

ORIENTATION BY HELICAL MOTION—II. CHANGING THE DIRECTION OF THE AXIS OF MOTION

- HUGH C. CRENSHAW
Department of Zoology,
Duke University,
Durham, NC 27706, U.S.A.

- LEAH EDELSTEIN-KESHET
Department of Mathematics,
University of British Columbia,
121-1984 Mathematics Road,
Vancouver, B.C., Canada V6T 1Y4

We analyse the helical motion of organisms, concentrating on the means by which organisms change the direction in space of the axis of the helical trajectory, which is the net direction of motion. We demonstrate that the direction of the axis is determined largely by the direction of the organism's rotational velocity. Changes in direction of the rotational velocity, with respect to the organism's body, change the direction in space of the axis of the helical trajectory. Conversely, changes in direction of the translational velocity, with respect to the body of the organism, have little effect on the direction in space of the axis of the trajectory. Because the axis of helical motion is the net direction of motion, it is likely that organisms that move in helices change direction by pointing their rotational velocity, not their translational velocity, in a new direction.

1. Introduction. Most free-swimming organisms whose bodies measure 5–500 μm swim in helices (see Jennings, 1901, 1904). Many of these organisms orient to external stimuli by aligning the axis of their helical trajectories to the direction of the stimulus (e.g. Jennings, 1904). Because the axis of the helix is parallel to the organism's rotational (angular) velocity when the rotational velocity is constant (see Crenshaw, 1993a) it is understood that these cells align the axis of their trajectories by pointing their rotational velocities in the direction of the stimulus (see Foster and Smyth, 1980).

The axis of the helix, however, is not always parallel to the organism's rotational velocity, especially when the rotational velocity is not constant, for example when the rotational velocity, and thus the axis of the helix, is changing direction. At such times the axis of the helix is a complex function of the organism's translational (linear) and rotational (angular) velocities and their first and second time derivatives (Crenshaw, 1989, 1993a). Consequently, the

mechanism by which the axis of the helix changes direction requires closer examination.

This paper analyses how an organism changes the direction of the axis of its helical trajectory. This is the second paper in a series of three describing how organisms can use helical motion to orient to a stimulus. The first paper (Crenshaw, 1993a) developed much of the mathematics used throughout the series. The third and final paper in this series (Crenshaw, 1993b) demonstrates how the mechanism of changing direction described in this second paper can be used by an organism to orient to a stimulus. For readers who do not want the details of the mathematical analyses, results are summarized without mathematics at the end of each paper in the series.

We begin here with the differential geometry of three-dimensional (3D) curves to describe a general case of motion in which the axis of a helical trajectory changes direction in space. This analysis discusses only smooth curves—the first and second derivatives of the curve are continuous. We then simulate the motion of an organism as a rigid body in rotation and translation and examine the resulting 3D trajectory. These simulations permit analysis of trajectories that are not smooth.

The general result of our analysis is that the axis of the helical trajectory is usually parallel to the organism's rotational velocity and that the axis of the helix changes direction in space whenever the organism changes the direction of its rotational velocity with respect to its body. Conversely, changes in the translational velocity lead only to transient changes in the direction of the axis, changes that persist only as long as the organism's translational acceleration is nonzero. When the translational acceleration returns to zero, the axis of the helix aligns with the rotational velocity, even if the final direction of the translational velocity has changed. Our results support independent work by Brokaw (1958—see discussion).

2. The Analysis

2.1. *Differential geometry.* We do not consider here the motion of an organism *per se*. Rather, we consider the motion of a point in the organism. This point describes a curve in three-dimensional (3D) space, and we analyse the geometry of that curve. We use three reference frames. (1) **XYZ** is fixed in space. (2) **TNB** is the Frenet trihedron in which **T** is the unit tangent vector; **N** is the unit normal vector; and **B** is the unit binormal vector. (The Frenet trihedron is conventionally used to describe the geometry of curves—see Gillett, 1984, pp. 690–699.) (3) **IJK** is fixed to a helical trajectory such that right-hand helical motion is described by the following vector function:

$$\mathbf{H}(t) = r \cos(\gamma t) \mathbf{I} + r \sin(\gamma t) \mathbf{J} + \left(\frac{p\gamma t}{2\pi} \right) \mathbf{K} \quad (1)$$

where \mathbf{K} is the axis of the helix; r is the radius; p is the pitch; and γ is the angular frequency of the vector (see Fig. 1 in Crenshaw, 1993a). In effect, the vector $\mathbf{H}(t)$ traces a helix. The endpoint moves around the cylinder once every $2\pi/\gamma$ units of time and moves the distance p in the direction of \mathbf{K} for every revolution around the cylinder.†

The Frenet trihedron \mathbf{TNB} moves along this curve such that the origin of \mathbf{TNB} is the endpoint of $\mathbf{H}(t)$. The motion of \mathbf{TNB} along the curve is described by a translational (linear) velocity \mathbf{V} and a rotational (angular) velocity known as the Darboux vector \mathbf{d} (see Crenshaw, 1993a). These are:

$$\mathbf{V} = \dot{\mathbf{H}} = V\mathbf{T} \tag{2}$$

$$\mathbf{d} = \tau\mathbf{T} + \kappa\mathbf{B} \tag{3}$$

where the dot indicates the derivative with respect to time, and τ and κ are the torsion and curvature, respectively, of the curve. \mathbf{d} describes the rotation of \mathbf{TNB} with respect to the arclength of the curve—it has units of radians/arclength. It will be helpful to define a rotational velocity with respect to time, \mathbf{d}^* , of \mathbf{TNB} as follows:

$$\mathbf{d}^* = V\mathbf{d} \tag{4}$$

where V is the speed of \mathbf{TNB} .

Crenshaw (1993a) demonstrates that \mathbf{d} , and thus \mathbf{d}^* , gives the axis of the helix \mathbf{K} . \mathbf{d}^* is parallel to \mathbf{K} for a right-hand helix and antiparallel to \mathbf{K} for a left-hand helix.

One additional parameter will assist later discussion. The pitch angle θ is the angle formed by the two vectors, \mathbf{V} and \mathbf{d}^* . It is given by:

$$\tan \theta = \frac{\kappa}{|\tau|} = \frac{2\pi r}{p} \tag{5}$$

(see Crenshaw, 1993a).

