Electrical Impedance Changes of the Cat's Foot Pad in Relation to Sweat Secretion and Reabsorption

DAVID P. C. LLOYD

From The Rockefeller Institute

ABSTRACT Impedance across the cat's foot pad, the glands being at rest, has a high quite constant value in a given preparation. Stimulation of the sudomotor nerves causes a decrease to a low constant value. After cessation of stimulation impedance returns slowly over a course that is linear with respect to the logarithm of time. The resistive and capacitative components vary with each other. Sweat reabsorption during recovery progresses linearly with respect to time. Hence impedance varies as the logarithm of reabsorption, and therefore as the mean level of sweat columns in the ducts. This relation can be accommodated by supposing that the sweat duct epithelium resembles a core conductor. An electrical model constructed on this principle is shown to behave as does the foot pad. During stimulation at a fixed frequency impedance change varies as the logarithm of duration showing that the amount of sweat produced per impulse at a given frequency is a constant. With frequency of a fixed number of stimuli varied the impedance change varies with it in a manner consistent with the view that the amount of sweat produced per impulse is a constant regardless of frequency.

That which follows is a description of the impedance changes that occur as the sweat glands of the cat's foot pad are thrown into activity by stimulation of their secretomotor supply and as they return to the fully resting state. A preliminary account of this material was presented at the Cambridge meeting of The Physiological Society (Lloyd (1958)).

Cats, in nembutal narcosis, were employed. The plantar nerves, which contain the secretomotor fibers, were exposed under oil, severed centrally, and fitted with stimulating electrodes. Zn–$ZnSO_4$ electrodes were placed one upon the central foot pad of the hind limb, the other subcutaneously below the ankle. These were held in place with plastic tape (Scotch electrical tape) and the entire foot bound with the same material to provide a barrier against evaporation. The leads from these electrodes were taken to an impedance bridge so that the tissues between the electrodes, most importantly the skin of the foot pad, constituted the unknown arm. The generator

Received for publication, June 29, 1959.

was set at 20 cycles which by trial was found to be a convenient fixed frequency, and the cathode ray oscilloscope with associated capacity-coupled amplifier served as detector. With the sweat glands at rest, or fully active, and during the slow course of recovery from activity to the resting state the oscilloscope could be used as a null-point instrument. During rapid changes, however, such as occur during stimulation, it was necessary to rely upon oscillographic recording of bridge imbalance, the width of the recorded band indicating the degree of imbalance. Examples of such recordings are to be found in an earlier paper (Lloyd (1959*b*)). The system was calibrated and measurements from recordings corrected for non-linearity.

TABLE I

EXAMPLES OF IMPEDANCE VALUES AT REST AND AT STEADY STATE OF MAXIMAL ACTIVITY IN INITIAL AND SUBSEQUENT TRIALS

	Resting		Active	
Trial No.	Ω	μ fd.	Ω	μ fd.
1	45,500	0.38	14,300	0.15
Final recovery	44,900	0.37	—	—
1	42,800	0.527	6,000	0.127
2 (60 min. rest)	31,400	0.426	6,600	0.146
(87 min. rest)	31,500	0.466	—	—
1	115,500	0.65	12,000	0.15
2	106,000	0.69	11,400	0.16
3	98,000	0.7	12,000	0.16
4	110,000	0.75	11,900	0.16
1	94,300	0.56	16,850	0.17
Final recovery	66,000	0.43	—	—
1	58,500	0.55	19,800	0.27
Final recovery	59,000	—	—	—

The foot pad provides a resistance with appreciable associated capacitative reactance. To obtain the best null when measuring A.C. resistance a variable capacitor was used. The comparison resistance and the variable capacitor then were adjusted alternately until full balance was achieved. With a little experience and knowledge of what to expect this could be done as frequently as once a minute.

IMPEDANCE AT REST AND IN MAXIMAL ACTIVITY Impedance across the foot pad of the cat is constant in three known circumstances: when the glands, their motor nerve supply severed, are at complete rest; when through stimulation of that motor nerve supply the glands are fully active and the ducts full; and when through appropriate selection of stimulus frequency the processes of secretion and reabsorption are on the average exactly in balance, the ducts not being full (Lloyd (1959*b*)).

