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Biological Motion of a Magnetotactic Bacterium

by

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ABSTRACT: We study the biological motion of a magnetotactic bacterium. Using the formalism of rigid body dynamics together with the fact that Reynolds number is small, we derive the equations of motion. Magnetotactic bacterium is treated in the formalism as a general case of a non-magnetotactic one. The equations of motion are integrated numerically and comparison with experimental data are made. It is showed how the model can help to treat experimental data. It is argued that it is biologicaly advantageous for a magnetotactic bacterium to have a flagellum highly asymmetric.

Key-words: Biological motion; Magnetotactic bacterium.

1) Introduction.

Motile bacteria swim by means of flagella (Berg, 1975), which consists of rigid helical tubes containing a single type of protein subunit. Each flagellum is attached to its base to a protein disc embedded in the bacterial membrane by a flexible hook. This disc is part of a molecular rotor (Manson *et al.*, 1977) that produces a torque on flagellum to rotate and turns it. Several flagellar filaments emerge randomically on the sides of the bacterial body. Usually, flagellum is a long organelle when compared to bacterial dimensions. In *E. Coli*, for example, each flagellum has typical dimensions of about three times the body lenght and each cell has about six flagellar filaments.

Two rotational directions with respect to the axis parallel to the velocity are observed. Counterclockwise rotation, when the angular velocity is anti-parallel to the velocity direction, and clockwise rotation. Counterclockwise rotation makes flagellar filaments to form a synchronous bundle that pushes bacterial body forward. On the other hand, clockwise rotation disperse flagellar filaments and each flagellum turns indepedently. In the first case the bacterium performs an helical motion while in the second case the bacterium tumbles.

It is observed that the cells align the axis of its helical trajectory with the direction of the stimulus. This behaviour is strikingly observed in the case of magnetotactic bacteria (Blakemore, 1975). Magnetotactic microorganisms are motile cells

that possess intracellular magnetic particles (Lins de Barros & Esquivel, 1985; Farina *et al.*, 1990; Mann *et al.*, 1990; Frankel & Blakemore, 1990) (iron oxide or iron sulfide crystallites) which impart the cell a permanent magnetic dipole moment. Each intracellular magnetic particle is enveloped by a membrane forming a specialized organelle, the magnetosome. The permanent cell magnetic moment interacts with an external magnetic field. This interaction produces a torque on the cell body that orients the cell to the field line. Reversion of the external field produces a new orientation of the cell and the trajectory makes a U-turn (Esquivel & Lins de Barros, 1986).

Two types of magnetotactic microorganisms with the respect to the relative magnetic dipole orientation are found in natural samples (Lins de Barros *et al.*, 1990). South-seeking microorganisms, found preferentially on the south magnetic hemisphere, are microorganisms in which the magnetic dipole is antiparallel to the motion direction. These organisms orient to the local field line and swim downward in the south magnetic hemisphere (where the field points upwards). North-seeking microorganisms are similar to the south-seeking cells but the magnetic dipole is in opposite direction. They swim downward in the north magnetic hemisphere. In geomagnetic equator the geomagnetic field is parallel to the earth surface and both magnetotactic microorganisms are found in the same approximate proportion (Frankel *et al.*, 1981). Magnetotaxis, that is, the motility directed by a magnetic field, seems to be an adaptative mechanism in which the magnetic field acts as a stimulus.

The orientation mechanism of magnetotactic cells is well

understood. The direct interaction between cell magnetic dipole moment and the external field produces a torque on the cellular body that orients the cell to the field line.

In this work we study the helical motion of a magnetotactic bacterium. The general case considered is that of a spherical magnetotactic bacterium swimming in an isotopic viscous medium under the flagellar action. Experimental observations were made using dark field high resolution optical microscopy with low exposure photo technique. This procedure enables to obtain a track of a bacterium swimming in a viscous medium (water). This track can be interpreted as the two-dimensional projection of a tridimensional helical path on the plane of emulsion.

2) Mathematical Introduction.

The motion of a bacterium in a viscous medium is characterized by a condition of low Reynolds number (Purcell, 1977). Reynolds number is a dimensionless parameter given by the ratio between inertial forces and viscous forces. In very low Reynolds number regimen no inertial effects are observed and in order to mantain a constant velocity it is necessary to apply a constant force. In this circumstance, force is proportional to velocity, in contrast to the Newtonian case where force is proportional to aceleration. This is accomplished *via* the equations of motion neglecting all inertial terms. This procedure is legitimate provided that Reynolds number is much less than unity, which is just the case of microorganisms swimming in water

(the case considered in this paper).

The helical trajectory observed in motile bacteria is a consequence of the net force applied on the cell body due to flagellar action. Torque generated by flagellar rotation is balanced by viscous drag due to counter-rotation of the cell and thrust generated by flagellum action is balanced by viscous drag due translation. It is assumed that a perfectly symmetric flagellum is not consistent with helical motion since in this case there is no way to change the direction of the net force (if no external magnetic field is present) and evidently the bacterium will move in a straight line. For example, if one considers the flagellum as a organelle possessing the shape of a circular cylindrical helix with an integer number of turns (Schreiner, 1971), rotation of flagellum will produce a net force responsible for translation only, that is, no torque is produced by such a force. On the other hand, if there is some kind of asymmetry, the resulting force that pushes the cell forward produces also a torque. Consequently, one can decompose the net force acting on the cell body into two components: one that does not produce torque and another one that, besides translation, produces a torque. This will be done in the next section without making special assumption about the shape of the flagellum.

