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A simple and fast approach for missing-wedge invariant classification of subtomograms extracted from filamentous structures

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Abstract

Unsupervised classification of subtomograms extracted from cryo-electron tomograms is often challenging due to the presence of a missing wedge in tomographic data. Here, we propose a simple new approach to classify subtomograms extracted from cryo-electron tomograms of filamentous objects. This unsupervised classification approach uses the 1D projections of the subtomograms for classification and works independently of the orientations of the missing wedge. We applied this approach to subtomograms from eukaryotic cilia and successfully detected heterogeneity including structural polymorphism of dynein molecules.

Introduction

Subtomogram averaging enables in vivo molecular structural analysis by cryo-electron tomography despite poor signal-to-noise ratio (S/N) of this technique. In subtomogram averaging, volumes including the target molecule are extracted computationally, aligned to have the same orientation and averaged. However, when there is heterogeneity in the data, it leads to imprecise alignments thereby resulting in a poor average. Image classification of subtomograms is done in order to get rid of heterogeneity of molecular structures due to enzymatic structural polymorphism, thermal fluctuation or coexistence of different molecules which are similar and cannot be distinguished visually. When there is *a priori* knowledge about heterogeneity, template based classification is possible and this has been applied successfully in eukaryotic flagellar tomography to look at conformations of dynein corresponding to the pre- and post-power stroke (Lin et al., 2014; Movassagh et al., 2010; Ueno et al., 2014). However, in general unsupervised (template free) classification is preferable, since no *a priori* knowledge is required and there is a less risk of bias.

Unsupervised classification of images (2D or 3D) by multivariate statistical analysis requires aligned image particles and this is often a challenge because alignment based on cross-correlation is imprecise when heterogeneous structures coexist. Simultaneous alignment and classification provides an

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