The sweat glands being initially at rest, stimulation of their nerve supply causes the foot pad impedance to fall from a high value to a low value. On the average at rest the impedance bridge is balanced with some 60 kilohms and 0.5 to 0.6 μ fd. in the comparison arm. These values decrease as stimulation progresses to reach a final steady value of some 9 kω and 0.15 μ fd. on the average. At the close of stimulation impedance begins slowly to return to or toward the initial resting value. Those values for resistance and capacity obtaining at the beginning of the experiment are not always reached when recovery has reached the level of no further change. Table I contains some values illustrative of the foregoing remarks.

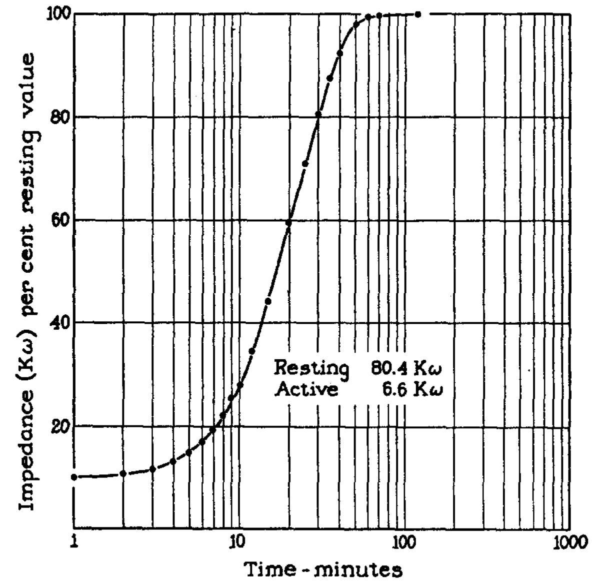

FIGURE 1. Course of impedance change following the end of a stimulation of the sudomotor nerves, at 10 per sec. frequency, sufficient in duration to bring the impedance level to a steady low value indicating full activity.

IMPEDANCE CHANGE FOLLOWING MAXIMAL ACTIVITY It is convenient to begin an account of impedance change with a consideration of that which occurs as the sweat glands recover, through reabsorption, from the fully active state to the fully resting condition. Fig. 1 exemplifies the change encountered. During the first few minutes after the close of stimulation there is but a slight increase in impedance of the foot pad. After this interval, which may vary from 2 to 8 minutes in duration, and until recovery is very nearly complete, the course of impedance change is linear with respect to the logarithm of time. The resting condition is reached in something under 2 hours.

Capacitance of the cat's foot pad varies *pari passu* with resistance during change from one state to another. In Fig. 2 are plotted, one against the other,

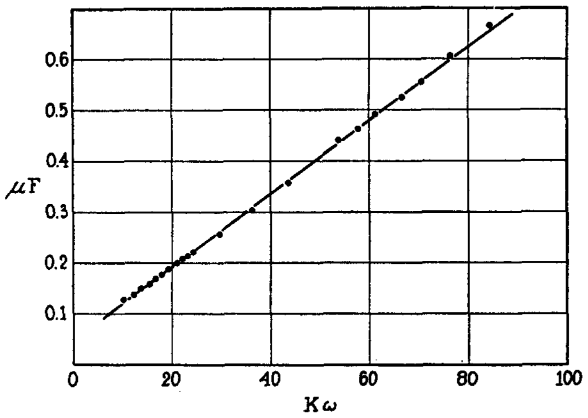

FIGURE 2. Relation between resistance and capacity of the cat's foot pad during recovery from maximal activity.

the capacitance and resistance readings at which exact bridge balance was achieved at various times during recovery from maximal activity.