\mathbf{d}^* is described relative to \mathbf{TNB} in equations (3) and (4), so \mathbf{d}^* changes direction with respect to \mathbf{TNB} whenever the ratio κ/τ of the curve changes. If \mathbf{K} is given by \mathbf{d}^* , what happens to the direction of \mathbf{K} in space when \mathbf{d}^* changes direction relative to \mathbf{TNB} ? Consider the two reference frames, \mathbf{TNB} and \mathbf{IJK} , both free to move in space. Suppose \mathbf{TNB} rotates in space with rotational velocity \mathbf{d}^* . When some vector \mathbf{r} changes direction relative to a reference frame rotating with rotational velocity \mathbf{d}^* , the change in direction of \mathbf{r} with respect to space is given by:

† For a left-hand helix, the sine and cosine terms are interchanged. We use right-hand helices throughout this analysis, but the results also apply to left-hand helices

$$\dot{\mathbf{r}}_s = \dot{\mathbf{r}}_b + \mathbf{d}_s^* \times \mathbf{r}_s \quad (6)$$

where the subscripts, s and b , indicate that the vector is described with respect to space or the rotating reference frame, respectively (see Symon, 1971, pp. 276–278). This says that the rate of change of \mathbf{r} with respect to space equals the rate of change of \mathbf{r} with respect to the body of the organism plus the change in the direction of \mathbf{r} due to rotation of the body. For the rotational velocity of **TNB** [equations (3–4)], this becomes:

$$\dot{\mathbf{d}}_s^* = \dot{\mathbf{d}}_b^* + \mathbf{d}_s^* \times \mathbf{d}_s^*. \quad (7)$$

If one assumes that the orientation in space of **TNB** does not instantaneously change with respect to the arclength of the curve (i.e. the curve is smooth),[†] then equation (7) simplifies to:

$$\dot{\mathbf{d}}_s^* = \dot{\mathbf{d}}_b^* \quad (8)$$

which says \mathbf{d}^* changes direction with respect to space only when \mathbf{d}^* changes direction with respect to the rotating reference frame **TNB**. Because \mathbf{d}^* gives the direction of \mathbf{K} , as discussed above, equation (8) also says that \mathbf{K} changes direction in space whenever \mathbf{d}^* changes direction with respect to **TNB**.

Using equations (3) and (4) we can restate this result. The direction of \mathbf{d}^* with respect to **TNB** is given by κ and τ [equations (3) and (4)]. Whenever the ratio of κ to τ changes, the direction of \mathbf{d}^* changes, and according to equation (5) the pitch angle θ of the helix also changes. Thus, whenever θ changes and the curve is smooth, \mathbf{K} changes direction in space. (It should be noted that some curves appear to violate this result, conical spirals for example. Such curves are discussed at the end of this section.)

To better demonstrate how \mathbf{K} can change direction in space, we have simulated this motion on a computer. The algorithm used in the following simulations is presented in Appendix A. Briefly, helical motion with a given r , p and γ is described by equation (1); however, **IJK** is now free to assume any orientation in **XYZ**. The position of $\mathbf{H}(t)$ in **XYZ** is then calculated at discrete time increments Δt . At a given point in time, r or p change. [We present changes in θ as changes in r and p to make the changes in motion more intuitive—see equation (5).] The new parameters effectively describe a new helix in space, which is joined to the preceding helix in such a way that (1) the origins of the Frenet trihedrons of the two helices coincide and (2) the axes of the Frenet trihedrons align at the point of transition. Motion then proceeds along the new helix. For any given simulation, successively smaller values of Δt are used until

[†] The unit vectors, **TNB**, are functions of the first and second derivations of \mathbf{H} (see Gillett, 1984, pp. 693–696), so if **TNB** does not change orientation at one point on the curve then the first and second derivatives of \mathbf{H} are continuous.

the trajectories converge to approximate continuous motion. All simulations are right-hand helices.

Figure 1a demonstrates that the direction of \mathbf{K} changes only when θ changes. r and p change at three points (marked by dots, \bullet), but the ratio r/p is constant, so θ is constant. As expected, the direction of \mathbf{K} does not change. In Fig. 1b, θ changes at three points, which are marked by dots. As expected, \mathbf{K} changes direction each time θ changes. The changes in θ presented in Fig. 1a and b are discrete changes. In Fig. 1c, θ is initially constant. At the dot (\bullet), θ begins to change continuously. At the circle (\circ), θ returns to a constant value. \mathbf{K} is straight in the initial and final sections of the trajectory because θ is constant, but the axis has changed direction between these two sections. The straight sections are included to better display the net change in the direction of \mathbf{K} .

In summary, \mathbf{d}^* is parallel or antiparallel to the axis of helical motion \mathbf{K} . Whenever the curve is smooth and the pitch angle (which is a function of the ratio of torsion to curvature or of radius to pitch) changes, the direction in space of \mathbf{d}^* , and thus \mathbf{K} , changes.

2.2. *Rigid body rotation.* In this section, we examine the motion of an organism, treating the organism's body as a rigid body represented by the reference frame \mathbf{ijk} , where the origin of \mathbf{ijk} is the organism's center of mass. The rotational and translational velocities of this body are:

$$\boldsymbol{\omega}_b = \omega_1 \mathbf{i} + \omega_2 \mathbf{j} + \omega_3 \mathbf{k} \tag{9}$$

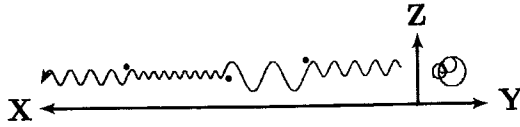
$$\mathbf{V}_b = V_1 \mathbf{i} + V_2 \mathbf{j} + V_3 \mathbf{k} \tag{10}$$

where the subscript, b , now indicates that the vector is described with respect to the body of the organism.

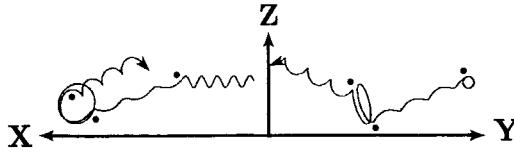
The trajectory traced by the center of mass of the organism is a curve in three dimensions, which as before can be described by the motion of a Frenet trihedron \mathbf{TNB} . Crenshaw (1993a) explains that the motion of \mathbf{TNB} is determined by the motion of the organism and presents equations describing \mathbf{TNB} , κ and τ as functions of \mathbf{V}_b , $\dot{\mathbf{V}}_b$, $\ddot{\mathbf{V}}_b$, $\boldsymbol{\omega}_b$ and $\dot{\boldsymbol{\omega}}_b$ [equations (7), (11), (12), (14) and (18)]. These equations are directly applicable to the discussion in the previous section. The axis of the helix changes direction in space whenever \mathbf{V}_b or $\boldsymbol{\omega}_b$ change such that the ratio of κ/τ , and thus θ , changes.