We will use the well established framework to treat a rigid body problem (Goldstein, 1980): rotation is analyzed in the center of mass reference frame considering the contribution of all the external torques. Translation of the cell is described as a translation of the center of mass reference frame.

Thermal disturbances are not considered despite brownian

effect is important in bacterial scale. In our case, however, thermal energy is much smaller than magnetic interaction or the flagellar energy and can be considered later as a randomic disturbance to be included in the numerical evaluation.

3) Mathematical Model.

One considers a spherical bacterium with radius R propelled by a net force $\vec{F}$ (due to flagellar rotation) that acts in a fixed point P on the cellular membrane. In order to take the effects of asymmetries of the flagellum in an appropriate way, one decomposes the net force into two components. The longtudinal component, $\vec{F}_L$, is along the direction that the bacterium would swim if there is no asymmetry. This direction is defined as the same of the segment OP where O is the center of the sphere. The other component, $\vec{F}_T$, arises from asymmetries of flagellum and it is perpendicular to the segment OP and acts at the point P. For this reason it is called transverse component. Since the transverse force accounts for the fact that the flagellum is not symmetric, one must have that, as the flagellum rotate with angular frequency ω, $\vec{F}_T$ rotates with the same frequency. The cell magnetic moment, $\vec{m}$, is considered, for simplicity, aligned parallel to OP and passing trough O. The case where the magnetic moment is in an arbitrary position in the interior of the cell body will be done in a future work as a generalization of the proposed model. However, this simplification does not alter the essential results of this paper. Flagellar geometry is not considered. The only contribution due to

flagellar rotation is described by the net force $\vec{F}$ (Fig. 1) and by a couple associated to the flagellar rotor. Non-magnetotactic bacterium is, in this treatment, a particular case of a magnetotactic one, in the sense that the non-magnetotactic bacterium is a magnetotactic bacterium with zero magnetic moment. Finally, the bacterium is considered to swim in a medium with viscosity η.

As usual, we use six coordinates to describe the general motion of a bacterium. Three of these coordinates will describe the rotation of the cell body in a reference frame where the center of mass O is at rest. The other three coordinates will describe the translation of center of mass with respect to an inertial frame.

a) Rotation of the cell body.

Neglecting inertial effects, the rotational equations of motion of the cell body are given, in vector form, as

$$\vec{N}_c + \vec{N}_T + \vec{N}_v + \vec{N}_m = \vec{0} \qquad (1)$$

In the above equation $\vec{N}_c$ denotes the reaction couple over the cell body due to the couple that generates flagellar rotation with frequency ω. $\vec{N}_T$ denotes the torque produced by the transverse force, $\vec{N}_v$ is the viscous torque and $\vec{N}_m$ is the magnetic torque.

Since flagellum rotates with a constant angular frequency ω, the reaction couple has a constant magnitude:

$$\vec{N}_c = -|\vec{N}_c|\,\vec{e}_3 \qquad (2)$$

where $(\vec{e}_1, \vec{e}_2, \vec{e}_3)$ is a set of unit vectors associated with a set of orthogonal axes, (x_1, x_2, x_3), fixed in the cell body, whose origin is at the center of mass. $\vec{e}_3$ is chosen to be collinear with *OP*.

$\vec{F}_T$ rotates with the flagellar frequency ω in a plane perpendicular to *OP*. Thus, assuming that the asymmetries of flagellum does not change as the system evolves (this means that the flagellum stays rigid as it rotates), the transverse force must have a constant magnitude and is given by

$$\vec{F}_T = |\vec{F}_T|\,(\cos\omega t\,\vec{e}_1 + \sin\omega t\,\vec{e}_2) \qquad (3)$$

$\vec{F}_T$ is applied at the point *P*, defined by the vector $\vec{R} = R\,\vec{e}_3$. Then

$$\vec{N}_T = \vec{R} \times \vec{F}_T = |\vec{N}_T|\,(-\sin\omega t\,\vec{e}_1 + \cos\omega t\,\vec{e}_2) \qquad (4)$$

where $|\vec{N}_T| = R\,|\vec{F}_T| = const.$

The viscous torque, $\vec{N}_v$, is due to rotational viscous drag of the spherical cell body rotating in a general way in a viscous fluid. At low Reynolds number one has, for a sphere (Landau & Lifshitz, 1959),

$$\vec{N}_v = -8\pi\eta R^3\,\vec{\Omega} = -8\pi\eta R^3\,(\omega_1\,\vec{e}_1 + \omega_2\,\vec{e}_2 + \omega_3\,\vec{e}_3) \qquad (5)$$

where $\vec{\Omega}$ is the vector angular velocity of the cell body, whose components are written, in terms of Euler angles, as

$$\omega_1 = \dot{\phi} \sin\theta \sin\psi + \dot{\theta} \cos\psi \qquad (6a)$$

$$\omega_2 = \dot{\phi} \sin\theta \cos\psi - \dot{\theta} \sin\psi \qquad (6b)$$

$$\omega_3 = \dot{\phi} \cos\theta + \dot{\psi} \qquad (6c)$$

where the dots denotes total time differentiation.

