[3] Frauenfelder, Babone, von Goller, Levine, Lewis, Peacock, Rossi, and Pasquali, *Phys. Rev.*, **106**, 386 (1957); Cavanaugh, Turner, Coleman, Gard, and Ridley, *Phyl. Mag.*, **21**, 1105 (1957).

[4] Page, L. A., and M. Heinberg, *Phys. Rev.*, **106**, 1220 (1957); Goldhaber, M., L. Grodzins, and A. W. Sunyar, *Phys. Rev.*, **106**, 826 (1957).

[5] Cox, R. T., C. G. McIlwraith, and B. Kurrelmeyer, these PROCEEDINGS, **14**, 544 (1928).

[6] In conformity with present practice we shall use the term helicity to describe the longitudinal polarization of particles. The helicity, H, being defined as $H = (\bar{\sigma}\cdot\bar{p})/(|\sigma|\cdot|p|)$. A positive helicity will thus mean that spin and momentum are parallel.

[7] Chase, C. T., *Phys. Rev.*, **34**, 1069 (1929).

[8] Chase, C. T., *Phys. Rev.*, **36**, 984 (1930).

[9] Chase, C. T., *Phys. Rev.*, **36**, 1060 (1930).

[10] See reviews of preceedings experiments in Dymond, E. G., *Proc.Roy. Soc.*, **A136**, 638 (1932); Tolhoek, H. L., *Rev. Mod. Phys.*, **28**, 277 (1956).

[11] Mott, N. F., *Proc. Roy. Soc. (London)*, *A***124**, 425 (1929); Mott, N. F., *Proc. Roy. Soc. (London)*, *A***135**, 429 (1932).

[12] Anishenko, I. U. V., and A. A. Rulchadze, *Soviet Phys. (JETP)*, **33**, 216 (1958); *J. Exptl. Theoret. Phys. (U.S.S.R.)*, **33**, 279 (1957); Tassic, L. J., *Phys. Rev.*, **107**, 1452 (1957); Gürsey, F., *Phys. Rev.*, **107**, 1734 (1957).

[13] de Shalit, A., S. Kuperman, H. J. Lipkin, and T. Rothen, *Phys. Rev.*, **107** 1459 (1957); *Phys. Rev.*, **109**, 223 (1958).

[14] Alikhanov, A. I., G. P. Eliseev, and V. A. Liubimov, 1957, Padua-Venice Conf.

[15] Heintze, J., *Zeits. für Physik*, **150**, 134 (1958).

[16] Selinger, H. H., *Phys. Rev.*, **78**, 491 (1950); *Phys. Rev.*, **85**, 724A (1952).

[17] Uhlenbeck, G. E., and S. A. Goudsmit, *Naturwissenschaften* **13**, 953 (1925).

SECRETION AND REABSORPTION IN SWEAT GLANDS

BY DAVID P. C. LLOYD

THE ROCKEFELLER INSTITUTE, NEW YORK

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The foot-pads of the cat are richly supplied with sweat glands of the eccrine type comparable to those that are distributed over the entire surface of the body in man. Sweat glands are blind-ended tubes leading to the skin surface. Each gland consists of a tortuously coiled secreting portion at its blind end and a duct that ends at the surface in a sweat pore. At the transition between secreting portion and duct the tube is particularly thin. Sweat glands are subject to nervous control by the central nervous system and are, in the intact animal or man, more or less constantly active.

Granting the obvious which is that sweat glands secrete, the question whether or or not they, like the kidney tubule, also reabsorb is frequently posed. Direct evidence of reabsorption appears to be lacking. However, reabsorption of water has been postulated by Lobitz and Mason[1] and by Schwartz, Thaysen, and Dole[2] to account for concentration differences between slowly and profusely secreted sweat. Also reabsorption of sodium is proposed by Schwartz and Thaysen[3] to account for sodium concentration differences between blood plasma and sweat. On the other hand, sweat ducts have been regarded as mere channels leading from the secretory portion to the skin surface.