A careful look at the assumptions underlying the analyses in the present and preceding sections will be helpful. The preceding section assumes the trajectory is smooth. This assumption is needed to describe the orientation of \mathbf{TNB} as κ and τ change. The present section uses results from the analyses of Crenshaw (1989, 1993a) that describe the relationships between the motion of the Frenet trihedron and the body of the organism. While these previous analyses do not consider changes in κ or τ , they can be applied here if again the curve is assumed

a



b



c

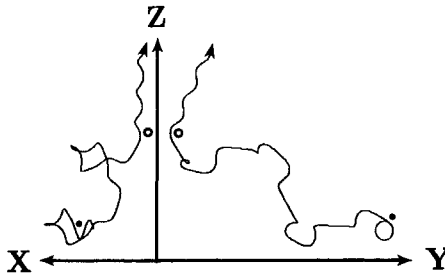


Figure 1. Simulation of changes in pitch angle, θ . (a) r and p of the trajectory change at three points (marked by dots, \bullet), total arclength s of curve equals 12: $s=0-3$, $r=0.1$, $p=0.3$; $s=3-6$, $r=0.2$, $p=0.6$; $s=6-9$, $r=0.05$, $p=0.15$; $s=9-12$, $r=0.1$, $p=0.3$. Because the ratio r/p does not change, θ does not change, and \mathbf{K} does not change direction in space. (b) r and p change at three points (marked by dots, \bullet), total arclength s of curve equals 12: $s=0-3$, $r=0.1$, $p=0.3$; $s=3-6$, $r=0.05$, $p=0.8$; $s=6-9$, $r=0.35$, $p=0.1$; $s=9-12$, $r=0.1$, $p=0.6$. Because r/p changes, θ changes and \mathbf{K} changes direction in space. (c) r and p change continuously between the point marked by a dot (\bullet) and the point marked by a circle (\circ). r always equals $1/p^2$. Total arclength s of curve equals 22. p changes as follows: $s=0-3$, $p=0.6$; $s=3-19$, $p=0.6-0.5 \sin(3(s-3))$; $s=19-22$, $p=0.984$. Because the ratio r/p changes, θ changes, so \mathbf{K} changes direction in space. Note: The trajectories are presented as two orthogonal two dimensional projections of the three dimensional curve. Each figure can be folded such that the axes form a right-hand reference frame.

to be smooth. Consequently, all equations presented here assume the curve is smooth. For rigid motion, this means that discrete changes in the direction of \mathbf{V}_b or in the orientation of \mathbf{ijk} with respect to the arclength of the trajectory are not considered by the equations.

This assumption of smoothness, however, is not needed in the simulations of the motion of a rigid body, because \mathbf{V}_b and $\boldsymbol{\omega}_b$ completely describe the motion of the body (see Beatty, 1986, Ch. 1). Consequently, discrete changes in the

direction of \mathbf{V}_b and the orientation of \mathbf{ijk} can now be considered. Violation of the assumption of smoothness at any point means that \mathbf{d}^* , and thus \mathbf{K} , is not defined at those points, and the equations presented here are not valid at those points. Nevertheless, the ability of the simulations in this section to address instantaneous changes has great relevance to the motion of microorganisms, as will be addressed in the discussion.

It is helpful if changes in \mathbf{V}_b and $\boldsymbol{\omega}_b$ are considered separately. Consider first the motion of an organism for which \mathbf{V}_b is held constant and only $\boldsymbol{\omega}_b$ varies. For simplicity, let $V_2 = V_3 = 0$ and $\omega_2 = 0$. In this case:

$$\kappa = \frac{\omega_3}{V}, \quad \tau = \frac{\omega_1}{V}, \quad \theta = \frac{\omega_3}{\omega_1} \tag{11}$$

$$\mathbf{d}_b^* = \boldsymbol{\omega}_b \tag{12}$$

[Crenshaw, 1993a, equation (30)]. Thus, κ , τ , θ and \mathbf{d}_b^* are not functions of the time derivatives of \mathbf{V}_b or $\boldsymbol{\omega}_b$. For such motion, \mathbf{ijk} and \mathbf{TNB} coincide. Both reference frames move in one direction relative to the rotating reference frame—in the direction of \mathbf{i} or \mathbf{T} . Both $\boldsymbol{\omega}_b$ and \mathbf{d}^* have two components, one parallel and one perpendicular to the direction of motion; in fact, \mathbf{d}^* is parallel to $\boldsymbol{\omega}$, as equation (12) shows. Consequently, θ , and thus the direction of \mathbf{K}_s , changes whenever the direction of $\boldsymbol{\omega}_b$ changes. In other words, the direction of \mathbf{K} in space changes whenever the direction of $\boldsymbol{\omega}$ changes with respect to the body of the organism.

Motion by a rigid body has been simulated with the computer program described in Appendix B. Briefly, an “organism” is given an initial orientation in space, and initial values of \mathbf{V}_b and $\boldsymbol{\omega}_b$ are defined according to equations (9) and (10). The organism proceeds in discrete time steps Δt , moving the distance $V\Delta t$ and rotating through the angle $\boldsymbol{\omega}\Delta t$. For each simulation, successively smaller values of Δt are used until the trajectories converge to approximate continuous motion.

Figure 2a shows a trajectory generated by simulating the motion of the organism described above ($V_2 = V_3 = 0$ and $\omega_2 = 0$). In this simulation, $\boldsymbol{\omega}_b$ changes only magnitude, not direction, at discrete points (marked by dots, \bullet). The axis of the helix \mathbf{K} does not change direction in space, agreeing with our predictions. In the trajectory in Fig. 2b the direction of $\boldsymbol{\omega}_b$ changes at three points (marked by dots). As expected, \mathbf{K} changes direction in space. Continuous changes in the direction of $\boldsymbol{\omega}_b$ are presented in Fig. 2c. Again, \mathbf{K} changes direction in space.