IMPEDANCE CHANGE AND REABSORPTION CORRELATED Figs. 3 and 4 are taken from an experiment in which impedance change during recovery was measured (Fig. 3) as was also the latent period for beginning sweat emergence following rest periods of varying duration (Fig. 4). The latter forms a measure of the course of sweat reabsorption (Lloyd (1959*a*)). Comparison indicates the relationship between the two events. Since impedance change, over most of

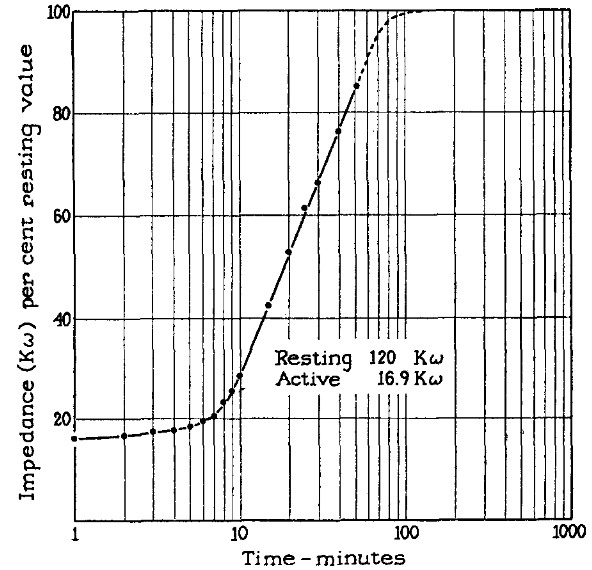

FIGURE 3. As Fig. 1, but from another experiment.

its course, is linear with respect to the logarithm of time, and sweat reabsorption, as determined by emergence latencies, is linear with respect to time itself it follows that impedance varies, over a considerable range, as the logarithm of reabsorption.

The early course of impedance change following maximal activity probably has no simple explanation. One certain cause is that the sweat glands, as Langley (1894) noted, continue to pour out sweat for a considerable period after a maximal stimulation. Another possible cause is that the foot pad is covered by a thick paste of kaolin-$ZnSO_4$, which it is not during visual inspection. This being so one may suppose that the reabsorptive force might need to act for a considerable period before the union between sweat column and kaolin paste is broken allowing the former to recede with attendant increase in impedance.

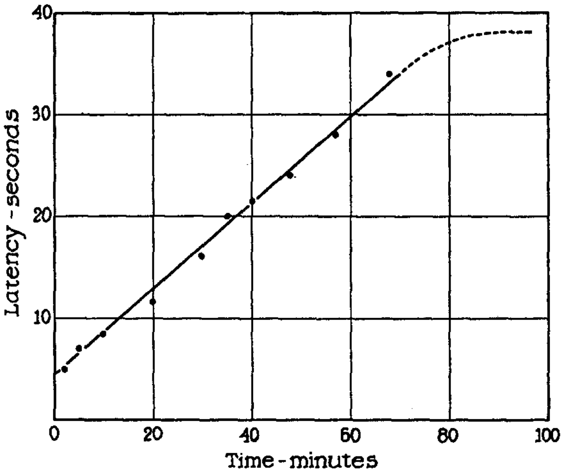

FIGURE 4. Latency for beginning sweat emergence at the surface of the foot pad as a function of rest period duration following a maximal stimulation. From the same experiment as Fig. 3. Figs. 3 and 4 taken in conjunction show the logarithmic relation between impedance of the foot pad and level of the sweat columns in the ducts.

AN ELECTRICAL MODEL OF A SWEAT GLAND The reason for logarithmic relation between impedance change and reabsorption (which is to say change in mean level of sweat columns in the ducts) may not be immediately obvious. It becomes so, however, if one considers the electrical structure of the foot pad and sweat glands, which is represented in Fig. 5. In the network as drawn R_0 represents the longitudinal resistance of the foot pad surface. R_s represents the transverse resistance of the skin which is high. R_d is the longitudinal resistance at the duct wall surface. It is presumably less per unit length than is R_s. R_e is the transverse resistance of the ductal epithelium. It would have a high value, but one that undoubtedly is less than is R_s. R_i represents the internal, or tissue, resistance, which is comparatively low. Finally R_f represents the longitudinal resistance of the fluid sweat column. It would have a low value, comparable per unit volume to R_i. R_f however, is variable according to length. The switch, S_1, is arranged to represent in successive positions equal increments, or decrements, in the sweat column. For the purpose of simplicity the capacitances of the network have been omitted. They would lie in parallel with R_s and R_e.