If one were to assume that the ducts of truly resting sweat glands are empty, then on activation by stimulation of the nerve supply, sweat *formation* in the secreting portion would begin, but a phase of duct filling would antecede sweat *emergence* (which is to say "sweating") at the skin surface. When stimulation is stopped, sweat formation and sweat emergence would cease, but the resting condition would be regained only when the ducts again become empty through reabsorption. Accordingly one might expect observations on the latency of sweat emergence to provide direct evidence concerning the occurrence or nonoccurrence of reabsorption and also to tell something of the dynamics of sweating.

The experiments to be described bring new evidence, of a physical rather than of a chemical nature, to bear upon the question of reabsorption in sweat glands. Study of sweat gland activity in the cat's foot-pad has a distinct advantage in that the secretomotor nerve supply, contained in the plantar nerves, is easily severed to permit the glands to assume the truly resting state and is easily stimulated to induce the active state. In the experiments presently considered, sweat emergence at the skin surface was observed with the aid of a low-power binocular microscope. A stimulator providing variable duration and frequency of electrical stimuli for application to the centrally severed plantar nerves and a stop watch completed the experimental arrangement. The preparations were anesthetized with nembutal, intraperitoneally administered. It is advantageous, in fact virtually imperative, to select cats with black rather than unpigmented foot-pads if one is to see adequately the appearance of sweat droplets. On the black pad, brightly illuminated, they appear as glistening beads upon an otherwise dull background.

After a prolonged rest, something approaching 90 min, stimulation of the secretomotor supply at a frequency of 10 per second, which is maximally effective, may require up to 60 sec duration before the first sweat drops appear. Repetition of the stimulation after a 2-min rest requires but 2.5 to 3 sec. As the duration of rest period is varied between these two extremes, the latency for sweat emergence varies with it in the manner illustrated by Figure 1. Over most of its course the relation

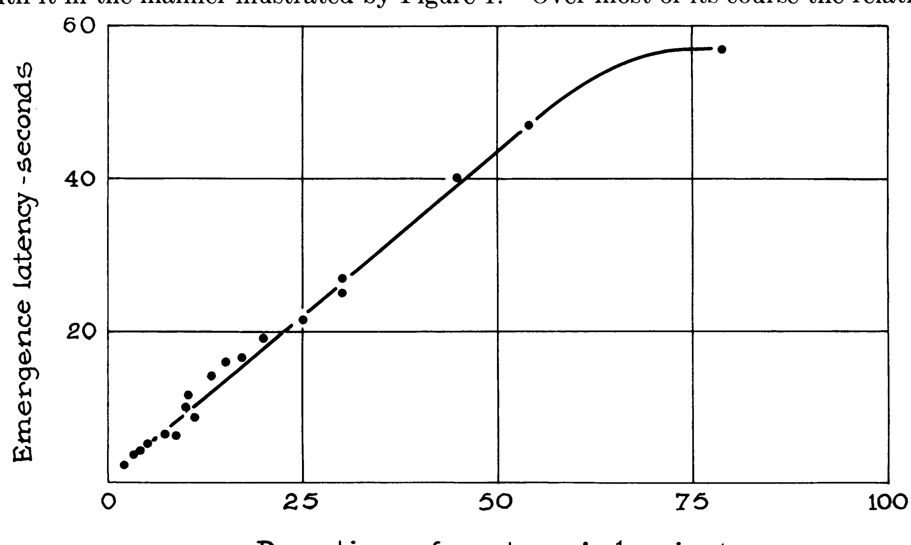

FIG. 1.—Latency for beginning sweat emergence at the surface of the central foot-pad of the cat as a function of rest period duration following a maximal stimulation.

is linear, although the rate of increase in latent period falls off after a rest period of approximately 60 min, and presumably reaches a final value.

When the ducts are full, as they certainly are a very short time after maximal activity, latency for emergence would provide a measure of the latency for sweat formation which on present evidence is some 2.5 to 3 sec. Since the latency for sweat formation would be fixed in fixed conditions of activation, the added time required for sweat emergence with increasing rest period must be time needed for duct filling. Therefore reabsorption must take place in the resting gland. Naturally these experiments do not reveal, except for water, what is reabsorbed by the sweat gland.