Consider now an organism that moves with three nonzero components of rotation. Suppose that, as before, the translational velocity is $\mathbf{V}_b = V_1\mathbf{i}$. In this case $\dot{\mathbf{V}}_b$ and $\dot{\mathbf{V}}_b$ both equal zero, so θ and \mathbf{d}_b^* are functions of \mathbf{V}_b , $\boldsymbol{\omega}_b$ and $\dot{\boldsymbol{\omega}}_b$

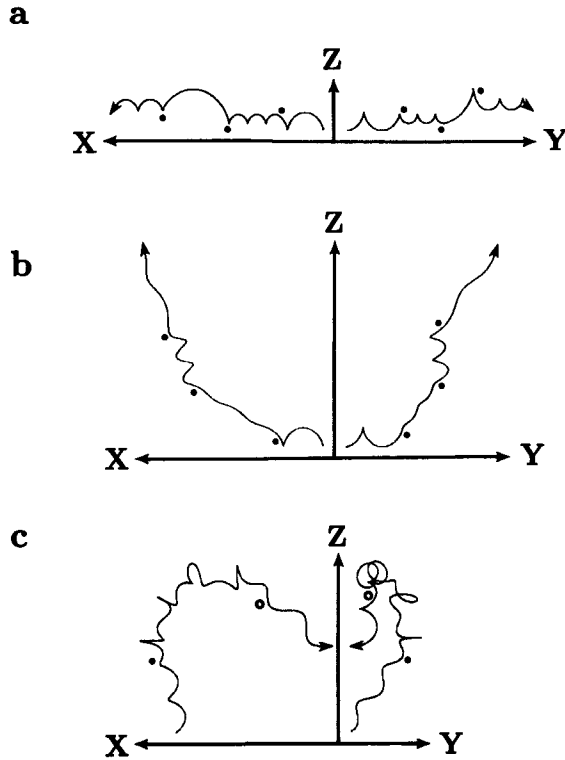


Figure 2. Simulation of changes in the direction, with respect to the body of the organism, of the organism's rotational velocity ω_b . Translational velocity is constant ($V_b = li$). $\omega_2 = 0$. (a) ω_b changes magnitude at three points (marked by dots, \bullet), total arclength s of curve equals 12: $s = 0 - 3, \omega_1 = 2, \omega_3 = 2$; $s = 3 - 6, \omega_1 = 4, \omega_3 = 4$; $s = 6 - 9, \omega_1 = 1, \omega_3 = 1$; $s = 9 - 12, \omega_1 = 3, \omega_3 = 3$. The direction of ω_b does not change, so K does not change direction in space. (b) ω_b changes at three points (marked by dots, \bullet), total arclength s of curve equals 12: $s = 0 - 3, \omega_1 = 2, \omega_3 = 2$; $s = 3 - 6, \omega_1 = 5, \omega_3 = 1$; $s = 6 - 9, \omega_1 = 2, \omega_3 = 4$; $s = 9 - 12, \omega_1 = 3, \omega_3 = 1$. The direction of ω_b changes, so K changes direction in space. (c) ω_b changes continuously between the point marked by a dot (\bullet) and the point marked by a circle (\circ), total arclength s of curve equals 22: $s = 0 - 3, \omega_1 = 2, \omega_3 = 2$; $s = 3 - 19, \omega_1 = 2 + 2 \sin(2(s - 3)), \omega_3 = 3 - \cos(5(s - 3))$; $s = 19 - 22, \omega_1 = 3.10, \omega_3 = 3.11$. The direction of ω_b changes, so K changes direction in space.

[Crenshaw, 1993a, equations (14) and (18)]. When ω_b does not vary, d_b^* is given by equation (12) [see Crenshaw, 1993a, equation (28)]. Consequently, K is parallel (or antiparallel) to ω_b before and after a change in the direction of ω_b . During the time that ω_b is changing direction, K is a function of both ω_b and $\dot{\omega}_b$.

Motion with all three components of rotation varying is presented in Fig. 3, where again $V_b = V_1 i$. ω_b changes at three discrete points. K changes direction in space at each point. Between changes in the direction of ω_b , K is parallel to ω_b . Continuous changes in the direction of ω_b also cause K to change direction in space. No simulations are presented.

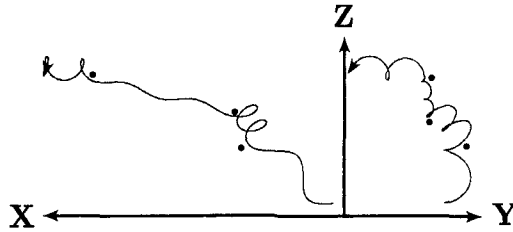


Figure 3. Simulation of changes in the direction, with respect to the body of the organism, of the organism's rotational velocity ω_b . Translational velocity is constant ($V_b = 1i$). ω_b changes at three points (marked by dots, \bullet), total arclength s of curve equals 12: $s=0-3, \omega_1=2, \omega_2=0, \omega_3=2$; $s=3-6, \omega_1=1, \omega_2=2, \omega_3=3$; $s=6-9, \omega_1=4, \omega_2=1, \omega_3=1$; $s=9-12, \omega_1=2, \omega_2=0, \omega_3=3$. The direction of ω_b changes, so \mathbf{K} changes direction in space.

Now consider the motion of an organism for which ω_b is constant and V_b varies. d_b^* , and thus \mathbf{K} , becomes a function of ω_b, V_b and the first and second derivatives of V_b [Crenshaw, 1993a, equations (14) and (18)]. If V_b changes only magnitude, not direction, then like the situation earlier with changes in the magnitude of ω_b, \mathbf{K} does not change direction in space. The only result of changing the magnitude of V_b is to change κ and τ such that their ratio, and thus θ , does not change [Crenshaw, 1993a, equations (26) and (27)].

If V_b changes direction, then \mathbf{K} changes direction in space, but in a way that is different than that for changes of ω_b . Consider an organism that moves with constant V_b and constant ω_b, d_b^* , and thus \mathbf{K} , is given by equation (12)— \mathbf{K} is parallel or antiparallel to ω_b [see Crenshaw, 1993a, equation (28)]. If V_b begins changing direction, then \mathbf{K} changes direction in space because \mathbf{B}, κ and τ , and thus d_b^* , are functions of \dot{V}_b [Crenshaw, 1993a, equations (12), (14) and (18)]. However, once V_b stops changing direction, \mathbf{K} is once again parallel or antiparallel to ω_b , which has not changed direction. Consequently, \mathbf{K} undergoes no net change in direction in space, even if there has been a net change in the direction of V_b —changes in the direction of V_b cause only a transient change in the direction of \mathbf{K} . As discussed earlier, however, θ has changed because the angle between \mathbf{V} and ω has changed.

