E. C. Anderson, R. L. Schuch, W. R. Fisher, W. H. Langham, *Science* **125**, 1273 (1957); E. C. Anderson, *ibid.* **128**, 882 (1958).
2. AEC Health and Safety Laboratory, *Laboratory Manual No. NYO-4700.*
3. W. H. Langham and E. C. Anderson, *Health Phys. J.*, in press.
4. The half-life of Cs^{137} is 26.6 years, that of Sr^{90} is 27.7.
5. E. P. Hardy, Jr., and S. Klein, *U.S. Atomic Energy Commission Health and Safety Lab. Publ. No. HASL-51* (1958), p. 52.
6. N. G. Stewart, R. G. D. Osmond, R. N. Crooks, E. M. R. Fisher, M. J. Owers, *U.K. Atomic Energy Authority Publ. No. AERE HP/R 2790* (1959), p. 9.
7. The soil samples were supplied through the courtesy of L. T. Alexander, Soil Survey Laboratory, U.S. Department of Agriculture.
8. The advice and cooperation of J. H. Harley of the Health and Safety Laboratory, U.S. Atomic Energy Commission, is gratefully acknowledged.
9. P. F. Gustafson, L. D. Marinelli, S. S. Brar, *Science* **127**, 1240 (1958).
10. This work was performed under the auspices of the U.S. Atomic Energy Commission. Many helpful discussions with L. D. Marinelli and J. E. Rose are hereby acknowledged. Credit in assisting with much of the spectral data goes to S. S. Brar.
11. P. F. Gustafson, *Argonne Natl. Lab. Rept. No. 5919* (1958), p. 62.
12. H. Nishita, B. W. Kowalewsky, A. J. Steen, K. H. Larson, *Soil Sci.* **81**, 317 (1956).
13. Data released by the Public Health Service, U.S. Department of Health, Education, and Welfare, Feb. 1959.

24 June 1959

Electrical Output of a Receptor Membrane

Abstract. The electrical output of the receptor membrane of the nonmyelinated ending of Pacinian corpuscles is a function of the electrical gradients across the receptor membrane. The generator potential of the receptor membrane in response to equal mechanical stimuli varies linearly with the intensity of polarizing currents passed through the membrane. The production of a generator potential leaves a refractory state in the receptor membrane which is independent of the amount of charge transferred across the membrane but is dependent on a factor related to the strength of the stimulus which produced the response.

The receptor membrane of the nonmyelinated nerve ending of Pacinian corpuscles has the peculiarity that small regions of it can be excited independently. When a mechanical stimulus is applied to a small portion of nerve ending, the resulting electric response is confined to that region which has been stimulated mechanically and is not propagated to nonstimulated regions of the same receptor membrane by local circuit excitation (*1-3*). The generator potential of the entire receptor membrane appears to be built up by spatial summation of the electric activity of small independently excitable membrane regions (*generator elements*) (*2*).

For analytical purposes, the output of each generator element may be considered all-or-nothing with respect to the strength of the mechanical stimulus. The entire input-output relation of the receptor membrane—namely, the finely graded relation between stimulus strength and generator potential amplitude—may then be accounted for by spatial summation of the activity of such generator elements (*2*). The experiments described in the present report reveal that, although the electrical output at each generator element may be all-or-nothing with respect to the strength of the mechanical stimulus, it is graded with respect to the electrical gradients across the generator element.

The membrane potential of the receptor membrane was changed by passing inward or outward currents through the nonmyelinated nerve ending, while generator potentials were produced in this membrane by mechanical stimulation with a piezoelectric crystal stimulator. The capsules of single isolated Pacinian corpuscles were removed by microdissection. Each such preparation, consisting mainly of a nonmyelinated ending, has already been shown to have essentially the same mechanoreceptor properties as it has in the intact corpuscle (*4*). The decapsulated preparation offered a relatively naked nonmyelinated ending onto which polarizing currents were directly applied, and from which mechanically elicited generator potentials were directly led off with nonpolarizable electrodes, as is shown in Fig. 1.