Finally, to evaluate $\vec{N}_m$ it is necessary to assume an applied external constant magnetic field $\vec{B}$. If (x, y, z) is a set of orthogonal axes representing a fixed reference frame where the translation of the center of mass is specified, there is no loss of generality to assume $\vec{B}$ pointed in the z-direction. The magnetic moment, $\vec{m}$, is assumed collinear to $\vec{e}_3$. Then

$$\vec{m} = | \vec{m} | \vec{e}_3 \qquad (7)$$

$$\vec{B} = - | \vec{B} | \vec{e}_z \qquad (8)$$

which gives the magnetic torque

$$\vec{N}_m = \vec{m} \times \vec{B} = | \vec{m} | | \vec{B} | \sin\theta \vec{e}_n \qquad (9)$$

where $\vec{e}_n$ is a unit vector directed along the line of nodes:

$$\vec{e}_n = \cos\psi \vec{e}_1 - \sin\psi \vec{e}_2 \qquad (10)$$

The Euler equations for the spherical bacterium are

$$\omega_1 = - \alpha \sin\omega t + \beta \sin\theta \cos\psi \qquad (11a)$$

$$\omega_2 = \alpha \cos\omega t - \beta \sin\theta \sin\psi \qquad (11b)$$

$$\omega_s = -\gamma \qquad (11c)$$

where $\alpha = |\vec{N}_T|/8\pi\eta R^3$, $\beta = |\vec{m}|\,|\vec{B}|/8\pi\eta R^3$ and $\gamma = |\vec{N}_C|/8\pi\eta R^3$. Solving Eqs. (11) for the angular velocities $\dot{\phi}$, $\dot{\theta}$ and $\dot{\psi}$ one obtains

$$\dot{\phi} = \alpha \csc\theta \cos(\omega t + \psi) \qquad (12a)$$

$$\dot{\theta} = \beta \sin\theta - \alpha \sin(\omega t + \psi) \qquad (12b)$$

$$\dot{\psi} = -\gamma - \alpha \cot\theta \cos(\omega t + \psi) \qquad (12c)$$

Thus, in this model, the net vector angular velocity acting in the cell body is given by

$$\vec{\Omega}' = \vec{\Omega} + \omega\,\vec{e}_s \qquad (13)$$

When $\beta=0$, the magnitude of the above vector is

$$\Omega' = [(\omega - \gamma)^2 + \alpha^2]^{1/2} \qquad (14)$$

Thus, as the flagellun undertakes counterclockwise rotation with angular frequency ω, the cell body rotates clockwise with angular frequency γ around the x_s-axis. The angular frequency α gives the rate of precession of the x_s-axis. This precession produces the helical motion obseved in tracks of flagellated bacteria.

On the other hand, when $\beta\neq0$, Ω' has the form

$$\Omega' = [(\omega - \gamma)^2 + \alpha^2 + \beta^2\sin^2\theta - 2\,\alpha\,\beta \sin(\omega t + \psi)]^{1/2} \qquad (15)$$

b) Translation of the Center of Mass.

Eqs. (12) describe the rotation of the cell body in a reference frame where the center of mass is at rest. The observed track in the film emulsion, or in a digitalized image from high resolution optical microscopy, is associated to the translation of the center of mass. The coordinates of the center of mass O are specified by the position vector $\vec{x} = x\,\vec{e}_x + y\,\vec{e}_y + z\,\vec{e}_z$.

Neglecting inertial effects, the Newton equation of motion is

$$\vec{F}_L + \vec{F}_T + \vec{F}_U = \vec{0} \qquad (16)$$

where $\vec{F}_U$ is the viscous drag force which, for a sphere, is given by Stoke's law (Landau & Lifshitz, 1959):

$$\vec{F}_U = -\,6\,\pi\,\eta\,R\,\vec{v} \qquad (17)$$

where $\vec{v}$ is the velocity vector whose components are $\dot{x}$, $\dot{y}$ and $\dot{z}$. Eq. (16) can be rewritten in the following form:

$$\begin{aligned}\vec{v} &= v_T\,(\cos\omega t\;\vec{e}_1 + \sin\omega t\;\vec{e}_2) + v_L\,\vec{e}_3 \\ &= \dot{x}\,\vec{e}_x + \dot{y}\,\vec{e}_y + \dot{z}\,\vec{e}_z \end{aligned} \qquad (18)$$

where $v_T = |\vec{F}_T|/6\pi\eta R$ and $v_L = |\vec{F}_L|/6\pi\eta R$.

The transformation of the unit vectors $(\vec{e}_1, \vec{e}_2, \vec{e}_3)$ fixed in the cell body to the unit vectors $(\vec{e}_x, \vec{e}_y, \vec{e}_z)$ is given by

$$\begin{aligned}\vec{e}_1 &= (\cos\psi\cos\phi - \cos\theta\sin\phi\sin\psi)\,\vec{e}_x \\ &+ (\cos\psi\sin\phi + \cos\theta\cos\phi\sin\psi)\,\vec{e}_y + \sin\psi\sin\theta\,\vec{e}_z \end{aligned} \qquad (19a)$$

$$\vec{e}_2 = (-\sin\psi\cos\phi - \cos\theta\sin\phi\cos\psi)\,\vec{e}_x + (-\sin\psi\sin\phi + \cos\theta\cos\phi\cos\psi)\,\vec{e}_y + \cos\psi\sin\theta\,\vec{e}_z \qquad (19b)$$

$$\vec{e}_3 = \sin\theta\sin\phi\,\vec{e}_x - \sin\theta\cos\phi\,\vec{e}_y + \cos\theta\,\vec{e}_z \qquad (19c)$$