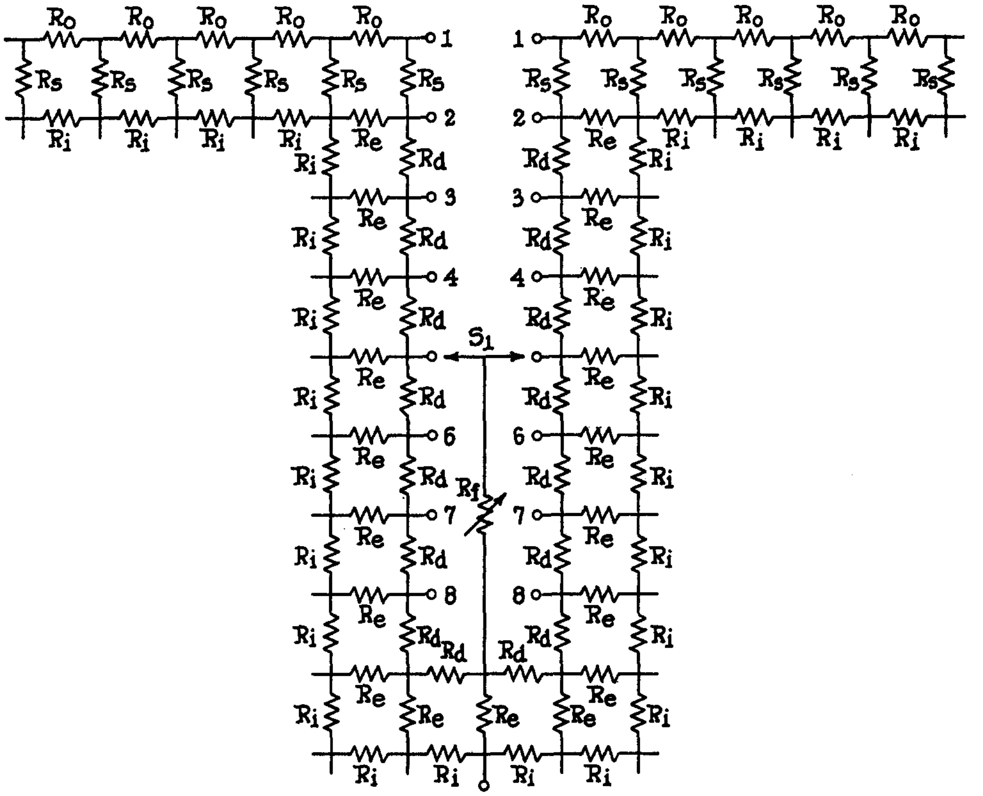

FIGURE 5. Electrical model of a sweat gland. Full description in the text.

It is evident from inspection that the electrical model of a sweat gland is none other than an especial case of the core conductor model advanced by Hermann (1879) to describe the muscle fiber membrane. Clearly the model as illustrated is oversimplified inasmuch as it is two dimensional whereas the foot pad is three dimensional. However, the general properties of the model are not altered thereby and, in fact, it is obvious that the model can be simplified still further and retain its essential electrical properties.

Fig. 6 describes a simplified model that was constructed and plots the A.C. resistance of the networks between points A and B (*i.e.* across the "foot pad") as S_1 is moved through its several positions (1 to 10) to represent linear decrements in length of the sweat column. The plotted result was obtained without a variable resistance R_f in the shunting arm. With R_f present, and varied linearly with length of the shunting arm, the slope of the resulting plot was altered without, however, changing the general relationship.