When steady inward or outward currents are passed through the receptor membrane, the amplitude of the generator potential in response to a mechanical stimulus of constant strength varies as a linear function of the polarizing current (Fig. 2). The rate of rise of the generator potential is also a func-

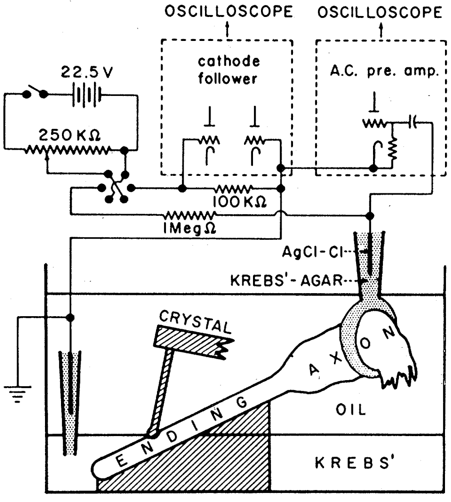

Fig. 1. Set-up for mechanical stimulation, polarization, and recording of the receptor membrane.

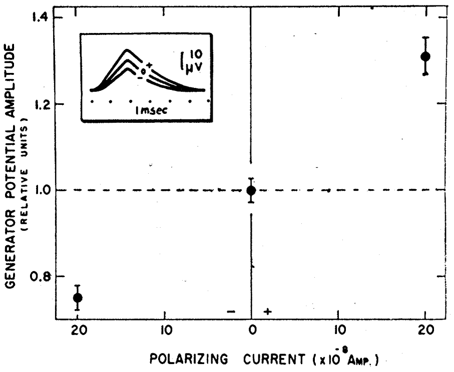

Fig. 2. Amplitude of mechanically elicited generator potential as a function of polarizing current. The mean amplitude of generator potential in response to equal mechanical stimuli is determined for various intensities of current flowing inward (hyperpolarizing, +) or outward (depolarizing, —) across the receptor membrane. The vertical bars subtend the standard error of the mean of approximately 30 generator potentials in each case. At any chosen current intensity, the polarizing current was on for at least 30 seconds before the start of each series of generator potential determinations. This allowed stable measurements. The inset shows three individual generator potentials (one of each series) whose mean amplitude is plotted in the main figure.

tion of the polarizing current. An analysis of these results, given elsewhere (*5*), suggests the following possibility: The mechanical stimulus causes the membrane potential across each generator element to drop to a certain fraction of the resting potential. This is equivalent to assuming that the transmembrane resistance across each generator element is shunted by a fixed leak resistor, when excited. This might occur, for example, if the activated generator element became permeable to all kinds of ions, as has been postulated for the end plate membrane of skeletal musculature (*6*). An increase in resting potential obtained by polarizing the receptor membrane with an inward current would then cause a proportionally increased fractional drop of membrane potential. Hence the generator potential, which is the aggregate result of all excited generator elements, should be directly proportional to the resting potential (*2*) (and to the polarizing current). It is of interest that the generator potential of a visual receptor has also been reported to increase as a function of the resting membrane potential (*7*).

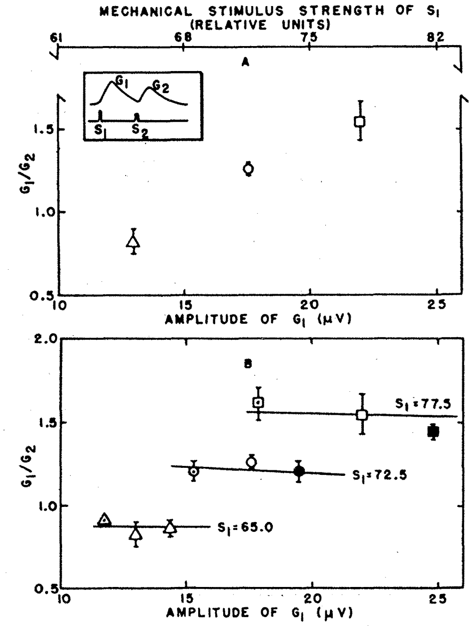

Fig. 3. Refractoriness of the receptor membrane unrelated to charge transfer. Two mechanical stimuli (S_1 and S_2) are successively applied so that the generator potential (G_2) in response to the second stimulus falls on the refractory trail of the generator potential (G_1) in response to the first. The ratio G_1/G_2 is determined while the amplitude of G_1—that is, the total amount of charge transferred—is varied in *A* by varying the stimulus strength (S_1) at constant resting membrane potential, and in *B*, by varying the resting potential across the receptor membrane at constant stimulus strength. (G_1 in response to three steps of stimulus strength was varied in *B* over a range of generator potential by polarizing currents.) Values of S_1 are displacements of the crystal stimulator given in relative units. S_2 was constant throughout all experiments. The vertical bars subtend a standard error of mean of approximately 30 generator potentials in each case. Curves in *B* were drawn by the method of least squaring.

