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Reporting Summary

Nature Research wishes to improve the reproducibility of the work that we publish. This form provides structure for consistency and transparency in reporting. For further information on Nature Research policies, see Authors & Referees and the Editorial Policy Checklist.

Statistics							
For	For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.						
n/a	Conf	firmed					
		The exact sai	mple size (n) for each experimental group/condition, given as a discrete number and unit of measurement				
		A statement	on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly				
\boxtimes		The statistical test(s) used AND whether they are one- or two-sided Only common tests should be described solely by name; describe more complex techniques in the Methods section.					
\times		A descriptior	of all covariates tested				
\times		A descriptior	description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons				
	\boxtimes	A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)					
\boxtimes		For null hypothesis testing, the test statistic (e.g. <i>F</i> , <i>t</i> , <i>r</i>) with confidence intervals, effect sizes, degrees of freedom and <i>P</i> value noted <i>Give P values as exact values whenever suitable.</i>					
\boxtimes	For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings						
\boxtimes	For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes						
\boxtimes	Estimates of effect sizes (e.g. Cohen's <i>d</i> , Pearson's <i>r</i>), indicating how they were calculated						
	1		Our web collection on <u>statistics for biologists</u> contains articles on many of the points above.				
Software and code							
Policy information about <u>availability of computer code</u>							
D	ata co	llection	EPU, FEI TIA				
D	ata an	nalysis	MotionCor2, CryoSPARC3.3.2, AlphaFold2, UCSF Chimera 1.14, UCSF ChimeraX 1.5, COOT 0.981, PHENIX 1.14, MolProbity.				
			tom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors/reviewers. e deposition in a community repository (e.g. GitHub). See the Nature Research guidelines for submitting code & software for further information.				

Data

Policy information about availability of data

All manuscripts must include a <u>data availability statement</u>. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A list of figures that have associated raw data
- A description of any restrictions on data availability

All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary information and source data are provided with this paper. The cryo-EM density maps and corresponding atomic models have been deposited in the EMDB and PDB, respectively. The accession codes are: for MCM-apo, EMD-38109 and PDB 8X7T [https://doi.org/10.2210/pdb8X7T/pdb] (the composite map), EMD-38110 (the map before local refinement), EMD-38112 to EMD-38118 (maps after local refinement); for MCM-ATP-dsDNA: EMD-38111 and PDB 8X7U [https://doi.org/10.2210/pdb8X7U/pdb] (the composite map), EMD-38119 (the map before local refinement), EMD-38120 to EMD-38127 (maps after local refinement); for CA Di-hexamer EMD-61286 and PDB 9JA0 [https://doi.org/10.2210/pdb9JA0/pdb]; for ScPol II EC: EMD-61287 and PDB 9JA1 [https://doi.org/10.2210/pdb9JA1/pdb].

Field-spe	ecific reporting
Please select the o	ne below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.
Life sciences	Behavioural & social sciences Ecological, evolutionary & environmental sciences
For a reference copy of	the document with all sections, see <u>nature.com/documents/nr-reporting-summary-flat.pdf</u>
Lite scier	nces study design
All studies must dis	sclose on these points even when the disclosure is negative.
Sample size	For cryo-EM SPA, sample sizes were those required for the resolution. The details of datasets, including sample sizes, are listed in the Supplementary Table 3 and 4.
Data exclusions	During cryo-EM SPA study, the particles were autopicked by a density threshold, which is a standard approach in cryoSPARC. 2D and 3D classifications were preformed to remove the junk particles in order to generate higher-resolution density maps.
Replication	For cyro-EM SPA study, two randomly divided half datasets were processed independently and combined to give rise to the final structures. The resolution of the structure is assessed by comparing the two independent maps.
Randomization	For each dataset of Cryo-EM SPA study, the dataset were randomly divided into two half sets, as a standard approach implementd in cryoSPARC.
Blinding	The cryo-FM SPA study including data collection and processing is not blinded

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Ma	terials & experimental systems	Methods		
n/a	Involved in the study	n/a	Involved in the study	
\boxtimes	Antibodies	\boxtimes	ChIP-seq	
\boxtimes	Eukaryotic cell lines	\boxtimes	Flow cytometry	
\boxtimes	Palaeontology	\boxtimes	MRI-based neuroimaging	
\boxtimes	Animals and other organisms	,		
\boxtimes	Human research participants			
\boxtimes	Clinical data			