Substituting Eqs. (19) into the first line of Eq. (18) and making some algebraic manipulations, one obtains

$$\dot{x} = \frac{4}{3}\alpha R\,[\cos\phi\cos(\omega t + \psi) - \sin\phi\cos\theta\sin(\omega t + \psi)] + \left[v^2 - \frac{16}{9}\alpha^2 R^2\right]^{1/2}\sin\theta\sin\phi \qquad (20a)$$

$$\dot{y} = \frac{4}{3}\alpha R\,[\sin\phi\cos(\omega t + \psi) + \cos\phi\cos\theta\sin(\omega t + \psi)] - \left[v^2 - \frac{16}{9}\alpha^2 R^2\right]^{1/2}\sin\theta\cos\phi \qquad (20b)$$

$$\dot{z} = \frac{4}{3}\alpha R\sin\theta\sin(\omega t + \psi) + \left[v^2 - \frac{16}{9}\alpha^2 R^2\right]^{1/2}\cos\theta \qquad (20c)$$

where $v^2 = v_T^2 + v_L^2$, with $v_T = (4/3)\alpha R$. The above equations describe the translation of the center of mass.

Eqs. (12) together with Eqs. (20) determines completely the motion of a magnetotactic bacterium. It must be noted that the frequencies β and γ are not present explicitly in Eqs. (20). This is due to the fact that the forces that produce the torques associated with these frequencies do not contribute to translation, that is, these torques are acted by couples.

c) Limit cases.

(i) $\alpha = 0$.

One has in this case a magnetotactic bacterium that swims with a symmetrical flagellum. The equations of motion (12) and (20) reduce to the set of equations

$$\dot{\phi} = 0 \qquad (21a)$$

$$\dot{\theta} = \beta \sin\theta \qquad (21b)$$

$$\dot{\psi} = -\gamma \qquad (21c)$$

$$\dot{x} = v \sin\phi \sin\theta \qquad (21d)$$

$$\dot{y} = -v \sin\theta \cos\phi \qquad (21e)$$

$$\dot{z} = v \cos\theta \qquad (21f)$$

The above equations can be integrated analytically and give a planar trajectory. This limit case corresponds to the Bean model (Esquivel & Lins de Barros, 1986). This model predicts the amount of time required for the magnetotactic bacterium aligns the magnetic moment to the magnetic field and the diameter of the U-turn. These quantities are given, after working the above equations and taking into account thermal disturbance in the initial condition θ_o, by the formulae

$$t_u = \frac{8\pi\eta R^3}{m B} \ln\left[\frac{2mB}{k T}\right] \qquad (22)$$

$$L = \frac{8\pi^2 R^3 \eta v}{m B} \qquad (23)$$

where k is the Boltzmann constant and T the absolute temperature. The time t_u given by Eq. (22) is time of the U-turn even in the

case $\alpha \neq 0$ because the U shaped trajectory of the Bean model is the mean trajectory in which the real one oscillates around. We will use t_u as a reference time for the following asymptotic argument that will be useful in the analysis of experimental data in the next section. When $t \geq t_u$, θ belongs to a small interval which have π as a lower or upper bound, depending on the case. The solution of Eq. (21b) is

$$\theta(t) = 2 \arctan\left[\exp(\beta t) \tan\left(\frac{\theta_0}{2}\right) \right] \qquad (24)$$

When $t \gg t_u$, θ tends to π asymptoticaly. This behaviour is due to the presence of the exponential function in the argument of the arctangent. Therefore, if β is not small when compared to α, the oscillating contribution from flagellar asymmetries is damped by the unperturbed solution and Ω' is given by the same expression as in the case in which $\beta = 0$. In the case of the Bean model, where $\alpha = 0$ and $\beta \neq 0$, one has $\Omega' = [(\omega - \gamma)^2 + \beta^2 \sin^2\theta]^{1/2}$ for all t. Then for $t \geq t_u$, $\theta = \pi$ and, therefore, $\Omega' = \omega - \gamma$.

(ii) $\alpha = \beta = 0$.

The equations of motion are the same as equations (21), except by Eq. (21b) which is now $\dot{\theta}=0$. The solution is a straight line. This very simple solution shows that a non-magnetotactic bacterium with a symmetric flagellum swims describing a straigth path, as expected. In this case $\Omega' = \omega - \gamma$ for all t.

(iii) $\alpha \ll \omega - \gamma$, $\beta = 0$.

This case corresponds to a limit in which the equations of

motion can be integrated regarding the flagellum asymmetries as a weak perturbation,that is, a non-magnetotactic bacterium with a quasi-symmetric flagellum. Using a well known perturbative treatment (Arnold, 1973) for ordinary differential equations (see appendix), one obtains an approximate solution which is an expansion of first order in the parameter $\alpha/(\omega - \gamma)$ around its zero value (that is, around the non-perturbed solution).

The approximate solutions in the center of mass reference frame are

$$\phi(t) \simeq \frac{\alpha \csc \theta_o}{\omega - \gamma} \sin[(\omega - \gamma)t] \qquad (25a)$$

$$\theta(t) \simeq \theta_o + \frac{\alpha}{\omega - \gamma} (\cos[(\omega - \gamma)t] - 1) \qquad (25b)$$

$$\psi(t) \simeq -\gamma t - \frac{\alpha}{\omega - \gamma} \cot \theta_o \sin[(\omega - \gamma)t] \qquad (25c)$$

with initial conditions $\phi(0)=\psi(0)=0$ and $\theta(0)=\theta_o$.