In view of the result plotted in Fig. 6 it would appear that the manner in which impedance varies with change in the level of sweat in the ducts is accounted for adequately by the supposition that the epithelium possesses core conductor properties.

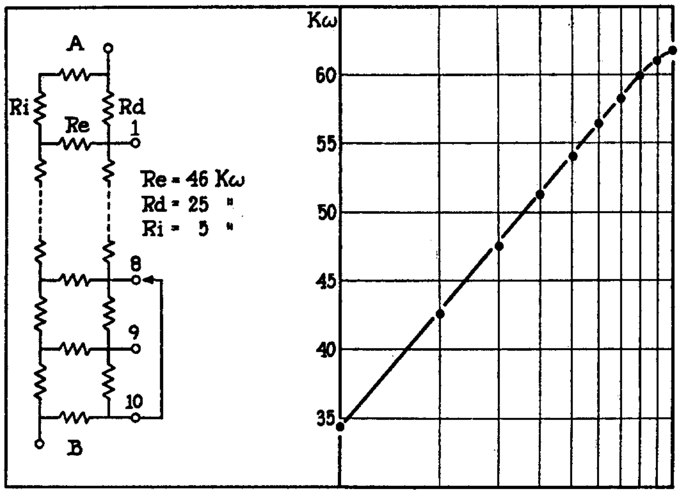

FIGURE 6. Left, schematic of simplified core conductor model of a sweat gland. Right, Impedance change between points A and B of the network shown on the left as the shunt is moved progressively from position 1 to position 10.

IMPEDANCE CHANGE DURING ACTIVITY Impedance change during activity is related, within limits, to duration of stimulation, frequency being fixed, and to the stimulus frequency. Fig. 7 illustrates the effect of altering the duration of stimulation at a fixed frequency of 10 per sec. To do the experiment a certain impedance level is selected as reference and the bridge balanced. Between each observation time is allowed for the bridge to return to that balance. Thus each point represents the degree of change from reference impedance level that is produced by a stimulation of the designated duration. It is impractical to allow rest periods long enough to secure full recovery.

Over most of the range impedance change runs a logarithmic course with respect to stimulus duration. The supposition would be that this logarithmic relation will hold provided all the ducts contain some sweat and none is full and hence not contributing to change. Since a logarithmic relation holds between impedance and the mean length of the sweat columns in the ducts (Figs.

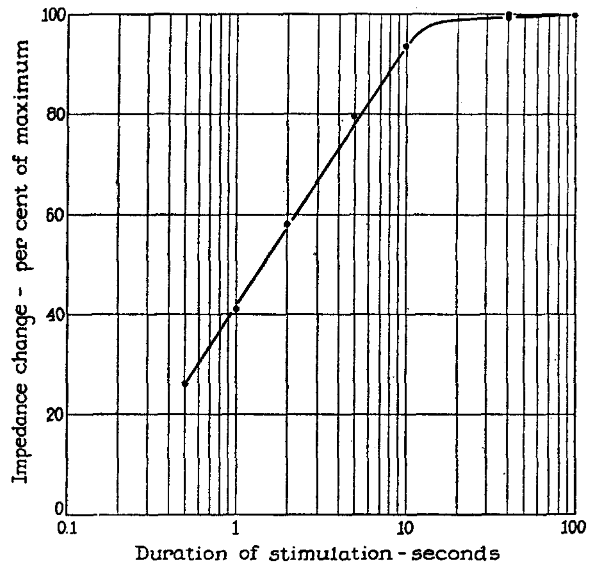

Figure 7. Impedance change across the cat's foot pad as a function of stimulus duration at a fixed frequency of 10 per sec.

3 and 4) it follows from the relation described by Fig. 7 that duct filling, which is to say sweat secretion, is linearly related to the duration of stimulation. Frequency being fixed it further follows that the amount of sweat produced per nerve impulse at a given frequency is a constant.

