

articles

The structure of the ubiquinol oxidase from *Escherichia coli* and its ubiquinone binding siteJeff Abramson¹, Sirpa Riistama², Gisela Larsson¹, Audrius Jasaitis², Margareta Svensson-Ek¹, Liisa Laakkonen², Anne Puustinen², So Iwata^{1,3} and Märten Wikström²

Cell respiration is catalyzed by the heme-copper oxidase superfamily of enzymes, which comprises cytochrome *c* and ubiquinol oxidases. These membrane proteins utilize different electron donors through dissimilar access mechanisms. We report here the first structure of a ubiquinol oxidase, cytochrome *bo*₃, from *Escherichia coli*. The overall structure of the enzyme is similar to those of cytochrome *c* oxidases; however, the membrane-spanning region of subunit I contains a cluster of polar residues exposed to the interior of the lipid bilayer that is not present in the cytochrome *c* oxidase. Mutagenesis studies on these residues strongly suggest that this region forms a quinone binding site. A sequence comparison of this region with known quinone binding sites in other membrane proteins shows remarkable similarities. In light of these findings we suggest specific roles for these polar residues in electron and proton transfer in ubiquinol oxidase.

Heme-copper oxidases are redox-driven proton pumps that couple the reduction of molecular oxygen to water to the vectorial translocation of protons across the membrane^{1,2}. This transmembrane proton and voltage gradient generated by heme-copper oxidases and the other members of the aerobic respiratory chain is directly converted to more useful energy forms via energy conserving systems such as the ATP synthase. The heme-copper oxidase superfamily is divided into two main branches based on the identities of the electron donating substrates³ — cytochrome oxidases use a water soluble protein, cytochrome *c*, as the electron donor whereas ubiquinol oxidases use a membrane soluble ubiquinol-8 (where 8 is the number of the isoprenoid units in the hydrophobic tail) molecule as their electron donor. The members of this superfamily share important structural and functional features.

Cytochrome *bo*₃ ubiquinol oxidase from *Escherichia coli* is a four-subunit heme-copper oxidase that catalyzes the four-electron reduction of O₂ to water and functions as a proton pump⁴ (Fig. 1). All redox centers are located within the largest subunit (subunit I), with a low spin protoheme (heme *b*_L) acting as the electron donor to a binuclear center that is composed of an O-type heme (heme *o*_L) and a copper ion (Cu_B). Subunits I, II and III of ubiquinol oxidase are homologous to the corresponding subunits in the aa₃-type cytochrome *c* oxidases, and the ligands of the two heme groups and of Cu_B have been identified as the invariant His residues⁵. Subunit IV has little or no sequence homology with other oxidases and its function is unknown. In contrast to the cytochrome *c* oxidases, subunit II of ubiquinol oxidase has no Cu_B center⁶, nor a cytochrome *c* binding site⁷. Instead, heme *b* receives electrons directly from a membrane solubilized ubiquinol molecule, and the protons produced are released on the positive side of the membrane⁴ (P-side; Fig. 1).

Here we present the crystal structure of the ubiquinol oxidase from *E. coli* at 3.5 Å resolution. The structure confirms that the overall architecture of this complex is very similar to that of cytochrome *c* oxidase. Using site-directed mutagenesis and

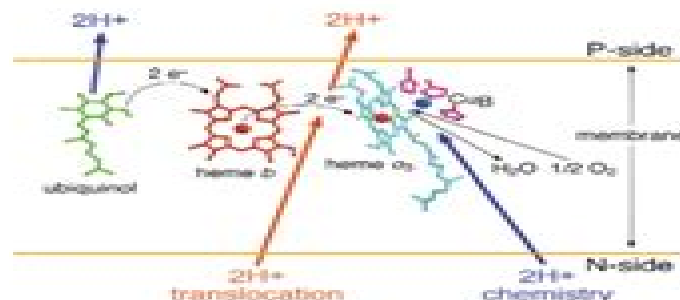


Fig. 1 Schematic representation of electron and proton transfer in ubiquinol oxidase.

sequence comparisons with known ubiquinone binding sites from other membrane proteins, we have identified a novel ubiquinone binding site within this enzyme. This study reveals how ubiquinol oxidase and cytochrome *c* oxidase can use a similar protein framework for oxygen reduction but with two entirely different electron donors.

Structure determination

Data from crystals diffracting to 3.5 Å resolution were used for molecular replacement (Table 1). Diffraction data beyond 4.0 Å were weak but were included for structure determination in order to use as many observations as possible. These additional observations were helpful for low resolution studies and proved particularly useful for density modification. A search model was constructed using the solved extrinsic domain of ubiquinol oxidase (Protein Data Bank (PDB) entry 1C9W; residues 125–283 of

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