By substitution of the above solutions in Eqs. (20) and making the same approximation and integrating, we obtain

$$x(t) \simeq \frac{v\,\alpha}{(\omega - \gamma)^2} - \frac{v\,\alpha}{(\omega - \gamma)^2} \cos[(\omega - \gamma)t]$$

$$+ \frac{4}{3} \frac{\alpha R}{\omega - \gamma} \sin[(\omega - \gamma)t] \qquad (26a)$$

$$y(t) \simeq \frac{4}{3} \frac{\alpha R}{\omega - \gamma} - \frac{4}{3} \frac{\alpha R}{\omega - \gamma} \cos[(\omega - \gamma)t]$$

$$- \frac{v\,\alpha \csc \theta_o}{(\omega - \gamma)^2} \sin[(\omega - \gamma)t]$$

$$+ \left[\frac{\alpha \csc \theta_o}{\omega - \gamma} - \sin \theta_o \right] v\,t \qquad (26b)$$

$$z(t) \simeq \frac{4}{3}\,\frac{\alpha R \sin\theta_0}{\omega-\gamma} - \frac{4}{3}\,\frac{\alpha R \sin\theta_0}{\omega-\gamma}\cos[(\omega-\gamma)t]$$

$$- \frac{\alpha R \sin\theta_0}{(\omega-\gamma)^2}\sin[(\omega-\gamma)t]$$

$$+ \left[\cos\theta_0 + \frac{\alpha \sin\theta_0}{\omega-\gamma}\right] v\, t \qquad (26c)$$

with the initial conditions $x(0)=y(0)=z(0)=0$.

The solution given by Eqs. (26) corresponds to the helical motion observed experimentally in a non-magnetotactic bacterium with a quasi-symmetric flagellum. It must be noted that only θ was not taken to be zero at $t=0$. This is because the range of values of θ in this coordinate system is the open interval $(0,\pi)$. In fact, 0 and π are singular poles of the θ coordinate. In this approximation, the contribution of α to Ω' is negligible and one has that $\Omega' \simeq \omega - \gamma$.

(iv) $\beta \ll \alpha$.

One proceeds in a way similar to that of the preceding limit case. Then, one considers the angular velocity $\dot{\theta}$ as a function of β and expands it in first order in β:

$$\dot{\theta} \simeq \dot{\theta}(\beta=0) + \beta \left.\frac{\partial\dot{\theta}}{\partial\beta}\right|_{\beta=0} \qquad (27)$$

From (21) one obtains

$$\dot{\theta} \simeq \beta \sin\left[\theta_o - \alpha \int_o^t dt' \sin(\omega t' + \psi(t';\beta=0)) \right] - \alpha \sin(\omega t + \psi) \qquad (28)$$

The first term in Eq. (28) acts as a small perturbing, time dependent factor because the sine is bounded and $\beta \ll \alpha$. In this case there is no U-turn because the argument of the sine in the first term of the above equation is no longer the same as the angle θ in which time diferentiation is taken. This case corresponds to a magnetotactic bacterium with a very short flagellum in a very small magnetic field.

4) Aplications.

Samples of magnetotactic bacterium were collected in the interface water-sediment in a costal brackish water lagoon. The samples were maintened by two weeks in laboratory without any chemical enrichment. To optical microscopy observation a drop of water with sediment was placed on the microscope. A coverslip was used to ensure good focus condition. A pair of coils adapted to the microscope furnished a homogeneous and stable magnetic field. Residual fields, as geomagnetic field or induced fields in the microscope, were not compensated because this does not alter essential results if the coils are well constructed and well adapted. Dark field ilumination was used to obtain the bacterium track on the film emulsion.

Experimental tracks obtained by low-exposure dark field optical microphotography technique give the projection of the

bacterium trajectory on the film emulsion plane, which is associated to the yz and xz planes (Fig. 2).

Theoretical parameters are connected to experimental observation. Electron scanning or transmission microscopy together with high resolution optical microscopy allows to estimate the bacterium radius R. U-turn analysis allows to obtain a mean value for the cell magnetic moment. This is achieved by means of formula (23) where, in addition, two more parameters are needed, namely, the applied field and the migration velocity. The viscosity, η, has value 0.01 Poise, that is, the water viscosity. The migration velocity that enters in formula (23) is the projection of the instantaneous velocity along the unperturbed trajectory given by the Bean model, which in the model described is just v_L . This velocity is measured directly in the photography or using recorded video images. v_T is obtained by measuring the mean angle between the perturbed trajectory and the associated unperturbed path (Fig. 2b). Then v_T is obtained by applying the formula

$$\frac{v_T}{v_L} = \tan \bar{\theta}_p \qquad (29)$$

where θ_p is the pitch angle of the helical path and the bar over the angle indicates a mean value over the measured angles. Since v_T is related to α by $v_T = (4/3)\alpha R$, one obtains immediately that $\alpha = 3\, v_L \tan\theta_p / 4R$.

As we have showed in the last section, when $t \gg t_u$ the magnitude of the angular frequency is the same as in regimen of zero field. This fact allows a good estimation of Ω'. This frequency is associated to the number of wavelengths of the

helical path divided by the time of exposure If this is made for the portion of the helical trajectory posterior to the U-turn, one can use as an approximate formula for Ω' Eq. (14). Thus, the angular velocity of rotation of the flagellum relative to the cell body is

$$\omega - \gamma = (\Omega'^2 - \alpha^2)^{1/2} \qquad (30)$$

The parameters ω and γ cannot be obtained separatedly. However, any value can be atributed to ω and γ if one mantains $\omega - \gamma$ fixed and $\gamma < \omega$. The case $\omega = \gamma$ is unstable and does not correspond to a real and viable bacterium.

