

mutant is phenotypically similar to the *aux1* mutant, which suggests that both genes act in the same process. Dharmasiri *et al.* now provide an explanation for this phenotypic similarity by identifying AXR4 as an endoplasmic reticulum-resident protein required for proper AUX1 sorting to the plasma membrane. AXR4 appears specific for AUX1 trafficking, because other membrane proteins such as the PINs are not mislocalized in the *axr4* mutant. Interestingly, in the root tissues examined, the only cell types affected by the *axr4* mutation were those in which AUX1 localization is polar. In the lateral root cap, where AUX1 is uniformly distributed, there are no obvious effects in the *axr4* mutant background, whereas in the epidermis and protophloem where AUX1 is polarly localized, AUX1 is retained in the endoplasmic reticulum. This suggests that AXR4 plays a specific tissue-dependent role in the polar sorting of AUX1 to

a particular plasma membrane face, rather than a general chaperone-like function. The biochemical basis for AXR4 action is not yet clear. Apart from a predicted transmembrane motif and a putative α/β hydrolase fold, AXR4 does not contain any known protein domains.

These discoveries demonstrate clear tissue-specific elements in the membrane targeting of both PIN and AUX1. So far, however, there is no evidence of any coordination of these events, although there is some suggestion of common elements because both are sensitive to the protein traffic inhibitor brefeldin A (13, 17). As the mechanisms for polar localization of these proteins are revealed, it will be interesting to see the extent to which they are independent.

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MATERIALS SCIENCE

Toward Devices Powered by Biomolecular Motors

Henry Hess

Biomolecular motors, such as the motor protein kinesin, convert chemical energy derived from the hydrolysis of individual adenosine triphosphate (ATP) molecules into directed, stepwise motion (1). This process enables them to actively transport designated cargo—such as vesicles, RNA,

or viruses—to predetermined locations within cells. For engineers, active transport in biology inspires visions of nano-

fluidic systems for biosensing, of active materials that can rearrange their components, and of molecular conveyor belts and forklifts for nanometer-scale manufacturing.

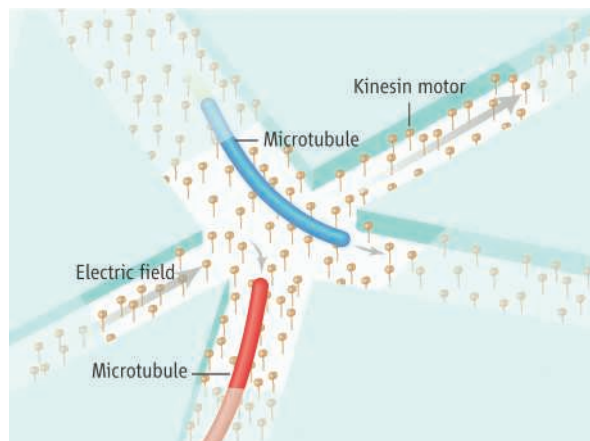
Nanofluidic devices, which extend the lab-on-a-chip paradigm to systems with picoliter volumes and submicrometer channel diameters, present an immediate opportunity for the application of biomolecular motors. On page 910 of this issue, van den Heuvel *et al.* (2) show that kinesin motor proteins can drive the directed transport of microtubules (filamentous assemblies of thousands of tubulin proteins) in closed channels

with submicrometer dimensions. Controlled application of an external electric field steers the microtubules into either one of two arms of a Y junction (see the figure).

The setup is an adaptation of the classic gliding motility assay (3), in which the kinesin motor proteins adhere to a surface via their rotationally flexible tails, bind to the leading ends of approaching microtubules with their two heads, and move the microtubules by stepping forward with alternating heads until they reach the trailing end and detach. In biological systems, the motors move and the microtubules are stationary. The key advantages of the inverted geometry used in the assay are that the microtubules are continuously bound to the surface over transport distances of more than a millimeter (4) and that the large microtubule allows the attachment of fluorescence tags for observation and of specific linkers for cargo binding (5).

Open or micrometer-scale closed channels have previously been fabricated to confine microtubule movements (6–8). Van den Heuvel

Biomolecular motors can be used in nanometer-scale devices to perform mechanical work. This approach will assist the development of active nanostructures.



Nanofluidics with molecular motors. In van den Heuvel *et al.*'s work (2), an electric field is used to steer the microtubules into one of two arms of a Y junction; the microtubules move perpendicular to the field. The microtubules are transported by kinesin motor proteins.

et al. have now created closed channels with submicrometer dimensions. The channels not only provide better confinement, but they also mimic the dimensions of axons, in which motor-driven transport plays a central role. They may thus enable more realistic model studies at the system level of active transport in biology. Electric fields for active steering provide direct control over the paths of individual microtubules. By coupling fluorescence detec-

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