The relation between rest period and emergence latency as represented in Figure 1 permits one to make some surmise as to the site of reabsorption in the sweat gland. Since the relation is linear over most its range, it may be supposed that the column of sweat in a duct decrements in length by equal amounts for equal increments in rest period. This presumably would be the case only if reabsorption were to occur near the base of the gland rather than along the length of the duct. Were reabsorption to take place along the entire length of the duct the expected relation between emergence latency and rest period would be logarithmic. Where in the depth of the gland reabsorption occurs remains problematical. Nevertheless it is reasonable to suppose, and the tentative suggestion is, that the initial thin segment of the duct near its junction with the secreting portion may be the locus of reabsorption. The final decline in rate of increase in latent period that occurs at rest periods in excess of approximately 60 min, may indicate that the fluid columns in the ducts of the sweat glands at such times following maximal activity are receding through the region of reabsorption.

In circumstances of maximal activation sweat formation is a rapid process whereas reabsorption is slow. According to the information contained in Figure 1 the relative rates are in the ratio of approximately 75 to 1 and in other experiments the ratio may be as high as 100 to 1. Thus reabsorption cannot be an important determinant of the final product when the glands are maximally active. When minimally active, however, the situation is quite different, as will be seen from experiments of a different sort discussed in connection with Figure 2.

Sweat glands vary in their functional power[4, 5] and it is an important point for consideration that the method of latency measurement here employed yields information concerning the most powerful rather than the average or least powerful sweat glands. One can make a rough visual estimate of the over-all effect of a standard stimulation having, as herein used, a duration of 1 min at 10 per second frequency. Such a stimulation following prolonged rest is not of sufficient duration to secure a full outpouring of sweat. The individual beads indeed may be neither large enough nor sufficiently closely spaced to coalesce. After a brief rest, however, the foot-pad will be drenched long before the end of the stimulation period. In brief, the amount of sweat appearing at the surface may be said to vary roughly inversely with duration of the antecedent rest period.

Unfortunately one cannot extract either from observation of the behavior of the most powerful glands or from observation of the over-all effect of stimulation information as to the exact temporal course of reabsorption in the less powerful glands. If, however, some of the sweat glands, namely those whose reabsorptive activity

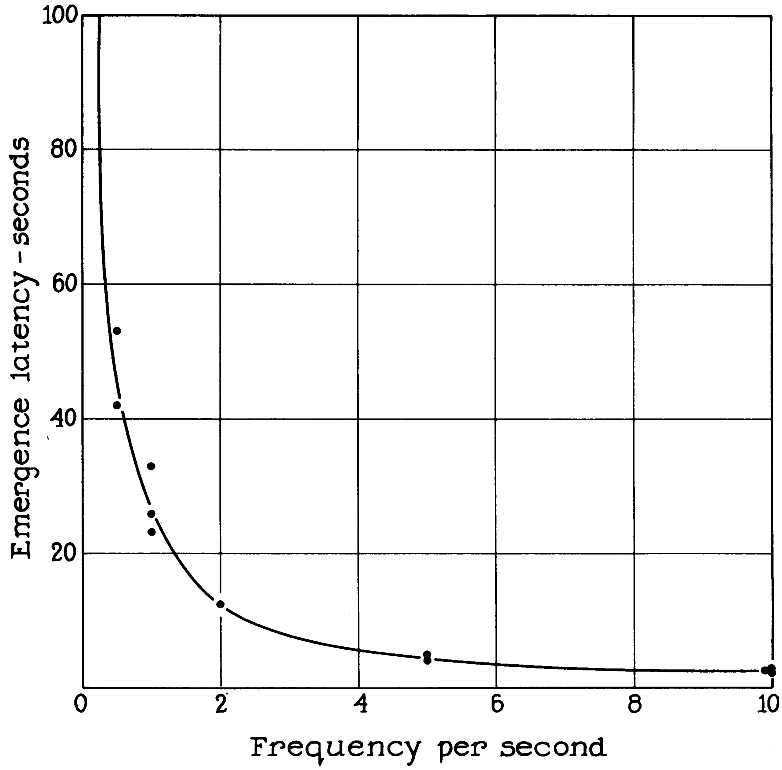

FIG. 2.—Latency for beginning sweat emergence at the surface of the central foot-pad of the cat as a function of stimulation frequency, the sweat ducts having been filled by an antecedent maximal stimulation.

can be measured by available technique, deplete their ducts of sweat content as a linear function of time, then the simplest and most reasonable assumption is that the others do likewise.