The equations of motion were integrated in a computer using a fourth order Runge-Kutta method. The parameters used were obtained from experiment in the described way. Fig. 3 shows the projection of the resulting 3d trajectory in the planes xy, yz, and xz. It must be noted that the trajectory obtained has a better alignment with the applied field than that of the experimental trajectory because in the equations of motion no residual field is taken into account. The diameter of the U-turn is almost the same as the diameter obtained from the photographic plate. Also the migration velocity in this computer trajectory is in good agreement with the observed one. The dashed curve in the yz plane is the associated path obtained from the Bean model. Fig. 4 shows the behaviour with time of the three Euler angles (θ, ϕ, ψ). Fig. 4a is directly associated with the way in which the cell magnetic moment aligns with the field and one identifies explicitly the time t_u. As in the yz plane in Fig. 3, the dashed curve in Fig. 4a is the

behaviour of θ with respect to time in the associated Bean model.

Fig. 5 shows the trajectory of the same bacterium in zero field condition. The resulting helical motion of the center of mass is modulated by another helical path with greater wavelength. A magnetic field considerably greater than the geomagnetic field breaks this modulation as is evidenced in Fig. 3. This strong modulation reflects the very high degree of asymmetry of the flagellum of the studied bacterium. This behaviour is typical in all magnetotactic bacteria observed in our laboratory. As α became small compared with $\omega - \gamma$, the modulation decreases until the trajectory reaches the approximated shape of a cylindrical helix (Fig. 6). This behaviour was predicted in the last section (limit case (iii)).

Fig. 7 shows the trajectory of the same bacterium at the presence of the local geomagnetic field. In this case the bacterium does not make any U-turn but the helical modulation is distorted by the field. This behaviour corresponds to the one predicted in the limit case (iv) in the last section. In fact, one has in this case $\alpha/\beta = 4 \times 10^{-3}$, which is much less than unity. This shows that flagellar asymmetries dominates. If one considers a transverse torque of about one tenth of the measured torque one obtains that, in the same interval of time, the bacterium begins to make a U-turn (Fig. 8).

5) Conclusion.

We have described a mechanical *ab initio* model for the motion of a magnetotactic bacterium where a non-magnetotactic one emerges

as a particular case. This approach allows a description of helical motion with six degrees of freedom. Previous works (Crenshaw, 1989; 1990; 1992, a, b & c) assume helical motion as given *a priori* and treat the kinematics of a microorganism using the framework of differential geometry.

The model presented can help experimentalists to extract parameters not directly accessible, as for example, the frequency of flagellar rotation relative to the cell body, $\omega - \gamma$, as well the torques and forces involved in the bacterial motion. The model also allows to obtain informations on the behaviour of magnetotactic bacteria in fields of the order of the geomagnetic field. In laboratory it is difficult to control such fields and the model can elucidate questions related to the biological efficiency of magnetic response in microorganisms (Lins de Barros & Esquivel, 1987).

In the last section, we show that if the flagellum is sufficiently asymmetrical, that is, if the flagellar bundle does not have an integer number of wavelengths, magnetotactic bacterium does not make a U-turn in low magnetic fields. Otherwise, if the degree of asymmetry is low, the magnetotactic bacterium performs a U-turn. The parameters obtained for the bacteria analyzed in laboratory conditions shows that these bacteria does not perform U-turn in the local geomagnetic field. This can be associated to adaptative factors in magnetotaxis. The geomagnetic field orients the cell but not limit the motion allowing to the bacterium to swim in any direction. Magnetotaxis can be related to the reduction of possibilities in the the motion direction when the field is present: if the magnetotactic interaction dominates the

flagellar action, the average motion is nearly constrained to one direction allowing a faster migration velocity but, a bacterium strongly constrained to the magnetic field line direction swims in a narrower region. This reduce the possibilities to find nutrients. On the other hand, asymmetrical flagellum introduces a disturbance in the movement and allows the cell to swim in any direction and to search nutrients more efficiently. In this sense asymmetrical flagellum can constitute a biological advantage to magnetotactic bacterium. Early data from electron microscopy (Lins de Barros *et al.*, 1990), both scanning and transmission, reveals that, in fact, some magnetotactic bacteria have a flagellum that typically possesses a shape of a half wavelength helix with an extension of about one body length. It is possible that a flagellum of this type has been developed to compensate the excess of biomineralization of magnetic material, avoiding, in this way, that the biological motion of the magnetotactic bacterium of being too much constrained to the geomagnetic field line. However, experimental observations of others species of magnetotactic microorganisms show that some cells are expected to make a U-turn in the geomagnetic field.

Aknowledgement.

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Appendix.

In this appendix we discuss the technique of variation of parameters used in the discussions of the limit cases (iii) and (iv). This technique is legitimated by the following theorem (Arnold, 1973).

Theorem. *If* $\vec{v} = \vec{v}(t, \vec{x}, \varepsilon)$ *is a vector field depending differentiably on a parameter* ε *(as well as on* t *and* $\vec{x}$*), then the value* $\vec{\xi}(t)$ *of the solution of the equation*

$$\dot{\vec{x}} = \vec{v}(t, \vec{x}, \varepsilon) \qquad (A1)$$

satisfying the initial condition $\vec{\xi}(t_0) = \vec{x}_0$ *depends differentiably on* t_0, $\vec{x}_0$, t *and* ε.