There is an exception to this rule. Define ψ as the angle between V_b and ω_b . If V_b changes direction such that ψ changes from an angle less than to one greater than $\pi/2$, or vice versa, then \mathbf{K} changes from parallel (or antiparallel) to ω to antiparallel (or parallel) to ω with a concomitant change in the handedness of the helix (Crenshaw, 1993a). Consider an organism that moves such that $\psi < \pi/2$. This organism moves along a right-hand helix for which ω is parallel to \mathbf{K} (Fig. 4a). If the direction of ω_b remains constant, but the direction of V_b reverses, then ψ becomes greater than $\pi/2$. Consequently, the helix switches handedness, and \mathbf{K} reverses direction (Fig. 4b). Note that if $\psi = \pi/2$ then the

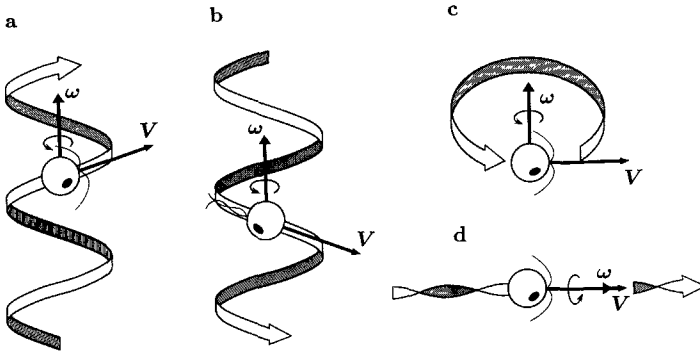


Figure 4. The angle ψ between the translational velocity \mathbf{V} and the rotational velocity $\boldsymbol{\omega}$ affects the handedness of the helix and the direction of the axis of the helix \mathbf{K} . (a) $\psi < \pi/2$: $\boldsymbol{\omega}$ is parallel to \mathbf{K} , and the helix is right-handed. (b) $\psi > \pi/2$: $\boldsymbol{\omega}$ is antiparallel to \mathbf{K} , and the helix is left-handed. (c) $\psi = \pi/2$: the trajectory is a circle. (d) $\psi = 0$: the trajectory is a straight line with $\boldsymbol{\omega}$ parallel to the direction of motion. (If $\psi = \pi$, the trajectory is a straight line with $\boldsymbol{\omega}$ antiparallel to the direction of motion.)

trajectory is a circle (Fig. 4c), and if $\psi = 0$ or π then the trajectory is a line (Fig. 4d).

Motion in which \mathbf{V}_b changes direction can also be simulated with the program presented in Appendix B. Now, $\boldsymbol{\omega}_b$ is constant. Figure 5a presents a trajectory for which the direction of \mathbf{V}_b changes at three discrete points (marked by dots). The changes in the direction of \mathbf{V}_b are visible as kinks in the trajectory, demonstrating how the assumption of smoothness in the previous section has been violated. Nevertheless, as expected, the axes of the helical trajectories between the kinks are all straight and parallel. \mathbf{K} has not changed direction in space.

Figure 5b presents a trajectory for which \mathbf{V}_b changes continuously over a finite period of time. The direction of \mathbf{V}_b is initially constant, resulting in an initially straight helix. At the dot (\bullet) the direction of \mathbf{V}_b begins to vary continuously. At the circle (\circ), the direction of \mathbf{V}_b is again held constant, producing a straight helix at the end of the trajectory. The straight helical portions are placed at the beginning and end of this trajectory to better demonstrate the net change in the direction of \mathbf{K} . As expected the direction in space of \mathbf{K} is the same in the two straight portions—there is no net change in the direction of \mathbf{K} .

Figure 5c presents a trajectory similar to that in Fig. 5b; however, now ψ has changed from less than $\pi/2$ to greater than $\pi/2$. As discussed earlier, \mathbf{K} reverses direction in space, and the helix changes from right-hand to left-hand.

In summary, the Darboux vector \mathbf{d} of an organism's trajectory is determined by the organism's translational and rotational velocities, \mathbf{V}_b and $\boldsymbol{\omega}_b$. In