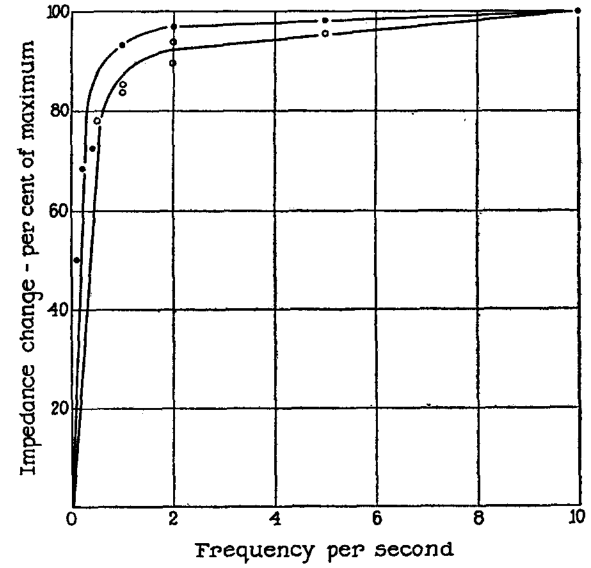

Figure 8. Impedance change across the cat's foot pad as a function of stimulus frequency the number of motor volleys being held constant at 20.

Fig. 8 shows the effect of varying frequency of stimulation. At each frequency the impedance change caused by a train of twenty stimuli is measured. Such trains in the circumstances are too brief to result in the appearance of sweat droplets on the foot pad surface (Lloyd, 1959*a*). Hence the plotted curves of Fig. 8 are not distorted by some glands being non-contributory, through completion, to impedance change. A fixed number of stimuli was chosen rather than a fixed duration of stimulation as the more suitable fixed parameter because the sweat formed per impulse at a given frequency is constant.

Impedance change due to a given number of impulse volleys increases in degree very rapidly as frequency is increased to 1 or 2 per sec. and thereafter more slowly. A frequency of 10 per sec. appears to secure the maximal effect. This curve of impedance change as a function of stimulation frequency has essentially the same form as does the curve describing the latency for beginning sweat emergence as a function of frequency (Lloyd, 1959*a*, Fig. 2). Interpretation of the one is best made in the light of the other. At high frequencies of stimulation reabsorption can have little effect upon the latency of sweat emergence because of the great disparity between secretory and reabsorptive power of the glands. As frequency is lowered, however, reabsorption is progressively a more important factor and there exists a threshold frequency below which sweat formation does not lead to sweat emergence. The range of frequencies within which these differences occur is that employed in the experiment of Fig. 8. Reabsorption rate presumably is a constant, but the rate of formation certainly is frequency-dependent.

Impedance of the foot pad depends upon the mean level of the sweat columns in the ducts (Lloyd, 1959*b*). At low frequency, with reabsorption relatively a significant factor the sweat columns in response to a given number of stimuli would not rise as high as they would at high frequency. This in turn would mean a lesser change in impedance for a given number of impulses.

Considering the form of the impedance change curve of Fig. 8 and that of latency it seems a sufficient explanation for, and correct interpretation of, the results depicted in Fig. 8 that the amount of sweat formed per impulse is a constant regardless of stimulation frequency, but that the degree of impedance change caused by a fixed number of impulses depends upon the relation between the rate of formation and the rate of reabsorption.

REFERENCES

HERMANN, L., Galvanische Erscheinungen am Muskel, *Handb. Physiol.*, 1879, **1**, 173.

LANGLEY, J. N., Further observations on the secretory and vasomotor fibres of the foot of the cat, with notes on other sympathetic nerve fibres, *J. Physiol.*, 1894, **17**, 296.

LLOYD, D. P. C., Impedance change in relation to duct filling and emptying in sweat glands of the central foot pad of the cat, *J. Physiol.* 1958, **143**, 48P.

LLOYD, D. P. C., Secretion and reabsorption in sweat glands, *Proc. Nat. Acad. Sc.*, 1959*a*, **45**, 405.

LLOYD, D. P. C., Average behavior of sweat glands as indicated by impedance changes, *Proc. Nat. Acad. Sc.*, 1959*b*, **45**, 410.