Let us apply the above theorem by treating perturbatively equation (A1) with respect to the parameter ε.

If ε is a small parameter, one can write that

$$\vec{v} = \vec{v}_0 + \varepsilon \vec{v}_1 + O(\varepsilon^2) \qquad (A2)$$

By the above theorem, the solution with fixed initial condition can be written in the form

$$\vec{x}(t) = \vec{x}_0(t) + \varepsilon \vec{y}(t) + O(\varepsilon^2) \qquad (A3)$$

where $\vec{x}_0(t)$ is the solution of the unperturbed equation

$$\dot{\vec{x}} = \vec{v}(\vec{x}, 0) \qquad (A4)$$

and $\vec{y}(t)$ is the derivative of the solution with respect to the parameter ε at $\varepsilon = 0$.

LEGENDS OF FIGURES.

Figure 1: The bacterium with a spherical cell body. We use two reference frames: one is defined by the set of orthogonal axes (x_1, x_2, x_3) in which the center of mass is at rest; the other reference frame is specified by the set of axes (x, y, z) where translation of the center of mass is taken into account.

Figure 2: (a) Photografic plate obtained from dark field high resolution optical microscopy showing the track of a magnetotactic bacterium performing a U-turn. (b) One of the tracks translated and better defined. The mean θ_p angle measured in this track allows an indirect estimation of α and $\omega - \gamma$. The applied field is B=2.5 G. The experimental parameters obtained directly are R=1.2 μm, L=25 μm, t_u=0.4 sec., m=2.2 *emu*, v_L=125 μm/sec., Ω'=220 rad/sec. For this bacterium, α=133.64 rad/sec and $\omega - \gamma$=175 rad/sec. The time of exposure is 1.6 sec. Bar=30 μm.

Figure 3: Computer trajectories. The parameters are taken from data of Fig. 2. The dashed curve represents the unperturbed trajectory of the Bean model.

Figure 4: The behaviour with time of the Euler angles (θ, ϕ, ψ). The dashed curve in the graph $\theta \times t$ represents the behaviour given by the Bean model.

Figure 5: Computer trajectories made with the same parameters as used in Fig. 3 , except that the bacterium is now in zero magnetic field.

Figure 6: Computer trajectories of a bacterium in zero magnetic field with a small α. The parameters are the same as in

Fig. 3, except that α is one tenth of the value used there and β=0. The trajectory obtained is roughly a cylindrical helix. Only the planes yz and xy are showed.

Figure 7: Computer trajectories made with the same parameters as used in Fig. 3, except that the bacterium is in the local geomagnetic field (0.25 G in Rio de Janeiro, Brazil). For these parameters there is no U-turn.

Figure 8: Computer trajectory in the yz plane where one uses the same parameters as in Fig. 7, except for the value of α which is taken as one tenth of the value used there. The time of integration is the same used in Fig. 7 for better comparison. We note that, in the same interval of time, the bacterium begins to perform a U-turn. The oscillatory behaviour of the path is not much visible due to smallness of α and the scale utilized.

