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Dynamics and regulation at the tip : a high resolution view on microtubule assembly

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Bibliography

- [1] Wells WA (2005) The discovery of tubulin. *J Cell Biol* **169**:552.
- [2] Borisy GG, Taylor EW (1967) The mechanism of action of colchicine: Binding of colchicine-3H to cellular protein. *J Cell Biol* **34**:525–533.
- [3] Borisy GG, Taylor EW (1967) The mechanism of action of colchicine: Colchicine binding to sea urchin eggs and the mitotic apparatus. *J Cell Biol* **34**:535–548.
- [4] Erickson HP (1995) FtsZ, a prokaryotic homolog of tubulin? *Cell* **80**:367–370.
- [5] Schlieper D, Oliva MA, Andreu JM, Lowe J (2005) Structure of bacterial tubulin BtubA/B: Evidence for horizontal gene transfer. *Proc Natl Acad Sci* **102**:9170–9175.
- [6] Desai A, Mitchison TJ (1997) Microtubule polymerization dynamics. *Annu Rev Cell Dev Biol* **13**:83–117.
- [7] Kirschner M, Mitchison T (1986) Beyond self-assembly: from microtubules to morphogenesis. *Cell* **45**:329–342.
- [8] Mitchison T, Kirschner M (1984) Dynamic instability of microtubule growth. *Nature* **312**:237–242.
- [9] Heald R, Nogales E (2002) Microtubule dynamics. *J Cell Sci* **115**:3–4.
- [10] Cassimeris L (1999) Accessory protein regulation of microtubule dynamics throughout the cell cycle. *Curr Opin Cell Biol* **11**:134–141.
- [11] Howard J, Hyman AA (2007) Microtubule polymerases and depolymerases. *Curr Opin Cell Biol* **19**:31–35.
- [12] Akhmanova A, Steinmetz MO (2008) Tracking the ends: a dynamic protein network controls the fate of microtubule tips. *Nat Rev Mol Cell Biol* **9**:309–322.
- [13] Morrison EE (2007) Action and interactions at microtubule ends. *Cell Mol Life Sci* **64**:307–317.

- [14] Lansbergen G, Akhmanova A (2006) Microtubule plus end: a hub of cellular activities. *Traffic* **7**:499–507.
- [15] Wu X, Xiang X, Hammer JA III (2006) Motor proteins at the microtubule plus-end. *Trends Cell Biol* **16**:135–143.
- [16] Vaughan KT (2004) Surfing, regulating and capturing: are all microtubule-tip-tracking proteins created equal? *Trends Cell Biol* **14**:491–496.
- [17] Carvalho P, Tirnauer JS, Pellman D (2003) Surfing on microtubule ends. *Trends Cell Biol* **13**:229–237.
- [18] Galjart N, Perez F (2003) A plus-end raft to control microtubule dynamics and function. *Curr Opin Cell Biol* **15**:48–53.
- [19] Mimori-Kiyosue Y, Tsukita S (2003) 'Search-and-capture' of microtubules through plus-end-binding proteins (+TIPs). *J Biochem* **134**:321–326.
- [20] Schuyler SC, Pellman D (2001) Microtubule 'plus-end-tracking proteins': the end is just the beginning. *Cell* **105**:421–424.
- [21] Slep KC, Vale RD (2007) Structural basis of microtubule plus end tracking by XMAP215, CLIP-170, and EB1. *Mol Cell* **27**:976–991.
- [22] Akhmanova A, Hoogenraad CC (2005) Microtubule plus-end-tracking proteins: mechanisms and functions. *Curr Opin Cell Biol* **17**:47–54.
- [23] Wittmann T, Desai A (2005) Microtubule cytoskeleton: a new twist at the end. *Curr Biol* **15**:R126–R129.
- [24] Galjart N (2005) CLIPs and CLASPs and cellular dynamics. *Nat Rev Mol Cell Biol* **6**:487–498.
- [25] Sandblad L, Busch KE, Tittmann P, Gross H, Brunner D, Hoenger A (2006) The *Schizosaccharomyces pombe* EB1 homolog Mal3p binds and stabilizes the microtubule lattice seam. *Cell* **127**:1415–1424.
- [26] Helenius J, Brouhard G, Kalaidzidis Y, Diez S, Howard J (2006) The depolymerizing kinesin MCAK uses lattice diffusion to rapidly target microtubule ends. *Nature* **441**:115–119.
- [27] Brouhard GJ, Stear JH, Noetzel TL, Al-Bassam J, Kinoshita K, Harrison SC, Howard J, Hyman AA (2008) XMAP215 is a processive microtubule polymerase. *Cell* **132**:79–88.
- [28] Al-Bassam J, van Breugel M, Harrison SC, Hyman A (2006) Stu2p binds tubulin and undergoes an open-to-closed conformational change. *J Cell Biol* **172**:1009–1022.

