

## Diffusible crosslinkers generate directed forces in microtubule networks

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Remodeling of cytoskeletal filament networks is essential to cell division and morphogenesis. The mechanical forces driving the restructuring processes are attributed to the activity of molecular motors and the dynamics of cytoskeletal filaments, which both consume chemical energy. Passive filament crosslinkers, on the other hand, are commonly regarded as mere friction-generating entities. Here, we report on the generation of directed forces by non-enzymatic, diffusible microtubule crosslinkers of the Ase1/PRC1/Map65 family. After experimentally confining Ase1 molecules between partially overlapping microtubules, we observed overlap expansion through directed microtubule sliding. Notably, the forces generated were sufficient to reverse the direction of motor-protein driven microtubule sliding. Force generation by Ase1 can be quantitatively explained by entropic expansion of confined Ase1 crosslinkers diffusing along microtubules in the overlap region. The thermal motion of confined filament crosslinkers is thus harnessed to generate mechanical work analogous to compressed gas propelling a piston in a cylinder. We argue that this mechanism constitutes an active, force-producing element of self-organizing filamentous networks inside cells.

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