Impedance Changes across the Footpad of the Cat in Relation to Action and Secretion in Sweat Glands*

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Abstract. Impedance changes across the footpad of the cat occur as the result of sweat gland activity after stimulation of the sudomotor nerves. It is possible to discern two phases of impedance change; one, early, associated with the action potential of sweat gland cells; the other, later, being the well-known change associated with secretion and reabsorption.¹ After a single stimulus, latency for the initial impedance change is about that of the sweat gland cell action potential, that of the secretory change approximately 1 additional second.

Electrical impedance across the footpad of the cat varies in the main inversely and in a logarithmic relation as the degree to which the sweat gland ducts traversing its thickness are filled.¹ Filling of the sweat ducts may occur as the result of sudomotor nerve activity or of injection of suitable excitatory substances. Emptying of them is a consequence of reabsorption. Many of the electrical concomitants of action by sweat glands differ in their expression by reason of difference in the degree to which the ducts are sweat filled at the time of that action.² After stimulation of the sudomotor nerve fibers there is recorded an action potential referable to the sweat gland cells. It is negative in sign at the footpad surface and, although representing maximal activity of the sweat gland cells in response to maximal sudomotor nerve stimulation, its recorded magnitude varies as the degree to which the ducts are filled, this merely because increased duct filling lowers the in-series resistance between the recording electrodes. There is, in brief, a “better” lead to the sweat gland cells, and the effect is essentially artifactual. During secretion and subsequent reabsorption there is a waxing and waning positive deflexion. Figure 1 (*top record*) stands in exemplification of these facts. The second recording of Figure 1 illustrates the decrease and recovery of impedance that parallels in its time course the positively directed secretory potential.

FIG. 1.—Potential changes (top) showing the individual negative action potentials incrementing in size as the baseline goes positive due to duct filling. Impedance change (bottom) parallels the positive secretory potentials of the upper record. Stimulation frequency: 0.5 Hz. Time: 0.05 Hz [from *Proc. Nat. Acad. Sci. USA*, 47, 351 (1961)].

If the ducts be full at the time of onset of activity, however engendered, only potential changes in the negative direction occur. If they be not full, potential changes in both directions (negative (action) and positive (secretory)) occur, the recorded response being the resultant. If the ducts be full at the onset, an impedance change of the sort recorded in Figure 1 does not occur, for once the ducts are full it matters not how much sweat pours out at the footpad surface; impedance change related to duct filling has reached its minimum value!

But, with the ducts initially full, another impedance change manifests itself in an unmistakable fashion. It is this change that is of major concern herein. The preparations were cats anesthetized by the intraperitoneal injection of chloralose-urethane mixture. Zinc-zinc sulfate electrodes were placed on the footpad and subcutaneously nearby. Sudomotor stimulation was effected through electrodes placed upon the centrally severed plantar nerves. Action potentials and impedance change were recorded by conventional means.

In Figure 2 there is in the top record the action potential (ducts full to avoid

FIG. 2.—Top: Single action potential of sweat gland cells in response to a sudomotor nerve impulse volley (ducts full). Bottom: *low*: impedance change recorded in similar circumstance but with ducts initially empty. Time: 10 Hz.

change in shape because of secretory potential) of the sweat gland cells in response to a single sudomotor volley. In the second record there is the impedance change produced by a single identical sudomotor volley (ducts empty to emphasize the secretory phase of impedance change). Comparison yields a crude indication of the relation between action potential and secretion—in a way analogous to the relation between action potential and contraction of skeletal muscle. The word “crude” is used advisedly because a careful analysis of the relation, as in Figure 3, demonstrates the existence of two phases in the impedance change. Drawn upwards in Figure 3 is the action potential of the sweat gland cells, downwards the concomitant impedance change. The initial impedance deflexion begins with or very shortly after potential change. Within

FIG. 3.—Tracing of sweat gland cell action potential response to a single sudomotor nerve volley (ducts full) plotted upward. Plotted downward is an analysis of impedance change (decrease) also in response to a single sudomotor nerve volley (ducts initially empty). St = time of nerve stimulus. Time: 10 Hz.

about 1 sec begins a second and larger change in impedance, this latter presumably related to secretion. Thus it would appear in the first approximation that latency differential between onset of sweat gland cell depolarization and measurable onset of sweat formation is slightly less than 1 sec.