-
- [29] Folker ES, Baker BM, Goodson HV (2005) Interactions between CLIP-170, tubulin, and microtubules: implications for the mechanism of CLIP-170 plus-end tracking behavior. *Mol Biol Cell* **16**:5373–5384.
- [30] Dragestein KA, van Cappellen WA, van Haren J, Tsibidis GD, Akhmanova A, Knoch TA, Grosveld F, Galjart N (2008) Dynamic behavior of GFP-CLIP-170 reveals fast protein turnover on microtubule plus ends. *J Cell Biol* **180**:729–737.
- [31] Nogales E, Whittaker M, Milligan RA, Downing KH (1999) High-resolution model of the microtubule. *Cell* **96**:79–88.
- [32] Chrétien D, Wade RH (1991) New data on the microtubule surface lattice. *Biol Cell* **71**:161–174.
- [33] Chrétien D, Metoz F, Verde F, Karsenti E, Wade RH (1992) Lattice defects in microtubules: protofilament numbers vary within individual microtubules. *J Cell Biol* **117**:1031–1040.
- [34] Chrétien D, Fuller S, Karsenti E (1995) Structure of growing microtubule ends: two-dimensional sheets close into tubes at variable rates. *J Cell Biol* **129**:1311–1328.
- [35] Hammond JW, Cai D, Verhey KJ (2008) Tubulin modifications and their cellular functions. *Curr Opin Cell Biol* **20**:71–76.
- [36] Peris L, Thery M, Faure J, Saoudi Y, Lafanechere L, Chilton JK, Gordon-Weeks P, Galjart N, Bornens M, Wordeman L, et al. (2006) Tubulin tyrosination is a major factor affecting the recruitment of CAP-Gly proteins at microtubule plus ends. *J Cell Biol* **174**:839–849.
- [37] Reed NA, Cai D, Blasius TL, Jih GT, Meyhofer E, Gaertig J, Verhey KJ (2006) Microtubule acetylation promotes kinesin-1 binding and transport. *Curr Biol* **16**:2166–2172.
- [38] Ikegami K, Heier RL, Taruishi M, Takagi H, Mukai M, Shimma S, Taira S, Hatanaka K, Morone N, Yao I, et al. (2007) Loss of α -tubulin polyglutamylation in ROSA22 mice is associated with abnormal targeting of KIF1A and modulated synaptic function. *Proc Natl Acad Sci* **104**:3213–3218.
- [39] Mandelkow E, Mandelkow E, Milligan R (1991) Microtubule dynamics and microtubule caps: a time-resolved cryo-electron microscopy study. *J Cell Biol* **114**:977–991.
- [40] Nogales E, Wang HW (2006) Structural intermediates in microtubule assembly and disassembly: how and why. *Curr Opin Cell Biol* **18**:179–184.

- [41] Browning H, Hackney DD, Nurse P (2003) Targeted movement of cell end factors in fission yeast. *Nat Cell Biol* **5**:812–818.
- [42] Gittes F, Mickey B, Nettleton J, Howard J (1993) Flexural rigidity of microtubules and actin filaments measured from thermal fluctuations in shape. *J Cell Biol* **120**:923–934.
- [43] Pampaloni F, Lattanzi G, Jonas A, Surrey T, Frey E, Florin EL (2006) Thermal fluctuations of grafted microtubules provide evidence of a length-dependent persistence length. *Proc Natl Acad Sci* **103**:10248–10253.
- [44] Janson ME, Dogterom M (2004) A bending mode analysis for growing microtubules: evidence for a velocity-dependent rigidity. *Biophys J* **87**:2723–2736.
- [45] Taute KM, Pampaloni F, Frey E, Florin EL (2008) Microtubule dynamics depart from the wormlike chain model. *Phys Rev Lett* **100**:028102.1–4.
- [46] Felgner H, Frank R, Schliwa M (1996) Flexural rigidity of microtubules measured with the use of optical tweezers. *J Cell Sci* **109**:509–516.
- [47] Felgner H, Frank R, Biernat J, Mandelkow EM, Mandelkow E, Ludin B, Matus A, Schliwa M (1997) Domains of neuronal microtubule-associated proteins and flexural rigidity of microtubules. *J Cell Biol* **138**:1067–1075.
- [48] Mickey B, Howard J (1995) Rigidity of microtubules is increased by stabilizing agents. *J Cell Biol* **130**:909–917.
- [49] Fygenon DK, Flyvbjerg H, Sneppen K, Libchaber A, Leibler S (1995) Spontaneous nucleation of microtubules. *Phys Rev E* **51**:5058–5063.
- [50] Wang HW, Long S, Rose FK, Nogales E (2005) Assembly of GMPCPP-bound tubulin into helical ribbons and tubes and effect of colchicine. *Cell Cycle* **4**:1157–1160.
- [51] Wang HW, Nogales E (2005) Nucleotide-dependent bending flexibility of tubulin regulates microtubule assembly. *Nature* **435**:911–915.
- [52] Wiese C, Zheng Y (2006) Microtubule nucleation: γ -tubulin and beyond. *J Cell Sci* **119**:4143–4153.
- [53] Particle Data Group (1990) Review of particle properties. *Phys Lett B* **239**:III.28–38.
- [54] Komarova YA, Vorobjev IA, Borisy GG (2002) Life cycle of MTs: persistent growth in the cell interior, asymmetric transition frequencies and effects of the cell boundary. *J Cell Sci* **115**:3527–3539.
- [55] Piehl M, Cassimeris L (2003) Organization and dynamics of growing microtubule plus ends during early mitosis. *Mol Biol Cell* **14**:916–925.