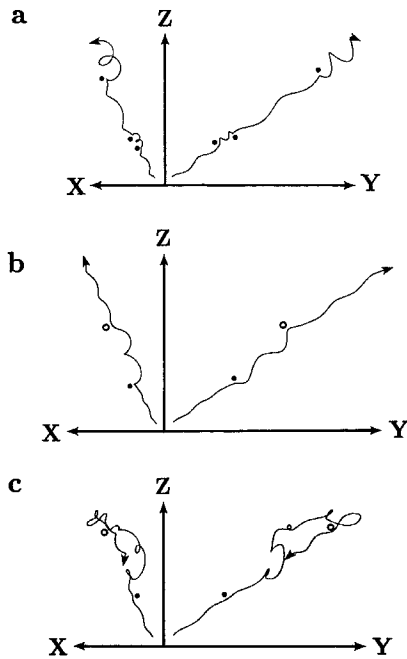


Figure 5. Simulation of changes in the direction, with respect to the body of the organism, of the organism's translational velocity \mathbf{V}_b . Rotational velocity is constant ($\boldsymbol{\omega}_b = 3\mathbf{i} + 2\mathbf{j} + 1\mathbf{k}$). (a) \mathbf{V}_b changes at three points (marked by dots, \bullet), total arclength s of curve equals 12: $s=0-3$, $V_1=1$, $V_2=1$, $V_3=1$; $s=3-6$, $V_1=3$, $V_2=0$, $V_3=0$; $s=6-9$, $V_1=0$, $V_2=3$, $V_3=0$; $s=9-12$, $V_1=0$, $V_2=0$, $V_3=3$. The direction of \mathbf{V}_b changes; however, the direction of $\boldsymbol{\omega}_b$ is constant. Consequently, \mathbf{K} does not change direction in space. (b) \mathbf{V}_b initially is constant and then changes continuously between the point marked by a dot (\bullet) and the point marked by a circle (\circ), total arclength s of curve equals 12: $s=0-3$, $V_1=2$, $V_2=2$, $V_3=1$; $s=3-9$, $V_1=2+2\sin(3(s-3))$, $V_2=4-2\cos(s-3)$, $V_3=1+\sin(2(s-3))$; $s=9-12$, $V_1=0.498$, $V_2=2.08$, $V_3=0.463$. The direction of $\boldsymbol{\omega}_b$ is constant, and ψ remains less than $\pi/2$. Consequently, when \mathbf{V}_b returns to zero, the final direction in space of \mathbf{K} remains unchanged. (c) \mathbf{V}_b changes continuously between the point marked by a dot (\bullet) and the point marked by a circle (\circ), total arclength s of curve equals 17: $s=0-3$, $V_1=2$, $V_2=2$, $V_3=1$; $s=3-13$, $V_1=2+4\sin(3(s-3))$, $V_2=2\cos(s-3)$, $V_3=\cos(2(s-3))$; $s=13-17$, $V_1=-1.95$, $V_2=-1.68$, $V_3=0.408$. This trajectory is similar to that in *b*; however, now ψ changes from less than $\pi/2$ to greater than $\pi/2$. Consequently, when \mathbf{V}_b returns to zero, the direction in space of \mathbf{K} has reversed, and the helical trajectory has switched from right-hand to left-hand.

particular, if the directions of \mathbf{V}_b and $\boldsymbol{\omega}_b$ are constant (i.e. if \mathbf{V} and $\boldsymbol{\omega}$ do not change direction with respect to the organism's body), then \mathbf{d}_b is parallel to $\boldsymbol{\omega}_b$. The resulting trajectory is a helix with \mathbf{K} parallel or antiparallel to $\boldsymbol{\omega}_b$. If the direction of $\boldsymbol{\omega}_b$ changes then \mathbf{K} changes direction in space. Changes in the direction of \mathbf{V}_b only transiently change the direction in space of \mathbf{K} .

One final type of curve must be considered. Some curves appear to contradict the result of this analysis—the pitch angle of these curves changes, but the axis appears straight. Figure 6a presents a trajectory generated by the simulation of rigid body motion (Appendix B). It is a conical spiral in which the pitch angle constantly increases. Other curves also appear to contradict the present results, for example a curve with constant radius but varying pitch. If a helix of constant pitch angle is fitted to each point of such curves, then the axis of the helix of constant pitch angle precesses around the axis of the curve of variable pitch angle. It is possible for organisms to follow such a trajectory. However, the results of the present analysis remain unchanged. Consider Fig. 6b. Here the simulation presented in Fig. 6a is repeated, but at the dot the pitch angle stops changing. The axis of the resulting helix after the dot is clearly different than that of the conical spiral. In fact, a diversity of motions can be imagined in which the axis of a helical trajectory changes over time such that the net change in the direction of the axis is zero. This by no means contradicts the present results.

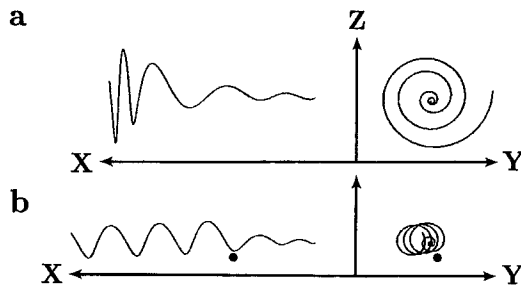


Figure 6. An apparent contradiction to the results. (a) A conical spiral in which the pitch angle changes, but the axis appears straight. Translational velocity is constant ($\mathbf{V}_b = 1\mathbf{i}$). The rotational velocity changes continuously: $\omega_1 = 0.1 + (10-s)^6/10^5$, $\omega_2 = 0$, $\omega_3 = 1 + (10-s)/5$, (b) The trajectory is the same as in (a) but now the rotational velocity is held constant at the dot. The trajectory after the dot is a straight helix for which the axis is not parallel to the axis of the conical spiral.

3. Discussion. The primary result of this analysis is that an organism changes the direction in space of the axis of its helical motion primarily by changing the direction of its rotational velocity with respect to its body. Changes in the direction of the rotational velocity produce both a transient change while the rotational acceleration is not zero and a net change if the rotational velocity undergoes a net change of direction. Conversely, changes in the direction of the translational velocity produce only transient changes in the direction of the axis—the axis changes direction only while the translational acceleration does

not equal zero, but there is no net change in the direction of the axis once the translational acceleration returns to zero, even if the translational velocity has undergone a net change in direction.

This result sounds less intuitive when expressed in common words: an organism that commences rotating more rapidly around its anterior–posterior axis, for example, begins moving in a new net direction. Conversely, an organism that swims in a more dorsal direction does not move in a new net direction.

The first section of this paper discusses the differential geometry of three-dimensional curves and deals strictly with smooth trajectories. (The Frenet trihedron makes no discrete changes in orientation along the arclength of the trajectory.) In the second section, which addresses the motion of a rigid body, this assumption implies that the organism does not instantaneously (with respect to the arclength of the curve) change the direction of its translational velocity or the orientation of its body. However, this assumption is not necessary in the simulations of rigid body motion. Consequently, these simulations permit discrete changes both in the orientation of the organism's body and in the direction of the translational velocity along the arclength of the trajectory.

It is important that the simulations of rigid body motion are able to address both continuous and discrete changes in orientation and direction because microorganisms probably perform both. Many ciliates and rotifers appear to move in smooth trajectories, continuously rotating and translating. Propulsion is generated by metachronal waves of cilia in these organisms, which produce a fairly continuous force (see Naitoh and Sugino, 1984; Sugino and Naitoh, 1988). However, as Purcell (1977) explains, the trajectories of the many microorganisms that propel themselves with oscillating appendages are kinked. For example, the flagellate *Chlamydomonas* propels itself with a “breast stroke” of its two anterior flagella. The resulting motion of the cell is forward during the effective stroke and then backward a shorter distance during the recovery stroke with a rotation during the cycle (Rüffer and Nultsch, 1985). When this motion is repeated with some constant translation and rotation per flagellar beat, the resulting trajectory is a helix (Kamiya and Witman, 1984; Rüffer and Nultsch, 1985). The simulations of rigid body motion address both types of motion.

