GUEST COMMENTARY

How *Spiroplasma* Might Swim

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Spiroplasmas are small helical bacteria without rigid walls. They have a cytoskeleton in the form of a flat ribbon that runs the length of the cell. In an ordinary liquid medium, a cell spins about its long axis, but it does not translate. In a gel-like medium, containing a viscous agent like methylcellulose, it moves rapidly in a direction parallel to its long axis. Here I suggest how a cytoskeletal ribbon might bend to generate such motion.

This commentary is inspired by a recent article describing the molecular organization of the “contractile cytoskeleton of the helical bacterium *Spiroplasma melliferum* BC3” (4). This is a flat ribbon made up of six or seven parallel fibrils attached to the cell membrane that “follows, seemingly, the shortest helical path of the cell. . . the innermost helical line in the coiled cell.” It is suggested that this ribbon propels the cell by contracting and expanding. For descriptions of *Spiroplasma* movement, see reference 2.

If the ribbon contracts and expands, it is not sufficient for it to do so reciprocally, i.e., merely to contract and expand: reciprocal motion does not generate net displacement in a microscopic environment (3). However, there is a simple way that the ribbon might propel the cell by bending about two axes in a cyclic manner. The scheme is outlined in Fig. 1 and 2. Figure 1 approximates the helical cell body as a cylinder that bends about two axes, one, **a**, normal to the plane of the page, and the other, **b**, in the plane of the page. As shown, the bend about **a** has moved the right end of the cylinder upwards and the bend about **b** has moved the tip of that segment out of the page. The complete cycle is shown in Fig. 2, where the cell of Fig. 1 is viewed end-on from the right and the segments of the cell subject to bends are reduced to lines. The cycle runs from configuration 1 to 4 and back to 1. The bend angles are indicated on the right image, and their progression with time is shown in the graph.

The primary effect of this cycle is to roll the cell about its longitudinal axis, clockwise as viewed in Fig. 2. Think of the circle as a floating tub viewed from above and the lines as an oar. Stroke backwards on the left (bend about axis **a**, transition 1 to 2), to the right behind (axis **b**, 2 to 3), forwards on the right (axis **a**, 3 to 4), and to the left in front (**b**, 4 back to 1): the tub turns clockwise. Of course, the stroking could be more complicated, and it could occur anywhere along the cell body, but

this is its simplest representation. Part of the cell gyrates one way, and the entire cell rolls the other way.

Leptospira swims in this way, gyrating its ends by means of two short subpolar periplasmic flagella (1). Its body is much longer than that of *Spiroplasma*, but it has a similar helix pitch and diameter. The motion of a cell with only one flagellum is particularly instructive. When the flagellar motor spins one way, the filament becomes helical, with a pitch and diameter much larger than those of the cell body. Rotation of the filament causes the end of the cell body to propagate a spiral wave from the head towards the tail. It also causes the cell to roll the other way about its local body axis. Propagation of the spiral wave drives the cell forward. This works both in an ordinary liquid medium and in 1% methylcellulose, but in the latter medium the roll of the cell body also contributes. When the flagellar motor spins the other way, the filament becomes coiled and the end of the cell gyrates, bent in the shape of a hook, rather like the handle of an old umbrella. As before, the cell body rolls the other way about its local body axis. But now there is no spiral wave, and the cell fails to translate in an ordinary liquid medium. However, it swims quite well in 1% methylcellulose, hook last. So, the roll of the cell body (a helix of small pitch and diameter) does not generate much thrust in an ordinary liquid medium, but it generates a lot of thrust in a gel-like medium. The helix screws its way through the latter like a corkscrew through a cork. And the gyration is more effective because there is more drag on a thin cylinder moving sideways in a gel-like medium than in an ordinary medium.

Therefore, to make *Spiroplasma* swim, all one has to do is

FIG. 1. A cell, simplified to a cylinder, viewed from the side. It bends about two axes, **a** normal to the page and **b** in the plane of the page. In the configuration shown, the bend about **a** is upwards and the bend about **b** is out of the page. In real life, the bending need not be so pronounced.

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FIG. 2. The same cell as that shown in Fig. 1 viewed end-on from the right, shown in four different configurations. Frame 1 is the configuration shown in Fig. 1. Here, the segments of the cell that are displaced by bends are reduced to lines. Bending proceeds through the cycle 1 to 4 and back to 1. The graph shows how the bend angles progress with time.

gyrate one end of the cell to generate torque that rolls the cell body. This will work if both ends of the cell gyrate, as long as the direction of gyration is the same when viewed from one end of the cell. If both ends gyrate but in opposite directions, then the cell will stop rolling and flex. However, one does not need a rotary joint to gyrate—try waving your arm—bending will do. Bending can be generated by differential contraction or expansion, e.g., of one part of the cytoskeleton relative to another or of the cytoskeleton relative to the cell membrane. A familiar example is the bimetallic strip, where bending is driven by thermal expansion.

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