-
- [56] Walker R, O'Brien E, Pryer N, Soboeiro M, Voter W, Erickson H, Salmon E (1988) Dynamic instability of individual microtubules analyzed by video light microscopy: rate constants and transition frequencies. *J Cell Biol* **107**:1437–1448.
- [57] Fygenon DK, Braun E, Libchaber A (1994) Phase diagram of microtubules. *Phys Rev E* **50**:1579–1588.
- [58] Carlier MF, Hill TL, Chen YD (1984) Interference of GTP hydrolysis in the mechanism of microtubule assembly: an experimental study. *Proc Natl Acad Sci* **81**:771–775.
- [59] Hyman AA, Salser S, Drechsel DN, Unwin N, Mitchison TJ (1992) Role of GTP hydrolysis in microtubule dynamics: information from a slowly hydrolyzable analogue, GMPCPP. *Mol Biol Cell* **3**:1155–1167.
- [60] Caplow M, Ruhlen RL, Shanks J (1994) The free energy for hydrolysis of a microtubule-bound nucleotide triphosphate is near zero: all of the free energy for hydrolysis is stored in the microtubule lattice. *J Cell Biol* **127**:779–788.
- [61] Jánosi IM, Chrétien D, Flyvbjerg H (2002) Structural microtubule cap: stability, catastrophe, rescue, and third state. *Biophys J* **83**:1317–1330.
- [62] Molodtsov MI, Ermakova EA, Shnol EE, Grishchuk EL, McIntosh JR, Ataullakhanov FI (2005) A molecular-mechanical model of the microtubule. *Biophys J* **88**:3167–3179.
- [63] VanBuren V, Cassimeris L, Odde DJ (2005) Mechanochemical model of microtubule structure and self-assembly kinetics. *Biophys J* **89**:2911–2926.
- [64] Cassimeris L, Gard DL, Tran PT, Erickson HP (2001) XMAP215 is a long thin molecule that does not increase microtubule stiffness. *J Cell Sci* **114**:3025–3033.
- [65] Spittle C, Charrasse S, Larroque C, Cassimeris L (2000) The interaction of TOGp with microtubules and tubulin. *J Biol Chem* **275**:20748–20753.
- [66] Arnal I, Heichette C, Diamantopoulos GS, Chrétien D (2004) CLIP-170/tubulin-curved oligomers coassemble at microtubule ends and promote rescues. *Curr Biol* **14**:2086–2095.
- [67] Diamantopoulos GS, Perez F, Goodson HV, Batelier G, Melki R, Kreis TE, Rickard JE (1999) Dynamic localization of CLIP-170 to microtubule plus ends is coupled to microtubule assembly. *J Cell Biol* **144**:99–112.
- [68] Shirasu-Hiza M, Coughlin P, Mitchison T (2003) Identification of XMAP215 as a microtubule-destabilizing factor in *Xenopus* egg extract by biochemical purification. *J Cell Biol* **161**:349–358.