Making use of the facts (1) that changes associated with secretion are deemphasized, and (2) that the electrical lead to the sweat gland cells is emphasized when the ducts are full, one can attain the optimum, if less than desirable, circumstance for observing the initial phase of impedance change and for establishing it as a (largely) distinct entity.

Figure 4 shows at the top (ducts full) a recording of the action potential of the sweat glands: it serves principally as a time reference for the other events

FIG. 4.—*Top*: single sweat gland action potential (ducts full). *Middle*: impedance change to single sudomotor volley (ducts initially empty). *Bottom*: impedance change to single sudomotor volley (ducts full). Time: 5 Hz.

depicted. The second record of Figure 4 shows impedance change caused by a single sudomotor nerve volley, the ducts being sweat impoverished. Superficially there is a single wave of impedance change of the sort that has been linked to sweat secretion (properly speaking, duct filling). However, if the ducts are filled as a result of prior tetanic sudomotor nerve stimulation impedance change recorded has the course illustrated in the third record of Figure 4. There is now a marked wave of impedance change located in time within the period of the action potential. It is unfortunate that the impedance records are marred by a superimposed differential recording of the action potential, but the difference in amplitude of this recorded nuisance in the second and third records is a further indication of how much more effective is the lead from the sweat gland cells when the ducts are full.

There is at least a reasonable indication that the initial impedance change is associable with membrane depolarization in the sweat gland cells during their action potential. Since the two components of impedance merge, one into the other, it is virtually impossible to denote the end of the earlier and the onset of the later.

In an attempt to formulate some sort of concluding statement concerning these observations, prior note should be made of the uncertainties and virtual impossibilities involved. This is necessarily a qualitative study. One cannot bear witness to the ducts at a given time all being full or at another time all or, in fact, any being empty. Nevertheless, to avoid tortuous circumlocution I use the words "full" and "empty" loosely. For the present purpose operational definitions of these words could be:

Full: The state of the sweat gland ducts at and shortly after tetanic stimulation of the sudomotor nerves for a duration and at a frequency known to cause profuse sweat emergence at the footpad surface.³

Empty: The state of the sweat gland ducts after a rest period approximating 90 min at which time impedance across the footpad, after change associable with reabsorption, becomes virtually constant at a high value.¹

Furthermore one cannot know how much sweat entering into the ducts is sufficient to cause measurable change from the empty state. And still further, since one cannot assert that all the ducts are really, to qualify the unqualifiable, full when the early impedance change is observed, as in Figure 4, it follows that this change usually, if not always, is distorted by the sequellae of some inter-current duct filling.

Mindful of the foregoing caveats, and undoubtedly properly apprehensive concerning the possibility of others, it is still possible to propose that there exist, after stimulation of the sudomotor nerves, two components of impedance change: one associable with the sweat gland cell action potential and possibly analogous to impedance change in other tissues during action, the other associable with duct filling and emptying through secretion and reabsorption.

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¹ Lloyd, D. P. C., "Electrical impedance changes of the cat's footpad in relation to sweat secretion and reabsorption," *J. Gen. Physiol.*, **43**, 713 (1960).

² Lloyd, D. P. C., "Action potential and secretory potential of sweat glands," *Proc. Nat. Acad. Sci. USA*, **47**, 351 (1961).

³ Lloyd, D. P. C., "Secretion and reabsorption in sweat glands," *Proc. Nat. Acad. Sci. USA*, **45**, 405 (1959).