

1. Answer: FFFFF

Feedback: Both plus-end directed, and minus-end directed myosins and kinesins have been identified; however, all known dyneins move toward the minus end of microtubules.

2. Answer: D

Feedback: Catastrophe is the transition from growth to shrinkage, while rescue is the transition from shrinkage to growth. The transition frequencies are generally higher in more dynamic microtubules, which also tend to be shorter.

3. Answer: CCBC

Feedback: Cilia are found in large numbers on ciliated cells such as those lining our respiratory tract. They are relatively short and beat with a whiplike motion. Axoneme constitutes the structural core of both cilia and flagella.

4. A. Centrosome lowers the critical concentration by providing nucleation sites for microtubule growth. Nucleation sites make it easier to start new microtubules; moreover, they protect the bound end from disassembly. Thus, once started, a microtubule is more likely to persist. In the absence of such a nucleation site, it is much more difficult to start a microtubule, and both ends serve as sites for disassembly.

B. The shapes of the curves in the presence and absence of centrosomes differ because of the nature of the assays to detect polymerization. In the absence of centrosomes (see Figure 16-26A), the assay was for total polymer formed, which depends only on the concentration of added  $\alpha\beta$ -tubulin. Thus, it increases indefinitely in a linear fashion with increasing concentration of tubulin. In the presence of centrosomes (see Figure 16-26B), the assay was the number of microtubules per centrosome. Since each centrosome has a limited number of nucleation sites (about 60 for the centrosomes used in this experiment), the measurement must reach a plateau at high tubulin concentrations.

5. Newly synthesized actin filaments still contain ATP as hydrolysis to ADP is slower than the assembly of a new filament. In older filaments the ATP hydrolysis is complete and only ADP is present.

6. The microtubule cap

7:

A) False. Actin filaments accomplish this list of functions. Microtubules determine the positions of membrane-enclosed organelles, direct intra-cellular transport, and form the mitotic spindle that segregates chromosomes during cell division.

B) True. The actin filaments that make up the actin bundle in stereocilia display the dynamic properties typical of all actin filaments.

8: Intermediate filaments provide mechanical stability and resistance to shear stress. Microtubules determine the positions of membranous organelles and direct intracellular transport. Actin filaments determine the shape of the cell's surface and are necessary for whole-cell locomotion.

9: Although the subunits are indeed held together by noncovalent bonds that are individually weak, there are a very large number of them, distributed among a very large number of filaments. As a result, the stress a human being exerts by lifting a heavy object is dispersed over so many subunits that their interaction strength is not exceeded. By analogy, a single

thread of silk is not nearly strong enough to hold a human, but a rope woven of such fibers is.

10: In cells, most of the actin subunits are bound to thymosin, which locks actin into a form that cannot hydrolyze its bound ATP and cannot be added to either end of a filament. Thymosin reduces the concentration of free actin subunits to around the critical concentration. Actin subunits are recruited from this inactive pool by profilin, whose activity is regulated so that actin polymerization occurs when and where it is needed. The advantage of such an arrangement is that the cell can maintain a large pool of subunits for explosive growth at the sites and times of its choosing.

11: Two tubulin dimers have a lower affinity for each other (because of a more limited number of interaction sites) than a tubulin dimer has for the end of a microtubule. At the end of an existing microtubule there are multiple possible interaction sites, both end-to-end as the tubulin dimers add to a protofilament, and side-to-side as they bind to adjacent protofilaments in the microtubule lattice. Thus, to initiate a microtubule from scratch, enough tubulin dimers must come together and remain bound to one another for long enough for other tubulin molecules to add to them. Only when several tubulin dimers have already assembled will the binding of the next subunit be favored.

12: The centrosome nucleates a three-dimensional, starburst array of microtubules that grow until they encounter an obstacle, ultimately the plasma membrane. Dynamic instability of the microtubules, coupled to the requirement for equal pushing of oppositely directed microtubules, eventually positions the centrosome in the middle of the cell. One way to think about the notion of equal and opposite forces is to realize that the microtubules are not absolutely rigid structures. Imagine pushing an object with a short steel rod versus a very long one; the short rod transmits force effectively, but the long rod will bend, delivering less force. The same principle may operate inside the cell, with microtubules of equal length delivering the same force. When all the oppositely directed microtubules emanating from a centrosome are the same length, the centrosome will be in the center of the cell.

13: The minus ends of the growing actin filaments are anchored to the rest of the actin cytoskeleton, which supports the growing actin filaments and allows them to push on the membrane without simply sliding back into the cell's interior. The solution to the problem at the plus end is not so straightforward. Once the filament contacts the membrane, there would be no room for a new subunit to be added onto the end of the growing chain. It is thought that random thermal motions briefly expose the plus end of the filament, allowing a new subunit to be added. By taking advantage of these small windows of opportunity, actin polymerization acts as a ratchet to capture random thermal motions. It is unclear what motions the actin ratchet is capturing. It could be that membranes "breathe" thermally, allowing polymerization. Alternatively, the actin filament may bend elastically, moving the plus end sufficiently to allow subunit addition.