- [69] van Breugel M, Drechsel D, Hyman A (2003) Stu2p, the budding yeast member of the conserved Dis1/XMAP215 family of microtubule-associated proteins is a plus end-binding microtubule destabilizer. *J Cell Biol* **161**:359–369.
- [70] Dogterom M, Yurke B (1997) Measurement of the force-velocity relation for growing microtubules. *Science* **278**:856–860.
- [71] Grishchuk EL, Molodtsov MI, Ataulakhanov FI, McIntosh JR (2005) Force production by disassembling microtubules. *Nature* **438**:384–388.
- [72] Inoué S, Salmon ED (1995) Force generation by microtubule assembly/disassembly in mitosis and related movements. *Mol Biol Cell* **6**:1619–1640.
- [73] Dogterom M, Kerssemakers G, Jacob W J and Romet-Lemonne, Janson ME (2005) Force generation by dynamic microtubules. *Curr Opin Cell Biol* **17**:67–74.
- [74] Maiato H, DeLuca J, Salmon ED, Earnshaw WC (2004) The dynamic kinetochore-microtubule interface. *J Cell Sci* **117**:5461–5477.
- [75] Tran P, Marsh L, Doye V, Inoue S, Chang F (2001) A mechanism for nuclear positioning in fission yeast based on microtubule pushing. *J Cell Biol* **153**:397–412.
- [76] Janson ME, Dogterom M (2004) Scaling of microtubule force-velocity curves obtained at different tubulin concentrations. *Phys Rev Lett* **92**:248101.
- [77] Janson ME, de Dood ME, Dogterom M (2003) Dynamic instability of microtubules is regulated by force. *J Cell Biol* **161**:1029–1034.
- [78] Mogilner A, Oster G (1999) The polymerization ratchet model explains the force-velocity relation for growing microtubules. *Eur Biophys J* **28**:235–242.
- [79] van Doorn GS, Tanase C, Mulder BM, Dogterom M (2000) On the stall force for growing microtubules. *Eur Biophys J* **29**:2–6.
- [80] Stukalin EB, Kolomeisky AB (2004) Simple growth models of rigid multifilament biopolymers. *J Chem Phys* **121**:1097–1104.
- [81] Peskin CS, Odell GM, Oster GF (1993) Cellular motions and thermal fluctuations: the Brownian ratchet. *Biophys J* **65**:316–324.
- [82] Brangwynne CP, MacKintosh FC, Kumar S, Geisse NA, Talbot J, Mahadevan L, Parker KK, Ingber DE, Weitz DA (2006) Microtubules can bear enhanced compressive loads in living cells because of lateral reinforcement. *J Cell Biol* **173**:733–741.
- [83] Brangwynne CP, MacKintosh FC, Weitz DA (2007) Force fluctuations and polymerization dynamics of intracellular microtubules. *Proc Natl Acad Sci* **104**:16128–16133.

-
- [84] Curmi PA, Andersen SSL, Lachkar S, Gavet O, Karsenti E, Knossow M, Sobel A (1997) The stathmin/tubulin interaction *in vitro*. *J Biol Chem* **272**:25029–25036.
- [85] Jourdain L, Curmi P, Sobel A, Pantaloni D, Carlier MF (1997) Stathmin: a tubulin-sequestering protein which forms a ternary T2S complex with two tubulin molecules. *Biochemistry* **36**:10817–10821.
- [86] McNally FJ, Vale RD (1993) Identification of katanin, an ATPase that severs and disassembles stable microtubules. *Cell* **75**:419–429.
- [87] Vale RD (2003) The molecular motor toolbox for intracellular transport. *Cell* **112**:467–480.
- [88] Caviston JP, Holzbaur EL (2006) Microtubule motors at the intersection of trafficking and transport. *Trends Cell Biol* **16**:530–537.
- [89] Karsenti E, Vernos I (2001) The mitotic spindle: a self-made machine. *Science* **294**:543–547.
- [90] Dujardin DL, Vallee RB (2002) Dynein at the cortex. *Curr Opin Cell Biol* **14**:44–49.
- [91] Banks JD, Heald R (2001) Chromosome movement: dynein-out at the kinetochore. *Curr Biol* **11**:R128–R131.
- [92] Bringmann H, Skiniotis G, Spilker A, Kandels-Lewis S, Vernos I, Surrey T (2004) A kinesin-like motor inhibits microtubule dynamic instability. *Science* **303**:1519–1522.
- [93] Wordeman L (2005) Microtubule-depolymerizing kinesins. *Curr Opin Cell Biol* **17**:82–88.
- [94] Moores CA, Milligan RA (2006) Lucky 13 - microtubule depolymerisation by kinesin-13 motors. *J Cell Sci* **119**:3905–3913.
- [95] Walczak CE (2006) Kinesin-8s: motoring and depolymerizing. *Nat Cell Biol* **8**:903–905.
- [96] Martin SG, McDonald WH, Yates JR III, Chang F (2005) Tea4p links microtubule plus ends with the formin for3p in the establishment of cell polarity. *Dev Cell* **8**:479–491.
- [97] Grigoriev I, Montenegro Gouveia S, van der Vaart B, Demmers J, Smyth JT, Honnappa S, Splinter D, Steinmetz MO, Putney JW Jr, Hoogenraad CC, et al. (2008) STIM1 is a MT-plus-end-tracking protein involved in remodeling of the ER. *Curr Biol* **18**:177–182.
- [98] Adames NR, Cooper JA (2000) Microtubule interactions with the cell cortex causing nuclear movements in *Saccharomyces cerevisiae*. *J Cell Biol* **149**:863–874.

