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# Effects of added divalent counterions on the properties and behaviors of microtubule filaments

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Microtubules are polymeric cytoskeletal filaments that define the shape of eukaryotic cells and are widely involved in intracellular active transport. Physiological regulation of microtubule mechanics and dynamics may be achieved through electrostatics based on their strong polyelectrolyte nature. Here, we report on the effects of counterions on microtubules at concentrations below the like-charge bundling phase boundary. We first show that the persistence length (Lp) is significantly increased in the presence of physiologically relevant amounts of certain divalent salts ($Mg^{2+}$, $Sr^{2+}$, and $Ba^{2+}$). These observations are counter to theoretical expectations and experimental observations in similar systems where biological rod-like polyelectrolytes (e.g., DNA) are reported to present lower Lp values due to counterion-induced condensation. The increase in microtubule LP was attributed to screened coulomb interactions between the filament surface and the highly negatively charged C-terminal tails. Suppression of depolymerization was also observed in the presence of $Ba^{2+}$ and in the absence of stabilization agents (e.g., paclitaxel). The observed correlation between structural stability and mechanical rigidity is consistent with prior work involving MAPs, which also affect dynamics through interaction with the C-terminal tails. Lastly, the counterion-induced increase in Lp also significantly affected the characteristics of kinesin-transport. Here the path trajectories of microtubules in the gliding motility assay transition from highly dispersed transport to deterministic transport following the addition of divalent ions. Overall these results establish a novel mechanism by which microtubules dynamics, mechanics, and interaction with molecular motors may be regulated by physiologically relevant concentrations of divalent salts.

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