Ref. 933 ment in linear motors was uncovered during the 1990s. The results started a wave of research on all other molecular motors found in nature. All molecular motors share several characteristic properties: molecular motors do not involve temperature gradients involved, as car engines do, they do not involve electrical currents, as electrical motors do, and they do not rely on concentration gradients, as chemically induced motion, such as the rising of a cake, does.

Linear molecular motors

The central element of the most important linear molecular motor is a combination of two protein molecules, namely myosin and actin. Myosin changes between two shapes and literally *walks* along actin. It moves in regular small steps, as shown in Figure 489. The motion step size has been measured with beautiful experiments to always be an integer multiple of 5.5 nm. A step, usually forward, but sometimes backwards, results whenever an ATP (adenosine triphosphate) molecule, the standard biological fuel, hydrolyses to ADP (adenosine diphosphate), thus releasing its energy. The force generated is about 3 to 4 pN; the steps can be repeated several times a second. Muscle motion is the result of thousand of millions of such elementary steps taking place in concert.

Ref. 933

How do molecular motors work? Molecular motors are are so small that the noise due to the molecules of the liquid around them is not negligible. But nature is smart: with two tricks it takes advantage of Brownian motion and transforms it into macroscopic molecular motion. Molecular motors are therefore also called *Brownian motors*. The transformation of disordered molecular motion into ordered macroscopic motion is one of the great wonders of nature. The first trick of nature is the use of an asymmetric, but periodic potential, a so-called *ratchet*.* The second trick of nature is a temporal variation of the potential, together with an energy input to make it happen. The most important realizations are shown in Figure 491.

Ref. 934

The periodic potential variation in a molecular motor ensures that for a short, recurring time interval the free Brownian motion of the moving molecule – typically 1 µm/s – affects its position. Subsequently, the molecule is fixed again. In most of the short time intervals of free Brownian motion, the position will not change. But if the position does change, the intrinsic asymmetry of the ratchet shape ensures that with high probability the molecule advances in the preferred direction. (The animation of Figure 489 lacks this irregularity.) Then the molecule is fixed again, waiting for the next potential change. On average, the myosin molecule will thus move in one direction. Nowadays the motion of single molecules can be followed in special experimental set-ups. These experiments confirm that muscles use such a ratchet mechanism. The ATP molecule adds energy to the system and triggers the potential variation through the shape change it induces in the myosin molecule. That is how our muscles work.

Another well-studied linear molecular motor is the kinesin–microtubule system that carries organelles from one place to the other within a cell. As in the previous example, also in this case chemical energy is converted into unidirectional motion. Researchers were able to attach small silica beads to single molecules and to follow their motion. Using laser beams, they could even apply forces to these single molecules. Kinesin was

* It was named by Walt Disney after by Ratchet Gearloose, the famous inventor from Duckburg.

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