- [99] Drechsel DN, Kirschner MW (1994) The minimum GTP cap required to stabilize microtubules. *Curr Biol* **4**:1053–1061.
- [100] Vandecandelaere A, Brune M, Webb MR, Martin SR, Bayley PM (1999) Phosphate release during microtubule assembly: what stabilizes growing microtubules? *Biochemistry* **38**:8179–8188.
- [101] Voter WA, O'Brien ET, Erickson HP (1991) Dilution-induced disassembly of microtubules: relation to dynamic instability and the GTP cap. *Cell Motil Cytoskeleton* **18**:55–62.
- [102] Carvalho P, Gupta ML Jr, Hoyt MA, Pellman D (2004) Cell cycle control of kinesin-mediated transport of Bik1 (CLIP-170) regulates microtubule stability and dynein activation. *Dev Cell* **6**:815–829.
- [103] Busch KE, Hayles J, Nurse P, Brunner D (2004) Tea2p kinesin is involved in spatial microtubule organization by transporting Tip1p on microtubules. *Dev Cell* **6**:831–843.
- [104] Honnappa S, Okhrimenko O, Jaussi R, Jawhari H, Jelesarov I, Winkler FK, Steinmetz MO (2006) Key interaction modes of dynamic +TIP networks. *Mol Cell* **23**:663–671.
- [105] Weisbrich A, Honnappa S, Jaussi R, Okhrimenko O, Frey D, Jelesarov I, Akhmanova A, Steinmetz MO (2007) Structure-function relationship of CAP-Gly domains. *Nat Struct Mol Biol* **14**:959–967.
- [106] Komarova YA, Akhmanova AS, Kojima Si, Galjart N, Borisy GG (2002) Cytoplasmic linker proteins promote microtubule rescue in vivo. *J Cell Biol* **159**:589–599.
- [107] Brunner D, Nurse P (2000) CLIP170-like tip1p spatially organizes microtubular dynamics in fission yeast. *Cell* **102**:695–704.
- [108] Beinhauer JD, Hagan IM, Hegemann JH, Fleig U (1997) Mal3, the fission yeast homologue of the human APC-interacting protein EB1 is required for microtubule integrity and the maintenance of cell form. *J Cell Biol* **139**:717–728.
- [109] Busch KE, Brunner D (2004) The microtubule plus end-tracking proteins Mal3p and Tip1p cooperate for cell-end targeting of interphase microtubules. *Curr Biol* **14**:548–559.
- [110] Tirnauer JS, Grego S, Salmon E, Mitchison TJ (2002) EB1-microtubule interactions in *Xenopus* egg extracts: role of EB1 in microtubule stabilization and mechanisms of targeting to microtubules. *Mol Biol Cell* **13**:3614–3626.

-
- [111] Manna T, Honnappa S, Steinmetz M, Wilson L (2008) Suppression of microtubule dynamic instability by the +TIP protein EB1 and its modulation by the CAP-Gly domain of p150^{Glued}. *Biochemistry* **47**:779–786.
- [112] Ligon LA, Shelly SS, Tokito M, Holzbaur EL (2003) The microtubule plus-end proteins EB1 and dynactin have differential effects on microtubule polymerization. *Mol Biol Cell* **14**:1405–1417.
- [113] Tirnauer JS, O’Toole E, Berrueta L, Bierer BE, Pellman D (1999) Yeast Bim1p promotes the G1-specific dynamics of microtubules. *J Cell Biol* **145**:993–1007.
- [114] Rogers SL, Rogers GC, Sharp DJ, Vale RD (2002) Drosophila EB1 is important for proper assembly, dynamics, and positioning of the mitotic spindle. *J Cell Biol* **158**:873–884.
- [115] Varga V, Helenius J, Tanaka K, Hyman AA, Tanaka TU, Howard J (2006) Yeast kinesin-8 depolymerizes microtubules in a length-dependent manner. *Nat Cell Biol* **8**:957–962.
- [116] Gupta ML Jr, Carvalho P, Roof DM, Pellman D (2006) Plus end-specific depolymerase activity of Kip3, a kinesin-8 protein, explains its role in positioning the yeast mitotic spindle. *Nat Cell Biol* **8**:913–923.
- [117] Moore AT, Rankin KE, von Dassow G, Peris L, Wagenbach M, Ovechkina Y, Andrieux A, Job D, Wordeman L (2005) MCAK associates with the tips of polymerizing microtubules. *J Cell Biol* **169**:391–397.
- [118] Mennella V, Rogers GC, Rogers SL, Buster DW, Vale RD, Sharp DJ (2005) Functionally distinct kinesin-13 family members cooperate to regulate microtubule dynamics during interphase. *Nat Cell Biol* **7**:235–245.
- [119] Maddox PS, Stemple JK, Satterwhite L, Salmon ED, Bloom K (2003) The minus end-directed motor Kar3 is required for coupling dynamic microtubule plus ends to the cortical shmoo tip in budding yeast. *Curr Biol* **13**:1423–1428.
- [120] Gard DL, Becker BE, Romney SJ (2004) MAPping the eukaryotic tree of life: structure, function, and evolution of the MAP215/Dis1 family of microtubule-associated proteins. *Int Rev Cytol* **239**:179–272.
- [121] Gard DL, Kirschner MW (1987) A microtubule-associated protein from *Xenopus* eggs that specifically promotes assembly at the plus-end. *J Cell Biol* **105**:2203–2215.
- [122] Vasquez RJ, Gard DL, Cassimeris L (1994) XMAP from *Xenopus* eggs promotes rapid plus end assembly of microtubules and rapid microtubule polymer turnover. *J Cell Biol* **127**:985–993.

