carried out the full derivation of Eq. 14, and used the method of Staverman (8) to derive an equation relating electric current flux I to potential difference Efor a membrane system in which active transport processes occur (10). This relation, which can now readily be shown to apply to any system of parallel phases and boundaries, is

$$\mathbf{I} = L_E E + \sum_{j} t'_{j} \Delta \mu_j + \sum_{j} z_j F \mathbf{J}_j^A \quad (15)$$

Here L_E is the electric permeability or conductance, t'_{j} the reduced transference numbers (8), and \mathbf{J}_{j}^{A} the active components of the flux.

Equation 15 is now seen to be quite general, applicable to any system of parallel membranes and phases regardless of the occurrence within the system of electric fields, fixed charges, polarizable molecules, or active transport processes. The equation takes on classical forms in simple cases. It reduces to Ohm's law when there are no chemical potential differences or active transport processes. When no current flows, in the absence of active transport, and with the same uni-univalent electrolyte on both sides of the membrane, it yields the Nernst liquid junction potential equation (2). When the chemical and electrical potential differences are zero, in the presence of active transport, the current flux is equal to the active transport current, as Ussing has shown for frog skin (11). For the more complicated situation across the membrane of the nerve axon, Eq. 15 readily yields the Hodgkin and Huxley equation for the resting current-voltage relation when the net active transport current is zero (12). Equation 15 is not readily reduced to the complex liquid junction equation of Planck (3), nor to the membrane equations of Teorell (4), Goldman (5), or Hodgkin and Katz (6). All of these use concentrations instead of chemical potentials, and the membrane equations utilize a number of assumptions about the membrane field and the concentration relations between the membrane and the external solutions. The constants in the resulting equations are consequently not comparable to the constants in Eq. 15, which are directly and simply related to the phenomenological coefficients.

In a previous report, I have noted the fact that for several types of biological membrane system, the resting current-voltage relation is linear, as Eq. 15 predicts (10). The equation is derived from thermodynamic considerations, and consequently is not related

to any mechanism of active transport; it cannot, therefore, be used by itself to test the validity of any such mechanism. It is not applicable in conditions which depart from the steady state, as in the excited nerve membrane. It should, however, have considerable value in the experimental study of diffusion, liquid junction potentials, and the important related phenomena in living membranes.

BRADLEY T. SCHEER

Department of Biology,

University of Oregon, Eugene

References and Notes

- A. Fick., Ann. Physik Leipzig 170, 59 (1855).
 W. Nernst, Z. physik. Chem. (Leipzig) 2, 613 (1888).
- 3. M. Planck, Ann. physik. Chem. n.f. 40, 561
- M. Planck, Ann. physik. Chem. n.t. 40, 561 (1890).
 T. Teorell, Proc. Soc. Exptl. Biol. Med. 33, 282 (1935); J. Gen. Physiol. 19, 917 (1936);
 Z. Elektrochem. 55, 460 (1951); Progress in Biophysics and Biophysical Chemistry, J. A. V. Butler and J. T. Randall, Eds. (Pergamon Press, New York, 1953), vol. 3, p. 155.
 D. E. Goldman, J. Gen. Physiol. 27, 37 (1945). 4.
- 5. D. (1943)
- (1943).
 6. A. L. Hodgkin and B. Katz, J. Physiol. (London) 108, 37 (1949).
 7. I. Prigogine, P. Mazur, R. Defay, J. chim. phys. 50, 146 (1953).
 8. A. J. Staverman, Trans. Faraday Soc. 48, 176 (1963). 1952
- (1952).
 9. I. Prigogine, Introduction to the Thermo-dynamics of Irreversible Processes (Thomas, Springfield, Ill., 1955). B. T. Scheer, Bull. Math. Biophys. 22, 269
- 10. B. (1960).
 11. H. H. Ussing and K. Zerahn, Acta Physiol.
- R. H. OSME and K. Leffin, New Physics Scand. 23, 110 (1951).
 A. L. Hodgkin and A. F. Huxley, J. Physiol. (London) 117, 500 (1952).

31 July 1961

Temporal Discrimination in Pigeons

Abstract. Pigeons trained to peck a lighted key were presented with a key that was alternately dark and lighted. The key was dark for intervals of from 3 to 30 seconds. Pecking of the lighted key was reinforced only after the shortest or, in a second experiment, the longest interval that the key was dark. The pigeons were able to discriminate the duration of the dark interval.

Previous studies (1) have shown that organisms can discriminate the duration of a stimulus. In a fixed-interval schedule of reinforcement (2), for example, a response is reinforced only after a fixed interval of time has elapsed since the previous reinforcement. The frequency of responding generally increases throughout the interval between two reinforcements, indicating that the organisms are to some extent sensitive to the passage of time.

Our procedure (3) was a modification of a standard procedure for the simultaneous study of stimulus discrimination

and generalization (4). In the standard procedure as applied to pigeons, several different stimuli, lights of different wavelength, for example, are successively presented to the pigeon. Pecks are reinforced with food in the presence of one wavelength and not in the presence of the other wavelengths. The frequency of pecking plotted against wavelength reveals both discrimination of the wavelength associated with reinforcement and generalization to wavelengths adjacent to it on the continuum. This procedure was modified in our work to accommodate a peculiarity of the continuum of duration, namely, that the duration of a stimulus does not have a single, unchanging value until the stimulus has terminated. Accordingly, in order precisely to define the durations to which our pigeons responded, we exposed them to various durations of a stimulus and allowed them to peck after, rather than during, the presentation of each duration. Pecking was reinforced after one duration and was not reinforced after the other durations.

