from tubulin and diffuse for $\sim 1 \mu s$, yet still have a 99% chance of returning to the substrate within 10 ms (our unpublished data), a time sufficiently short (compared with the ATP turnover rate) for movement to appear largely unaffected. Qualitatively, the occcasionally jittery character of bead motion driven by low numbers of kinesin molecules, including events of the kind shown in Fig. 1e-f, might be explained by a small number of longer-lived detached states. Detailed comparisons await data from tracking experiments that can follow fine structure of the motion¹⁴. Until now, it has not been possible to relate this motion to the action of single molecules.

The spontaneous bead detachments that we observe might be due to kinesin molecules operating with just a single active head, if, for example, the second head were inactivated by being bound to the bead surface. In this fashion, cooperativity between the two heads would be precluded and single-headed interactions would lead to premature release. Implicit in this interpretation is that the two kinesin heads are capable of independent motion, as seems to be the case for myosin⁸. This suggestion could be tested by studying motion driven by genetically engineered, single-headed kinesin²⁰.

How can movement over relatively long distances (5 µm and more) in moving microtubule assays driven by single molecules be reconciled with our observations of spontaneous release after \sim 1.4 µm? Figure 4b illustrates two effects that conspire to keep a microtubule moving near the glass, thereby obscuring the releases revealed by our moving bead assays. First, despite its narrow diameter, a microtubule has a smaller translational diffusion coefficient along the direction normal to the surface than a bead. Second, diffusional rotation of a moving microtubule about its long axis will present an equivalent surface lattice of potential binding sites, whereas rotation of a bead carrying a few kinesin molecules can destroy the possibility of favourable binding. Howard et al.⁹ recognized that movement driven by single kinesins might be consistent with a strokerelease model, and suggested that a detachment of less than 1 ms could be accommodated. Our data favour precisely such a model, and are fitted well by a microsecond-long inactivation of kinesin followed by a rebinding step that is diffusion-limited, taking a variable time, up to milliseconds. It is not clear how release time relates to measured rate constants of the biochemical $cycle^{21,22}$. We found no significant dependence of the speed of bead movement on the kinesin density; average speeds all fell in the range 0.35–0.45 μ m s⁻¹. The rate-limiting step for movement seems not to be associated with the reassociation step following release.

The existence of a detached state calls into question the feasibility of using (constant) tension probes, such as optical tweezers or glass microneedles, to measure the force of translocation for beads or microtubules that are driven by small numbers of motors. This is because beads or microtubules are likely to be driven backwards once molecules detach. Measurements of the average force generated by larger numbers of kinesin molecules may ultimately be more meaningful. \Box

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CORRECTION

Light-emitting diodes based on conjugated polymers

J. H. Burroughes, D. D. C. Bradley, A. R. Brown, R. N. Marks, K. Mackay, R. H. Friend, P. L. Burn & A. B. Holmes

Nature 347, 539-541 (1990)

In the published version of this paper the name of one of the authors was incorrectly cited as P. L. Burns rather than P. L. Burn. His address is the University Chemical Laboratory, Cambridge, rather than the University Chemistry Laboratory as stated.

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