- [123] Al-Bassam J, Larsen NA, Hyman AA, Harrison SC (2007) Crystal structure of a TOG domain: conserved features of XMAP215/Dis1-family TOG domains and implications for tubulin binding. *Structure* **15**:355–362.
- [124] Bieling P, Laan L, Schek HT III, Munteanu EL, Sandblad L, Dogterom M, Brunner D, Surrey T (2007) Reconstitution of a microtubule plus-end tracking system in vitro. *Nature* **450**:1100–1105.
- [125] Hayashi I, Wilde A, Mal TK, Ikura M (2005) Structural basis for the activation of microtubule assembly by the EB1 and p150^{Glued} complex. *Mol Cell* **19**:449–460.
- [126] Ashkin A (1997) Optical trapping and manipulation of neutral particles using lasers. *Proc Natl Acad Sci* **94**:4853–4860.
- [127] Svoboda K, Block SM (1994) Biological applications of optical forces. *Annu Rev Biophys Biomol Struct* **23**:247–285.
- [128] Svoboda K, Schmidt CF, Schnapp BJ, Block SM (1993) Direct observation of kinesin stepping by optical trapping interferometry. *Nature* **365**:721–727.
- [129] Visscher K, Schnitzer MJ, Block SM (1999) Single kinesin molecules studied with a molecular force clamp. *Nature* **400**:184–189.
- [130] Carter NJ, Cross RA (2005) Mechanics of the kinesin step. *Nature* **435**:308–312.
- [131] Valentine MT, Fordyce PM, Krzysiak TC, Gilbert SP, Block SM (2006) Individual dimers of the mitotic kinesin motor Eg5 step processively and support substantial loads *in vitro*. *Nat Cell Biol* **8**:470–476.
- [132] Mallik R, Carter BC, Lex SA, King SJ, Gross SP (2004) Cytoplasmic dynein functions as a gear in response to load. *Nature* **427**:649–652.
- [133] Gennerich A, Carter AP, Reck-Peterson SL, Vale RD (2007) Force-induced bidirectional stepping of cytoplasmic dynein. *Cell* **131**:952–965.
- [134] Finer JT, Simmons RM, Spudich JA (1994) Single myosin molecule mechanics: piconewton forces and nanometer steps. *Nature* **368**:113–119.
- [135] Molloy JE, Burns JE, Kendrick-Jones J, Tregear RT, White DCS (1995) Movement and force produced by a single myosin head. *Nature* **378**:209–212.
- [136] Davenport RJ, Wuite GJ, Landick R, Bustamante C (2000) Single-molecule study of transcriptional pausing and arrest by *E. coli* RNA Polymerase. *Science* **287**:2497–2500.
- [137] Wuite GJ, Smith SB, Young M, Keller D, Bustamante C (2000) Single-molecule studies of the effect of template tension on T7 DNA polymerase activity. *Nature* **404**:103–106.