The experiments were conducted in a standard pigeon chamber containing a feeder for delivering grain to the pigeon and a circular plastic key that could be illuminated with orange light. For observing the birds, there was dim overhead illumination throughout each session. The pigeons were maintained at 80 percent of free-feeding weight and had previously been trained to peck a lighted key.

In each daily session, intervals of various durations during which the key was dark were each followed by a 30second interval during which the key was lighted. The dark-key intervals ranged from 3 to 30 seconds in steps of 3 seconds. They were presented in an irregular order (5). Each duration occurred 12 times per session. In the first experiment, pecks on the lighted key were reinforced only after a darkkey interval of 3 seconds, and were not reinforced after longer dark-key intervals. In the second experiment, pecks on the lighted key were reinforced only after a dark-key interval of 30 seconds, and were not reinforced after shorter dark-key intervals. Reinforcement was a presentation of grain for 3 seconds, according to a variable-interval schedule with an average interreinforcement interval of 20 seconds.

Figure 1 shows the results of the two experiments for each of four pigeons. The median number of pecks on the lighted key during the last five sessions of each experiment is plotted against the duration of the preceding dark-key interval. The open circles show the frequencies when pecking was reinforced after a dark-key interval of 3 seconds; the solid circles show the frequency when pecking was reinforced after a dark-key interval of 30 seconds. The lighted key was pecked most frequently after the dark-key interval preceding reinforcement. The frequency of pecking was lower after dark-key intervals that were longer or shorter than the interval preceding reinforcement. The pigeons both discriminated the duration of the dark-key interval and generalized to similar duration.

The relations in Fig. 1 are adequately fitted by power functions of the form $N = kt^{\circ}$, where N is the number of responses and t is the duration of the preceding dark-key period. The functions differ in the value of the constants k and c.

Observation of the birds revealed no systematic changes in their behavior within individual presentations of the dark key. The number of pecks on the dark key never exceeded 40 per session, an average of one peck for every three presentations of the dark key.

The data in Fig. 1 indicate that pigeons can discriminate a difference as small as 3 seconds in 30 in the duration of a stimulus. Pigeon 236, for example, increased its frequency of pecking from about 300 pecks per session after 27-second intervals to about 550 pecks after 30-second intervals. From this large change in the frequency of pecking, however, it seems certain that the pigeon could discriminate differences in duration of less than 3 seconds in 30. Our procedure could be modified



Fig. 1. Median number of key-pecks per session during the presentation of a lighted key, as a function of the duration of the preceding dark-key interval for four pigeons. For the open circles, pecking on the lighted key was reinforced only after dark-key intervals of 3 seconds; for the solid circles, only after dark-key intervals of 30 seconds. The bottom right graph shows the effect of 2.5 mg of chlorpromazine on the discrimination of duration by pigeon 236. Reinforcement occurred only after the key was dark for 30 seconds.

26 JANUARY 1962

to measure directly, at different points on the continuum of duration, the change in duration that produces a given small change in the frequency of pecking. One duration, always followed by reinforcement, could be held constant, while a second duration is progressively made less different from the first.

A problem encountered with the present series of stimuli was the tendency of the pigeons to peck infrequently after any interval that followed reinforcement. This tendency came from the fact that reinforcement was always followed by nonreinforcement, because two dark-key intervals associated with reinforcement were never presented successively. The low rate of pecking just after reinforcement accounts for the systematic depression in the number of pecks after 21-second stimuli in Fig. 1. This artifact disappears when the correlation between reinforcement and nonreinforcement is reduced by arranging the sequence of dark-key intervals so that the interval associated with reinforcement recurs two or three times in succession.

Factors that affect the discrimination of duration, such as drugs, may be accurately studied with the present procedure. For example, the bottom graph in the right column of Fig. 1 shows the performance obtained when 2.5 mg of chlorpromazine was injected into the breast muscle of pigeon 236, 30 minutes before the start of a session (solid circles). Reinforcement occurred only after a dark-key interval of 30 seconds. The open circles show the undrugged, control performance from the previous day. This dosage of chlorpromazine does not abolish pecking, but it attenuates the discrimination of duration of a stimulus.

G. S. REYNOLDS A. CHARLES CATANIA Psychological Laboratories, Harvard

University, Cambridge, Massachusetts

References and Notes

- C. F. Sams and E. C. Tolman, J. Comp. and Physiol. Psychol. 5, 255 (1925); H. Woodrow, *ibid.* 8, 395 (1928). Additional citations in P. Fraisse, Psychologie du Temps (Presses Universitaires, Paris, 1957), especially pp. 51-59.
 C. B. Ferster and B. F. Skinner, Schedules of Reinforcement (Appleter Construct Constru-tion)
- Reinforcement (Appleton-Century-Crofts, New York, 1957).
- Research supported by grant G-8621 from the National Science Foundation.
 4. For example, R. Pierrel, J. Exptl. Anal. Behav.
- 303 (1958)
- 5. The order of presentation of the durations The order of presentation of the durations was as follows, the bird starting in a different place in the series each day: 24, 30, 21, 6, 27, 12, 18, 9, 15, 3, 12, 6, 18, 27, 9, 24, 3, 30, 15, 21, 15, 30, 9, 27, 12, 24, 18, 6, 3, 21seconds.

27 October 1961

315