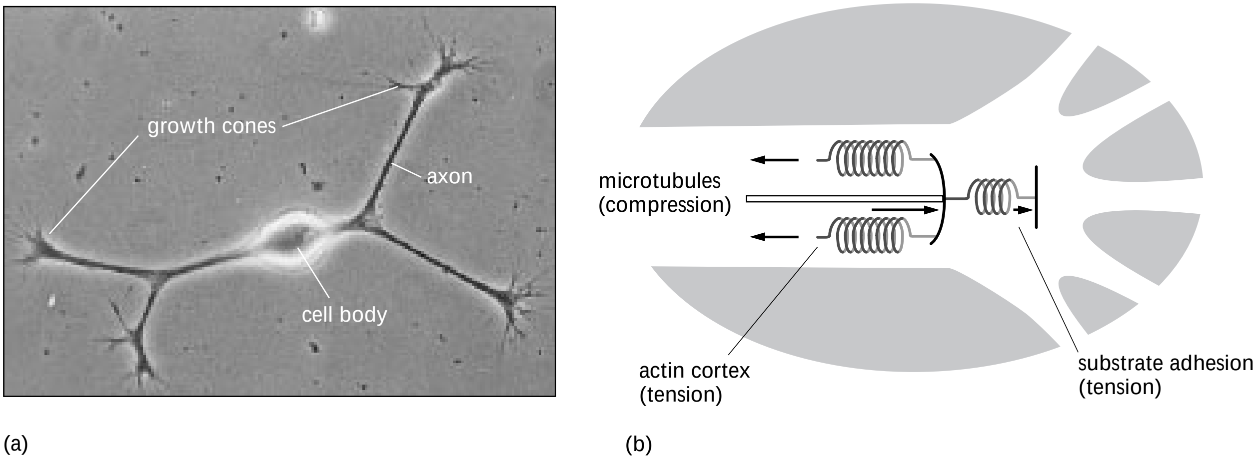

Figure 18-7 Mechanical balance in a nerve cell. (a) Light micrograph of a single nerve cell in tissue culture. Short axons tipped by growth cones are growing out from the cell body. (b) Principal contributions to the mechanical balance of each axon.

cytoskeleton seem to be highly localized and not distributed across the whole cell. It is also clear that chemical signals play an essential part in integrating changes in different regions, as we see below.

Myosin II makes a major contribution to cortical tension

The earliest measurements of the mechanical properties of living cells, some of them dating to the 1930s, focused on the deformation of very large cells. Sea urchin eggs, which are over 100 μm in diameter, spherical, and easily obtained in large numbers, were favorite objects of study. Individual eggs were mounted under a microscope, held in various kinds of jigs and clamps, and then depressed by probes such as strips of metal foil or flexible needles. The forces applied were estimated from the deflection of the foil or needle, and the deformations of the cell surface measured in the microscope.

Since then, techniques have become increasingly precise and rapid. Glass needles with tip diameters in the micrometer range can be maneuvered onto or into cells and their bending deflections measured with nanometer accuracy. Vibrating electrodes can be used to probe the surface elasticity of cells, changes in the amplitude and frequency of the tip being a sensitive indicator of the mechanical properties of the material it contacts. The tips of glass probes can be coated with specific antibodies or other molecules so that they adhere selectively to particular molecules such as integrins on the cell surface. Yet another approach is to grow cells on a thin elastic skin on the surface of silicone rubber. Cell contractions produce wrinkles in the underlying sheet, providing a graphic portrayal of the distribution of contractile forces (Figure 18-8).

One inescapable conclusion from these disparate measurements is that the surfaces of animal cells are under a steady level of tension. Moreover, given that the cortex is full of actin filaments, an obvious candidate for the source of this tension is myosin. Indeed, mutants of *Dictyostelium* lacking myosin II have a much reduced cortical tension, whereas a cell with a mutant myosin light chain kinase that works all the time has a

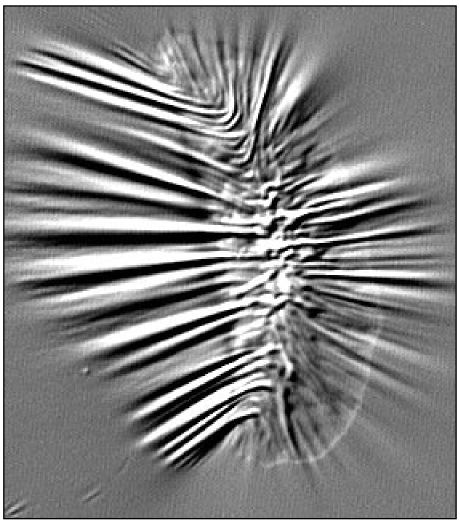

Figure 18-8 Wrinkles in rubber caused by a cell. A goldfish keratocyte (skin cell) is moving from left to right on a transparent silicone rubber substratum. Traction forces generated by the cell compress the rubber into a series of wrinkles. The cell was viewed by Normarski differential interference contrast microscopy. The field of view is 60 μm. (Courtesy of Kevin Burton.)