-
- [138] Noom MC, van den Broek B, van Mameren J, Wuite GJL (2007) Visualizing single DNA-bound proteins using DNA as a scanning probe. *Nat Meth* **4**:1031–1036.
- [139] Kellermayer MSZ, Smith SB, Granzier HL, Bustamante C (1997) Folding-unfolding transitions in single titin molecules characterized with laser tweezers. *Science* **276**:1112–1116.
- [140] Cecconi C, Shank EA, Bustamante C, Marqusee S (2005) Direct observation of the three-state folding of a single protein molecule. *Science* **309**:2057–2060.
- [141] Bechtluft P, van Leeuwen RGH, Tyreman M, Tomkiewicz D, Nouwen N, Tepper HL, Driessen AJM, Tans SJ (2007) Direct observation of chaperone-induced changes in a protein folding pathway. *Science* **318**:1458–1461.
- [142] Kerssemakers JWJ, Janson ME, van der Horst A, Dogterom M (2003) Optical trap setup for measuring microtubule pushing forces. *Appl Phys Lett* **83**:4441–4443.
- [143] Kerssemakers JWJ, Munteanu EL, Laan L, Noetzel TL, Janson ME, Dogterom M (2006) Assembly dynamics of microtubules at molecular resolution. *Nature* **442**:709–712.
- [144] Schek HT, Hunt AJ (2005) Micropatterned structures for studying the mechanics of biological polymers. *Biomed Microdevices* **7**:41–46.
- [145] Gibbons IR, Fronk E (1979) A latent adenosine triphosphatase form of dynein 1 from sea urchin sperm flagella. *J Biol Chem* **254**:187–196.
- [146] Pierce DW, Vale RD (1998) Assaying processive movement of kinesin by fluorescence microscopy. *Methods Enzymol* **298**:154–171.
- [147] Tselutin K, Seigneurin F, Blesbois E (1999) Comparison of cryoprotectants and methods of cryopreservation of fowl spermatozoa. *Poult Sci* **78**:586–590.
- [148] Nicastro D, Schwartz C, Pierson J, Gaudette R, Porter ME, McIntosh JR (2006) The molecular architecture of axonemes revealed by cryoelectron tomography. *Science* **313**:944–948.
- [149] Landau L, Lifshitz E (1986) Theory of elasticity, volume 7. New York: Pergamon.
- [150] Schek HT III, Gardner MK, Cheng J, Odde DJ, Hunt AJ (2007) Microtubule assembly dynamics at the nanoscale. *Curr Biol* **17**:1445–1455.
- [151] Laan L, Husson J, Munteanu EL, Kerssemakers JWJ, Dogterom M (2008) Force-generation and dynamic instability of microtubule bundles. *Proc Natl Acad Sci* :accepted.

- [152] Dogterom M, Husson J, Laan L, Munteanu EL, Tischer C (2007) Microtubule forces and organization. In: Lenz P, editor, *Cell Motility*, Springer New York. pp. 93–115.
- [153] Kinoshita K, Arnal I, Desai A, Drechsel DN, Hyman AA (2001) Reconstitution of physiological microtubule dynamics using purified components. *Science* **294**:1340–1343.
- [154] Jánosi IM, Chrétien D, Flyvbjerg H (1998) Modeling elastic properties of microtubule tips and walls. *Eur Biophys J* **27**:501–513.
- [155] Howard J, Hyman AA (2003) Dynamics and mechanics of the microtubule plus end. *Nature* **422**:753–758.
- [156] Carter BC, Vershinin M, Gross SP (2008) A comparison of step-detection methods: how well can you do? *Biophys J* **94**:306–319.
- [157] Popov AV, Pozniakovskiy A, Arnal I, Antony C, Ashford AJ, Kinoshita K, Tournebise R, Hyman AA, Karsenti E (2001) XMAP215 regulates microtubule dynamics through two distinct domains. *EMBO J* **20**:397–410.
- [158] Waterman-Storer CM, Desai A, Bulinski JC, Salmon ED (1998) Fluorescent speckle microscopy, a method to visualize the dynamics of protein assemblies in living cells. *Curr Biol* **8**:1227–1230.
- [159] Danuser G, Waterman-Storer CM (2006) Quantitative fluorescent speckle microscopy of cytoskeleton dynamics. *Annu Rev Biophys Biomol Struct* **35**:361–387.
- [160] Waterman-Storer CM, Salmon ED (1998) How microtubules get fluorescent speckles. *Biophys J* **75**:2059–2069.
- [161] Waterman-Storer CM, Salmon ED (1999) Fluorescent speckle microscopy of microtubules: how low can you go? *FASEB J* **13**:S225–S230.
- [162] Danuser G, M WSC (2003) Quantitative fluorescent speckle microscopy: where it came from and where it is going. *J Microsc* **211**:191–207.
- [163] Hess ST, Huang S, Heikal AA, Webb WW (2002) Biological and chemical applications of fluorescence correlation spectroscopy: a review. *Biochemistry* **41**:697–705.
- [164] Rigler R, Mets U, Widengren J, Kask P (1993) Fluorescence correlation spectroscopy with high count rate and low background: Analysis of translational diffusion. *Eur Biophys J* **22**:169–175.
- [165] Tirado MM, López Martínez C, García de la Torre J (1984) Comparison of theories for the translational and rotational diffusion coefficients of rod-like macromolecules. Application to short DNA fragments. *J Chem Phys* **81**:2045–2052.