Sweating as a Function of Stimulus Frequency.—From the fact that reabsorption occurs in sweat glands it follows that sweating is something that occurs normally when the rate of formation exceeds the rate of reabsorption. In the usual preparation one cannot vary the reabsorption rate but one can, by varying the frequency of stimulation, vary the rate of sweat formation. To observe the behavior of the sweat glands in response to varied frequencies of stimulation, it is a practical convenience to fill the ducts by use of a maximal conditioning stimulation, then to allow a brief rest period of standard duration: 2 min was selected, for at this interval after maximal activation a further maximal stimulation leads to sweat emergence at minimal latency (cf. Fig. 1). In this way standard initial conditions are obtained. A test stimulation of variable frequency then is applied to the secretomotor supply and the latency for sweat emergence observed.

In every instance stimulation at 6 per minute was quite ineffective, although impedance changes in similar circumstances prove the glands active.[6] When stimulated at a frequency of 12 per minute there usually is no visible sweating or, after some 5 to 6 min of stimulation, a few beads may appear. Stimulation at 10 per second induces profuse sweating within 2.5 to 3 sec. As the frequency of stimulation is varied between these two extremes, latency for beginning sweat emergence varies with it in the manner illustrated by Figure 2. At the lower frequencies, latency is quite variable, the flow scanty. With increasing frequency, latency diminishes, becomes more stable, and flow increases progressively.

An interesting fact is that a threshold frequency exists below which sweat formation cannot lead to sweat emergence. In this there is a clear indication that reabsorption takes place in the active gland. For instance, in the experiment illustrated by Figure 2, in the absence of reabsorption one might have expected sweating after 2 min at 12 per minute stimulation frequency and after some 4 min at 6 per minute whereas, in fact, there was none. The threshold stimulation frequency as determined in this way is about 10 per minute, which is to say that the ratio of threshold frequency to maximal frequency is approximately 1 to 60. On the assumption that the sweat formed per secretomotor impulse volley is constant this would indicate that the secretory and reabsorptive actions of the glands come into balance when the secretory action is proceeding at some 1.65 per cent of capacity. Otherwise put, the secretory power of the sweat glands is about 60 times greater than their reabsorptive power, which is in essential agreement with the result discussed in connection with Figure 1.

Again, of course, one must bear in mind the fact that latency measurements as here employed concern the activity of the most powerful glands. As the frequency of test stimulation is lowered from that which is maximally effective, the amount of sweat produced declines. To judge by this fact rather than latency of sweating, the average glands come into secretory-reabsorptive balance at somewhat higher frequencies than do the most powerful glands.

[1] Lobitz, W. C., Jr., and H. L. Mason, "Chemistry of Palmar Sweat. VII Discussion of Studies on Chloride, Urea, Glucose, Uric Acid, Ammonia-Nitrogen and Creatinine," *Arch. Dermatol. Syphilol.*, **57**, 907–915 (1948).

[2] Schwartz, I. L., J. H. Thaysen, and V. P. Dole, "Urea Excretion in Human Sweat as a Tracer for Movement of Water Within the Secreting Gland," *J. Exper. Med.*, **97**, 429–437 (1953).

[3] Schwartz, I. L., and J. H. Thaysen, "Excretion of Sodium and Potassium in Human Sweat," *J. Clin. Invest.*, **35**, 114–120 (1956).

[4] Dole, V. P., and J. H. Thaysen, "Variation in the Functional Power of Human Sweat Glands," *J. Exper. Med.*, **98**, 129–144 (1953).

[5] Lloyd, D. P. C., "Average Behavior of Sweat Glands as Indicated by Impedance Changes," these PROCEEDINGS, **45**, 410–413 (1959).

[6] Lloyd, D. P. C., "Electrical Impedance Change of the Cat's Foot-pad in Relation to Sweat Secretion and Reabsorption" (in preparation).