

the presence of valinomycin, respectively. When the electrode was withdrawn (third arrow) the potential returned to approximately the original value. In a similar experiment (1) at the same KCl concentration (1 mM) and with electrodes filled with 2M KCl the corresponding potentials were  $16.8 \pm 1.0$  and  $-14.0 \pm 3.0$  mv.

The experiments discussed by Rottenberg (5) and presumed to provide evidence for a metabolically induced membrane potential, are most readily interpretable on the basis of a nonelectrogenic  $H^+$  pump (6). In this model the  $H^+$  exchanges for a cation for which the mitochondrial membrane is sufficiently permeable (for example,  $K^+$  in the presence of valinomycin or a lipophilic cation). Alternatively, the  $H^+$  could be accompanied by an anion (for example, a lipophilic anion). The results of Wikström and Saari (7) are consistent with the presence of a significant metabolically induced membrane potential if the assumptions of the study are correct (for example, the assumption that the Nernst equation can be used to calculate a membrane potential at all  $K^+$  concentrations). However, these results do not correspond to a definite proof. The interpretation of Wikström and Saari (7), that the spectral shifts in ferric cytochromes  $aa_3$  are due to proton binding to this complex may well be in harmony with a model involving proton shifts alone without involving a membrane potential. Similarly, we have no quarrel with the concept that a diffusion potential induces spectral and fluorescence changes in aurovertin and ferric cytochromes  $aa_3$ , respectively, or a conformational change in  $F_1$  (adenosine triphosphatase). We have considerable corroborative evidence for an absence of a significant metabolically induced membrane potential. Using four electrofluorimetric dyes we have obtained evidence that in rat liver mitochondria, the magnitude of the metabolically induced membrane potential change is within the range of 0 to  $-60$  mv (4).

We have also conducted a variety of experiments on the decay of the  $K^+$  diffusion potential using the same electrofluorimetric dyes (4). The potential, as detected by the fluorescence, decays with time but only in the presence of certain cations (for example,  $Mg^{2+}$  or, alternatively, a high concentration of  $Na^+$  or choline). In the absence of these ions the decay is very slow, as it is in other systems such as liposomes and red blood cells (8) or Ehrlich ascites cells (9). Burckhardt (9), for example, selects

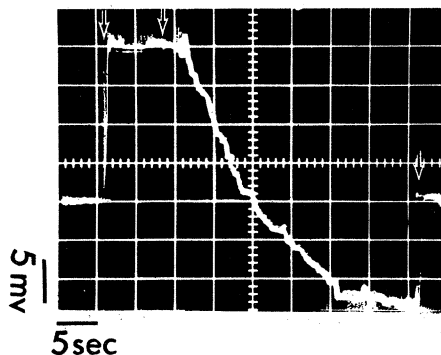


Fig. 1. Except for the use of the electrodes filled with NaCl, this experiment is approximately equivalent to that previously reported (2). The arrows indicate in chronological sequence, impalement, addition of valinomycin, and removal of the electrode. Valinomycin was added to the agar overlay about 0.1 mm in thickness to a final concentration of  $10^{-7}M$ . The medium was maintained at approximately  $18^\circ$  to  $25^\circ C$ . The medium contained 0.30 osmolal sucrose, 1 mM tris(hydroxymethyl)aminomethane, 1 mM KCl at pH 7.4.

steady state fluorescence as a reflection of membrane potential after 30 minutes.

The stability of the  $K^+$  diffusion potential in the presence of valinomycin results from the fact that the  $K^+$  must leave with an accompanying anion (or in exchange for another cation). A rapid decay from mitochondria would be expected only from considerations based on the chemi-osmotic hypothesis. We regard the lack of a rapid decay as further evidence that the high internal  $K^+$  concentration of mitochondria is not the result of a metabolically induced membrane potential postulated by others.

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