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CONVERSION OF BIOMEMBRANE-PRODUCED ENERGY  
INTO ELECTRIC FORM

## I. SUBMITOCHONDRIAL PARTICLES

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## SUMMARY

✓ The hypothesis of an electric membrane potential generated by respiration or ATP hydrolysis in submitochondrial particles has been verified. To this end a number of synthetic ions penetrating lipid membranes were used.

Penetrating anions of phenyl dicarbaundecaborane ( $\text{PCB}^-$ ), tetraphenyl boron and picrate were shown to accumulate in sonicated submitochondrial particles in an energy-dependent manner. The process was inhibited by rotenone, antimycin and cyanide if supported by respiration, and by oligomycin, if ATP was used as the energy source. Uncouplers were inhibitory in both cases. The following oxidation reactions were found to support the energy-dependent accumulation of  $\text{PCB}^-$ : oxidation of NADH by oxygen or fumarate; oxidation of succinate or ascorbate by oxygen; oxidation of NADPH by  $\text{NAD}^+$ . In the latter case, which is the reverse of the energy-requiring transhydrogenase reaction, ion transport was inhibited by NADH and  $\text{NADP}^+$  as well as by uncouplers. Oxidation of NADH by  $\text{NADP}^+$  in the energy-requiring transhydrogenase reaction was accompanied by an efflux of  $\text{PCB}^-$  anions which had accumulated during succinate oxidation. The redox 'succinate-ferricyanide' couple could not be used as a supply of energy for the accumulation of  $\text{PCB}^-$ .

Particles deprived of the coupling factor  $F_1$  showed a decreased ability for respiration-dependent anion uptake, the process being stimulated by oligomycin. ATP-driven  $\text{PCB}^-$  accumulation was completely absent in  $F_1$ -deprived particles but could be reconstituted after preincubation with  $F_1$ .

The active accumulation of anions penetrating into particles was readily distinguished from passive anion absorption, since the latter did not require energy and could be demonstrated both in native particles and in those deprived of  $F_1$ , as well as in phospholipid micelles. The energy-dependent accumulation of anions

Abbreviations:  $\text{PCB}^-$ , phenyl dicarbaundecaborane anion;  $\text{DDA}^+$ , *N,N*-dibenzyl *N,N*-dimethyl ammonium cation; FCCP, *p*-trifluoromethoxycarbonyl cyanide phenylhydrazone; TMPD, *N,N,N',N'*-tetramethyl-*p*-phenylenediamine; TTFB, tetrachlorotrifluoromethyl benzimidazole.