This analysis assumes that organisms change the direction of their rotational velocities with respect to their bodies. This is difficult to measure, but there are numerous reports of organisms changing the radius or pitch of their helical trajectory, reflecting changes in the direction of the rotational velocity. Jennings (1904) describes changes in the radius and pitch of several organisms (flagellates, ciliates, rotifers). In fact, Jennings states that changes in the radius of a microorganism's helical path change the organism's net direction of

motion ("the path"). Jennings (1904, p. 54), however, is unable to explain his observation.

In independent work, Brokaw (1958) also recognizes that changes in the direction of the rotational velocity of a cell change the direction of the axis of the helix. Brokaw demonstrates that spermatozoids of the bracken fern *Pteridium aquilinum* decrease the radius of their helical trajectory when exposed to concentration gradients of malate (see also Brokaw, 1974). Brokaw recognizes that this decrease in radius reflects a change in the cell's rotational velocity that causes the axis of the helix to change direction. (For a more complete description of Brokaw's work, see Crenshaw, 1993b.)

Other observations of cells changing the radius or pitch of their helical trajectories include the ciliates, *Ophryoglena* sp. (Párducz, 1964) and *Paramecium caudatum* (Machemer, 1989), and the spermatozoa of many invertebrates (Miller, 1985). Furthermore, Crenshaw (1990) presents three-dimensional trajectories of spermatozoa of the sea urchin *Arbacia punctulata*. These spermatozoa change the pitch angle of their motion. At the same time, the axis of their helical trajectory changes direction.

Interestingly, many of the observations of changes in radius and pitch mentioned above occur when the microorganisms and spermatozoa are stimulated. This raises the possibility that changes in the rotational velocity of an organism might orient an organism to a stimulus. Crenshaw (1993b) examines this question and demonstrates that the axis of helical motion automatically aligns to a stimulus field (a ray of light or a chemical concentration gradient) if the components of the organism's rotational velocity are simple functions of stimulus intensity.

4. Summary of Results. (1) The major result of this analysis is that an organism changes the direction in space of the axis of its helical motion primarily by changing the direction of its rotational (angular) velocity with respect to its body. Changes in the direction of the translational (linear) velocity have little or no effect on the direction of the axis of the helical trajectory. The axis of a helical trajectory is the net direction of motion, indicating that many microorganisms change their direction of motion by changing the direction of their rotational velocity, not their translational velocity.

(2) Changes in the direction of the rotational velocity produce both a transient change in the direction of the axis while the rotational acceleration is not zero and a net change if the rotational velocity undergoes a net change of direction. For example, if an organism commences rotating more rapidly around its anterior-posterior axis, then the axis of its helical trajectory changes direction in space—the organism begins moving in a new direction.

(3) Changes in the direction of the translational velocity produce only

transient changes in the direction of the axis—the axis changes direction only while the translational acceleration does not equal zero, but there is no net change in the direction of the axis once the translational acceleration returns to zero, even if the translational velocity has undergone a net change in direction. For example, an organism that begins swimming more to its left-hand side does not move in a new direction in space.

(4) Changes in the direction of the rotational velocity are seen as changes in the radius, pitch, or pitch angle of an organism's trajectory. In agreement with the present analysis, there are several published examples of organisms that change the radius, pitch, or pitch angle of their helical trajectories with concomitant changes in the direction of the axis.

During the early stages of this work, H.C.C. was supported by predoctoral fellowships from the U.S. Office of Naval Research and Duke University, and L.E.-K. was supported by N.S.F. Grant No. DMS-8601644. H.C.C. is currently supported by N.S.F. Grant No. DCB-8819271 and L.E.-K. by National Sciences and Research Council of Canada operating Grant No. OGPIN 021. Discussions with W. Conner (Wake Forest University), the Duke BLIMP Group, and the Duke Fluid Mechanics Discussion Group helped greatly. D. Crenshaw, J. Long and S. Vogel (Duke University) made helpful comments on the manuscript. Thanks to D. Egloff (Oberlin) for pointing out several pertinent papers and to C. J. Brokaw (California Institute of Technology) for providing a copy of his Ph.D. thesis.

A Note about Approximation Errors. First, to minimize round-off error these programs use double precision, floating point numbers. All programs are written in AmigaBasic (MicroSoft, Inc.), compiled with AC-Basic (Absoft Corp.), and run on an Amiga 1000 (Commodore Business Machines, Inc.). Copies of the programs can be obtained from H. C. Crenshaw. Second, to ensure that approximation error is negligible, the same simulation is run repeatedly with successively smaller values of Δt . Approximation error is considered small when the shape of the trajectory and the endpoint of the trajectory cease to change appreciably.

APPENDIX A

Simulations of Changing Radius and Pitch. We begin with equation (1), the vector function of a right-hand helix. This helix is constrained to move with \mathbf{K} as its axis. To describe a helix with any orientation and location in space, we describe \mathbf{IJK} relative to \mathbf{XYZ} .

Future manipulations are made easier by reparameterizing equation (1) to arclength s :

$$\mathbf{H}(s) = r \cos\left(\frac{s}{\sqrt{C}}\right) \mathbf{I} + r \sin\left(\frac{s}{\sqrt{C}}\right) \mathbf{J} + \left(\frac{ps}{2\pi\sqrt{C}}\right) \mathbf{K} \quad (\text{A1})$$

where $c = r\sqrt{1 + \delta^2}$, and $\delta = p/2\pi r$.

The task now at hand is to describe changes in r and p along the trajectory of the organism. Consider an organism swimming along a helical path with the orientation of **IJK** known with respect to **XYZ**. r and p are known and constant. At one point the organism changes r or p of its motion and continues moving uninterrupted along a new helix with new r or p . The first helix is described by equation (A1). All of the variables in equation (A1) are known. The second helix can be described by an identical equation:

$$\mathbf{H}(s') = r' \cos\left(\frac{s'}{\sqrt{C'}}\right) \mathbf{I}' + r' \sin\left(\frac{s'}{\sqrt{C'}}\right) \mathbf{J}' + \left(\frac{p's'}{2\pi\sqrt{C'}}\right) \mathbf{K}' \tag{A2}$$

where the primed variables pertain to the second helix. If r' and p' are known, either *a priori* or as the functions of some external variable, the values of s' , \mathbf{I}' , \mathbf{J}' and \mathbf{K}' are still unknown. Furthermore, the position of the origin of $\mathbf{I}'\mathbf{J}'\mathbf{K}'$ relative to **XYZ** is unknown.