It has previously been shown that excitation of a small region of the receptor membrane leaves a refractory condition behind so that a subsequent application of a mechanical stimulus to the same region elicits a response that is considerably smaller than normal. The refractory state, like the excited state, is confined to the mechanically stimulated region but does not spread to adjacent regions (*1, 2*). If a generator potential is produced by applying a mechanical (conditioning) stimulus to a relatively large area of receptor membrane—that is, to an area containing a relatively large number of generator elements—a subsequent equal (test) stimulus, falling on the refractory trail of the first, elicits a generator potential of an amplitude inversely related to that of the conditioning generator potential (*8, 9*). The measure of this effect has been called the "size factor of refractoriness" (*10*).

Since the amplitude of the generator potential increases as a function of the number of excited generator elements (*2*), and as a function of the electrical gradients across each excited generator element as well, the question arises whether it is the amount of charge transferred in response to the conditioning stimulus or the number of generator elements excited by the conditioning stimulus which determines the size factor of refractoriness. The present set-up gave us the opportunity to explore this question. The conditioning generator potential could be varied either by (i) changing the strength of the stimulus or by (ii) polarizing the receptor membrane at constant stimulus strength. By the first procedure, the number of conditioning-excited generator elements is varied at constant resting membrane potential of generator elements; by the second, the membrane potential of a given excited population of generator elements is varied. The results are shown in Fig. 3. It is seen that with procedure (i) the size factor—namely, the ratio of conditioning (G_1) to test generator potential (G_2)—increases progressively with the amplitude of conditioning generator potential (Fig. 3*A*), while this ratio remains approximately constant with procedure (ii) (Fig. 3*B*). It is clear from this result that the size factor of refractoriness does not depend on the amount of charge transferred but on another factor related to the strength of the stimulus.

The following explanation may be offered for this result: The conditioning stimulus excites a number of generator elements out of a statistically fluctuating population of excitable elements. Excitation of a generator element is followed by a refractory period. The first of these assertions has a good experimental basis (*9, 11*); the second is an assumption. If, then, a test stimulus is applied during the refractory period, the number of nonrefractory generator elements available for excitation at the instant of application of the test stimulus may be expected to decrease with an increase in the number of generator elements excited by the conditioning stimulus. Hence the amplitude of test generator potential, which is a function of the number of excited generator elements (*2*), will expectedly decrease as a function of conditioning generator potential. A quantitative analysis of this question is given elsewhere (*5*) (*12*).

NOBUSADA ISHIKO*
WERNER R. LOEWENSTEIN
Department of Physiology,
Columbia University College of
Physicians and Surgeons, New York

References and Notes

1. W. R. Loewenstein, *Nature* **183**, 1724 (1959).
2. ———, *Ann. N.Y. Acad. Sci.* **81**, 367 (1959).
3. For a general treatment of this matter see H. Grundfest, *Physiol. Revs.* **37**, 337 (1957).
4. W. R. Loewenstein and R. Rathkamp, *ibid.* **41**, 1245 (1958).
5. W. R. Loewenstein and N. Ishiko, *ibid.*, in press.
6. P. Fatt and B. Katz, *J. Physiol. (London)* **115**, 320 (1951).
7. M. G. F. Fourtes, *Am. J. Ophthalmol.* **46**, 13 (1958).
8. J. A. B. Gray and M. Sato, *J. Physiol. (London)* **122**, 610 (1953).
9. W. R. Loewenstein, *J. Gen. Physiol*, **41**, 825 (1958).
10. W. R. Loewenstein and R. Altamirano-Orrego, *J. Gen. Physiol.* **41**, 805 (1958).
11. ———, S. Socolar, S. Cohen, *ibid.*, in press; N. Ishiko and W. R. Loewenstein, *ibid.* **183**, 1725 (1959).
12. This work was aided by research grants from the National Institute of Neurological Diseases and Blindness (B-1466) and the National Science Foundation.

* On leave of absence from Kumamoto University Medical School, Kumamoto, Japan.

30 June 1959

Molecular Pumping

Abstract. A method is described for producing high vacua. A magnetically suspended molecular pumping rotor is operated inside a sealed glass vacuum system. The system is free of lubricants and can be baked out. The system gives promise of producing pressures below those previously used.

Gaede (*1*), Holweck (*2*), Siebahn (*3*), and others (*4, 5*) have amply demonstrated the effectiveness of molecular pumping for producing vacua. In some of their experiments the lowest pressure obtained was limited only by the vapor