

## SHAPE SHIFTING

Several factors interact to determine the three-dimensional structure of cells and organelles. First and foremost, the physical properties of the molecules that comprise the structure have preferred positions that minimize the energetic costs of the shape they take. If both layers of a lipid membrane have an identical composition, for example, that membrane will naturally lay flat **1**. Membrane monolayers composed of different lipids, on the other hand, may curve **2**.

Proteins also play a key role in determining cell and organelle shape. In the endoplasmic reticulum (ER), BAR domain proteins and reticulons insert into the lipid membrane, causing it to bend **3**. The proteins have an affinity for curved surfaces such that their attraction to the ER membrane overcomes the energetic cost of the bending.

Finally, some basic mathematical principles can dictate shape. For example, surface-to-volume ratio, which is a function of organelle size, can influence how spherical a structure is. The ER, which has a high surface area and a relatively low volume, takes the shape of a stack of pancakes **4**. The connections between these layers is once again determined by the physics of the system, with spiral connecting structures resulting in minimal energy output from the ER's lipid membranes.