As the orientation and position of $\mathbf{I}'\mathbf{J}'\mathbf{K}'$ are unknown, the value of s' can arbitrarily be assigned the value of zero. The values of \mathbf{I}' , \mathbf{J}' and \mathbf{K}' and the position of the origin of this coordinate system can be determined from the geometry, assuming the path of the organism is smooth at the point of transition. If the path is smooth then $\mathbf{T} = \mathbf{T}'$, $\mathbf{N} = \mathbf{N}'$ and $\mathbf{B} = \mathbf{B}'$.

\mathbf{I}' can be determined as follows: At $s' = 0$, $\mathbf{N}' = -\mathbf{I}'$. $\mathbf{N}'(0) = \mathbf{N}(s)$, which is known, so \mathbf{I}' is known.

\mathbf{K}' is parallel to $(\tau'/|\tau'|)\mathbf{d}'$ (Crenshaw, 1993a). \mathbf{d}' is given by equation (3). τ' and κ' are functions of r' and p' (see Crenshaw, 1993a), which are known. \mathbf{T}' and \mathbf{B}' are known, as discussed above, so \mathbf{K}' is known.

\mathbf{J}' equals $\mathbf{K}' \times \mathbf{I}'$.

Finally, the following equations determine the position of the origin (**O**) of $\mathbf{I}'\mathbf{J}'\mathbf{K}'$ relative to **XYZ**:

$$\mathbf{H}(s) = \mathbf{H}'(0) \tag{A3}$$

$$\mathbf{O} = \mathbf{H}'(0) - r'\mathbf{I}'. \tag{A4}$$

APPENDIX B

Simulations of Varying V_δ and ω_B . Two reference frames are used in this program—**XYZ** and **ijk**. From here on we will refer to **XYZ** as δ and to **ijk** as ξ . Vectors with subscript δ , therefore, are described relative to δ , and vectors with subscript ξ are described relative to ξ .

The motion of the organism is described relative to δ , so ξ is also described relative to δ . For example, **i**, which has the coordinates (1, 0, 0) in ξ , may have the coordinates $(1/\sqrt{3}, 1/\sqrt{3}, -1/\sqrt{3})$ in δ . (Note: It would then be referred to as \mathbf{i}_δ .) This permits the organism to assume any orientation in δ . The flow of the program is as follows.

Step 1—Determine Initial Location and Orientation. The organism is placed at an initial point \mathbf{P}_δ , and \mathbf{i}_δ , \mathbf{j}_δ and \mathbf{k}_δ are given initial values.

Step 2—Determine ω and V . V_ξ and ω_ξ can either change or remain the same in this step:

$$\mathbf{V}_\xi = V_{\xi 1} \mathbf{i} + V_{\xi 2} \mathbf{j} + V_{\xi 3} \mathbf{k}$$

$$\omega_\xi = \omega_{\xi 1} \mathbf{i} + \omega_{\xi 2} \mathbf{j} + \omega_{\xi 3} \mathbf{k}.$$

(Note: \mathbf{i} , \mathbf{j} and \mathbf{k} do not have subscripts. These equations are correct, regardless of the reference frame.)

Step 3—Move to a New Position. Now that the organism has a defined position, orientation, \mathbf{V}_ξ , and $\boldsymbol{\omega}_\xi$, the organism moves forward at the designated velocity over a predefined period of time, Δt :

$$\mathbf{P}'_\delta = \mathbf{P}_\delta + \mathbf{V}_\delta \Delta t$$

where \mathbf{P}'_δ is the new position in δ (at time $t + \Delta t$); \mathbf{P}_δ is the previous position (at time t); $\mathbf{V}_\delta \Delta t$ is the distance travelled; and \mathbf{V}_δ is given by

$$\mathbf{V}_\delta = (V_{\xi 1} \mathbf{i}_{\delta 1} + V_{\xi 2} \mathbf{j}_{\delta 1} + V_{\xi 3} \mathbf{k}_{\delta 1}, \dots, \dots).$$

Step 4—Rotate to a New Orientation. After moving forward, the organism rotates at the rotational velocity determined in Step 2 over the period of time Δt . This is done as follows:

$$\begin{aligned} \mathbf{i}'_\delta &= \mathbf{i}_\delta + \dot{\mathbf{i}}_\delta \Delta t \\ \mathbf{j}'_\delta &= \mathbf{j}_\delta + \dot{\mathbf{j}}_\delta \Delta t \\ \mathbf{k}'_\delta &= \mathbf{k}_\delta + \dot{\mathbf{k}}_\delta \Delta t \end{aligned}$$

where $\mathbf{i}'_\delta \mathbf{j}'_\delta \mathbf{k}'_\delta$ describes the new orientation

$$\begin{aligned} \dot{\mathbf{i}}_\delta &= \boldsymbol{\omega}_\delta \times \mathbf{i}_\delta \\ \dot{\mathbf{j}}_\delta &= \boldsymbol{\omega}_\delta \times \mathbf{j}_\delta \\ \dot{\mathbf{k}}_\delta &= \boldsymbol{\omega}_\delta \times \mathbf{k}_\delta \end{aligned}$$

and

$$\boldsymbol{\omega}_\delta = (\omega_{\xi 1} \mathbf{i}_{\delta 1} + \omega_{\xi 2} \mathbf{j}_{\delta 1} + \omega_{\xi 3} \mathbf{k}_{\delta 1}, \dots, \dots).$$

Step 5—Repeat Steps 2 Through 4. Now that the organism's new position and orientation are known, the program returns to Step 2 and repeats the process as many times as required.

NOMENCLATURE

γ	angular frequency of helical motion
θ	angle between axis and tangent of helical path
κ	curvature
τ	torsion
ψ	angle between \mathbf{V} and $\boldsymbol{\omega}$
$\boldsymbol{\omega}$	rotational (angular) velocity of organism
\mathbf{B}	unit binormal vector
\mathbf{d}	Darboux vector (units of radians/arclength)
\mathbf{d}^*	converted Darboux vector (units of radians/time)
\mathbf{H}	vector function of a helical trajectory
\mathbf{ijk}	reference frame fixed to organism
\mathbf{IJK}	reference frame fixed to helical trajectory
\mathbf{XYZ}	reference frame fixed in space
\mathbf{N}	unit normal vector

<i>p</i>	pitch of helical motion
<i>r</i>	radius of helical motion
<i>s</i>	arclength of curve
<i>t</i>	time
T	unit tangent vector
V	translational (linear) velocity of organism

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Received 2 July 1991

Revised 16 December 1991