-
- [166] Magde D, Elson EL, Webb WW (1974) Fluorescence correlation spectroscopy. II. An experimental realization. *Biopolymers* **13**:29–61.
- [167] Hess ST, Webb WW (2002) Focal volume optics and experimental artifacts in confocal fluorescence correlation spectroscopy. *Biophys J* **83**:2300–2317.
- [168] Krouglova T, Vercammen J, Engelborghs Y (2004) Correct diffusion coefficients of proteins in fluorescence correlation spectroscopy. Application to tubulin oligomers induced by Mg^{2+} and paclitaxel. *Biophys J* **87**:2635–2646.
- [169] Meseth U, Wohland T, Rigler R, Vogel H (1999) Resolution of fluorescence correlation measurements. *Biophys J* **76**:1619–1631.
- [170] Gaskin F, Cantor CR, Shelanski ML (1974) Turbidimetric studies of the *in vitro* assembly and disassembly of porcine neurotubules. *J Mol Biol* **89**:737–755.
- [171] Perez F, Diamantopoulos GS, Stalder R, Kreis TE (1999) CLIP-170 highlights growing microtubule ends *in vivo*. *Cell* **96**:517–527.
- [172] Mimori-Kiyosue Y, Shiina N, Tsukita S (2000) Adenomatous polyposis coli (APC) protein moves along microtubules and concentrates at their growing ends in epithelial cells. *J Cell Biol* **148**:505–518.
- [173] Mimori-Kiyosue Y, Shiina N, Tsukita S (2000) The dynamic behavior of the APC-binding protein EB1 on the distal ends of microtubules. *Curr Biol* **10**:865–868.
- [174] Akhmanova A, Hoogenraad CC, Drabek K, Stepanova T, Dortland B, Verkerk T, Vermeulen W, Burgering BM, De Zeeuw CI, Grosveld F, et al. (2001) CLASPs are CLIP-115 and -170 associating proteins involved in the regional regulation of microtubule dynamics in motile fibroblasts. *Cell* **104**:923–935.
- [175] Vaughan PS, Miura P, Henderson M, Byrne B, Vaughan KT (2002) A role for regulated binding of p150^{Glued} to microtubule plus ends in organelle transport. *J Cell Biol* **158**:305–319.
- [176] Kodama A, Karakesisoglou I, Wong E, Vaezi A, Fuchs E (2003) ACF7: an essential integrator of microtubule dynamics. *Cell* **115**:343–354.
- [177] Ding DQ, Chikashige Y, Haraguchi T, Hiraoka Y (1998) Oscillatory nuclear movement in fission yeast meiotic prophase is driven by astral microtubules, as revealed by continuous observation of chromosomes and microtubules in living cells. *J Cell Sci* **111**:701–712.
- [178] Hayles J, Nurse P (2001) A journey into space. *Nat Rev Mol Cell Biol* **2**:647–656.
- [179] Brunner D, Nurse P (2000) New concepts in fission yeast morphogenesis. *Phil Trans R Soc Lond B* **355**:873–877.

- [180] Browning H, Hayles J, Mata J, Aveline L, Nurse P, McIntosh JR (2000) Tea2p is a kinesin-like protein required to generate polarized growth in fission yeast. *J Cell Biol* **151**:15–28.
- [181] Browning H, Hackney DD (2005) The EB1 homolog Mal3 stimulates the ATPase of the kinesin Tea2 by recruiting it to the microtubule. *J Biol Chem* **280**:12299–12304.
- [182] West RR, Malmstrom T, Troxell CL, McIntosh JR (2001) Two related kinesins, klp5(+) and klp6(+), foster microtubule disassembly and are required for meiosis in fission yeast. *Mol Biol Cell* **12**:3919–3932.
- [183] Ohkura H, Garcia MA, Toda T (2001) Dis1/TOG universal microtubule adaptors - one MAP for all? *J Cell Sci* **114**:3805–3812.
- [184] Lata S, Piehler J (2005) Stable and functional immobilization of histidine-tagged proteins via multivalent chelator headgroups on a molecular poly(ethylene glycol) brush. *Anal Chem* **77**:1096–1105.
- [185] Tirnauer JS, Salmon ED, Mitchison TJ (2004) Microtubule plus-end dynamics in *Xenopus* egg extract spindles. *Mol Biol Cell* **15**:1776–1784.
- [186] Gildersleeve RE, Cross AR, Cullen KE, Fagen AP, Williams RC Jr (1992) Microtubules grow and shorten at intrinsically variable rates. *J Biol Chem* **267**:7995–8006.
- [187] Vitre B, Coquelle FM, Heichette C, Garnier C, Chretien D, Arnal I (2008) EB1 regulates microtubule dynamics and tubulin sheet closure *in vitro*. *Nat Cell Biol* **10**:415–421.
- [188] Moudjou M, Bornens M (1994) Isolation of centrosomes from cultured animal cells. In: Celis JE, editor, *Cell biology: A laboratory handbook*, Academic Press, Inc. pp. 595–604.
- [189] Tran PT, Walker RA, Salmon ED (1997) A metastable intermediate state of microtubule dynamic instability that differs significantly between plus and minus ends. *J Cell Biol* **138**:105–117.
- [190] Chrétien D, Fuller SD (2000) Microtubules switch occasionally into unfavorable configurations during elongation. *J Mol Biol* **298**:663–676.