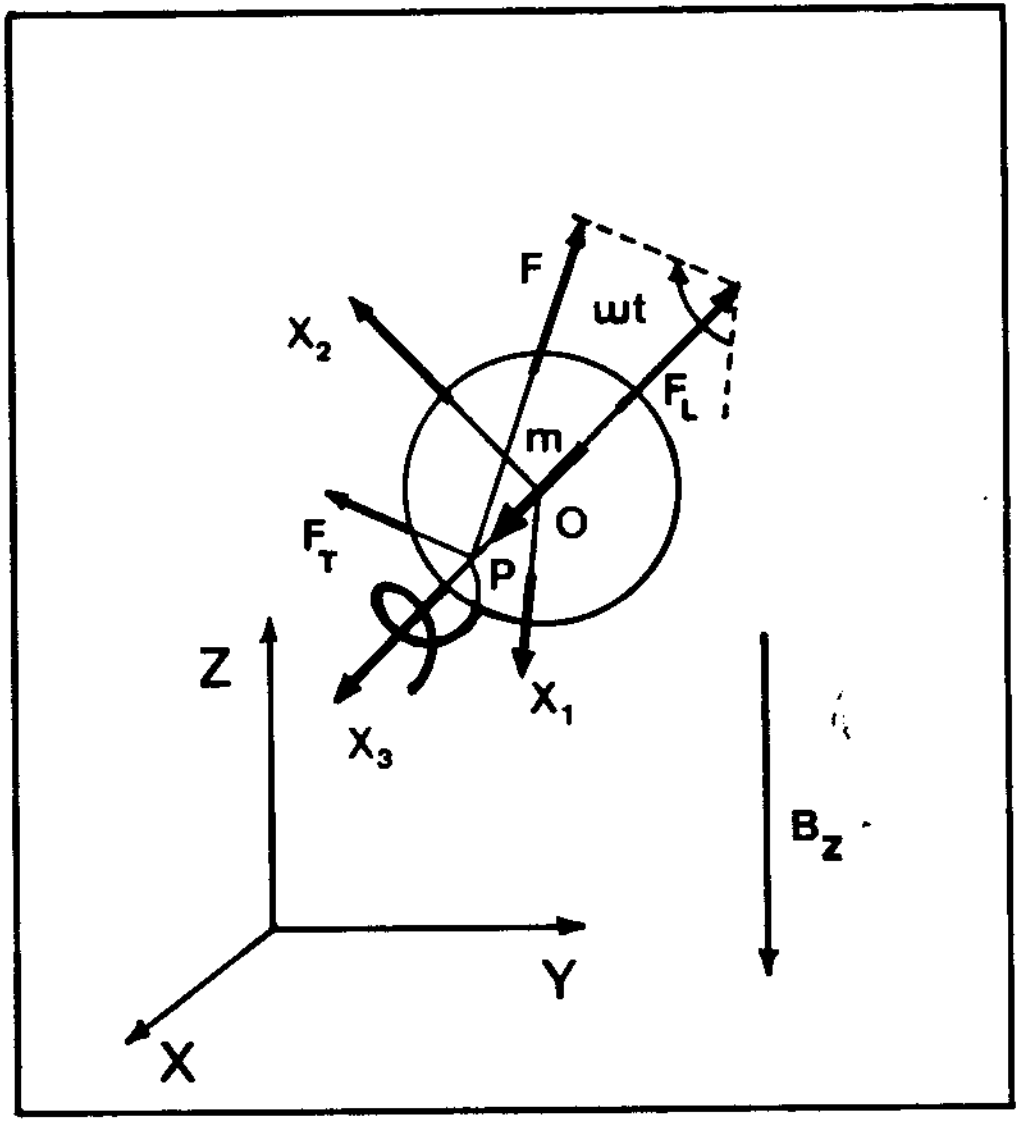


FIGURE 1

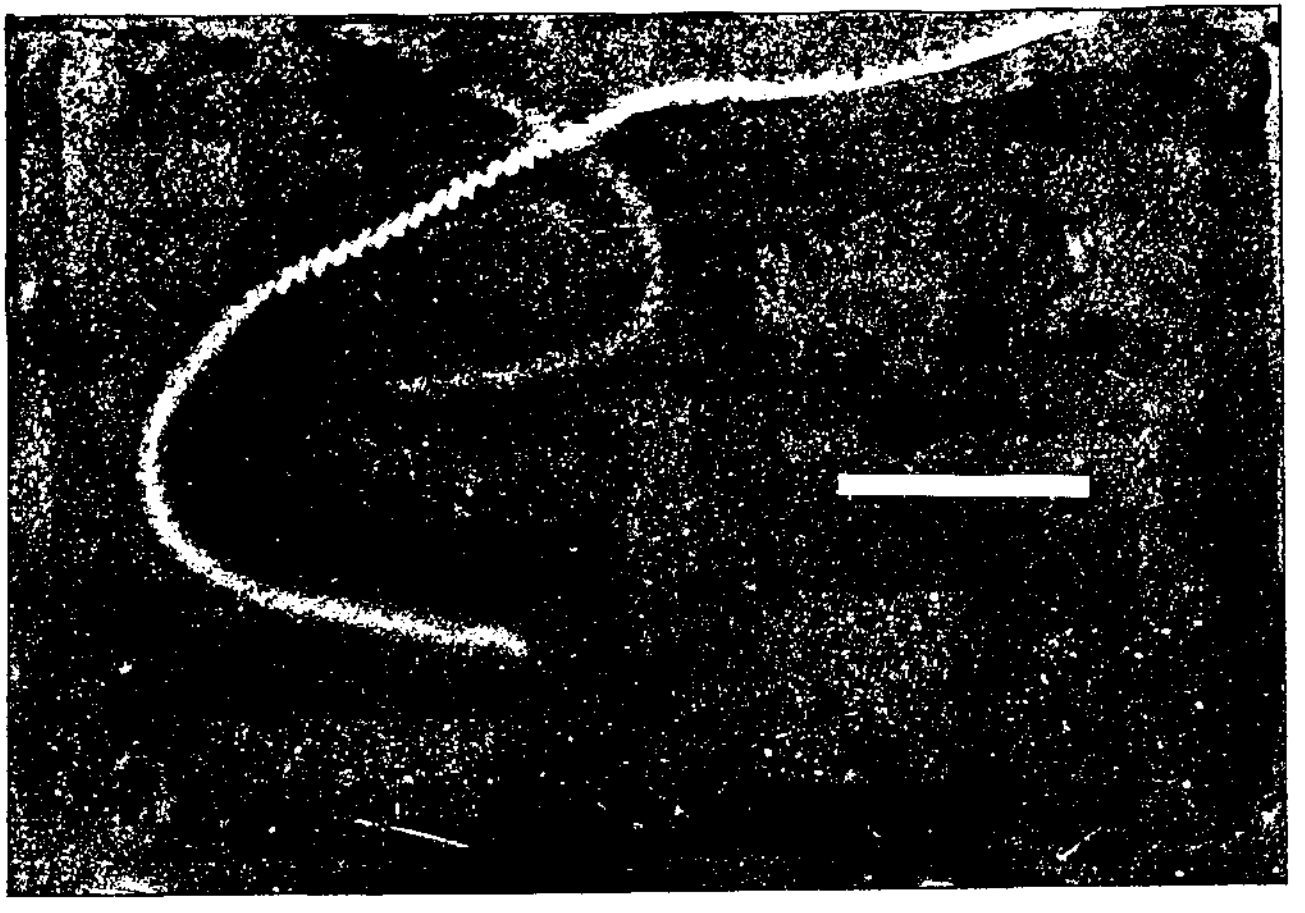


FIGURE 2a

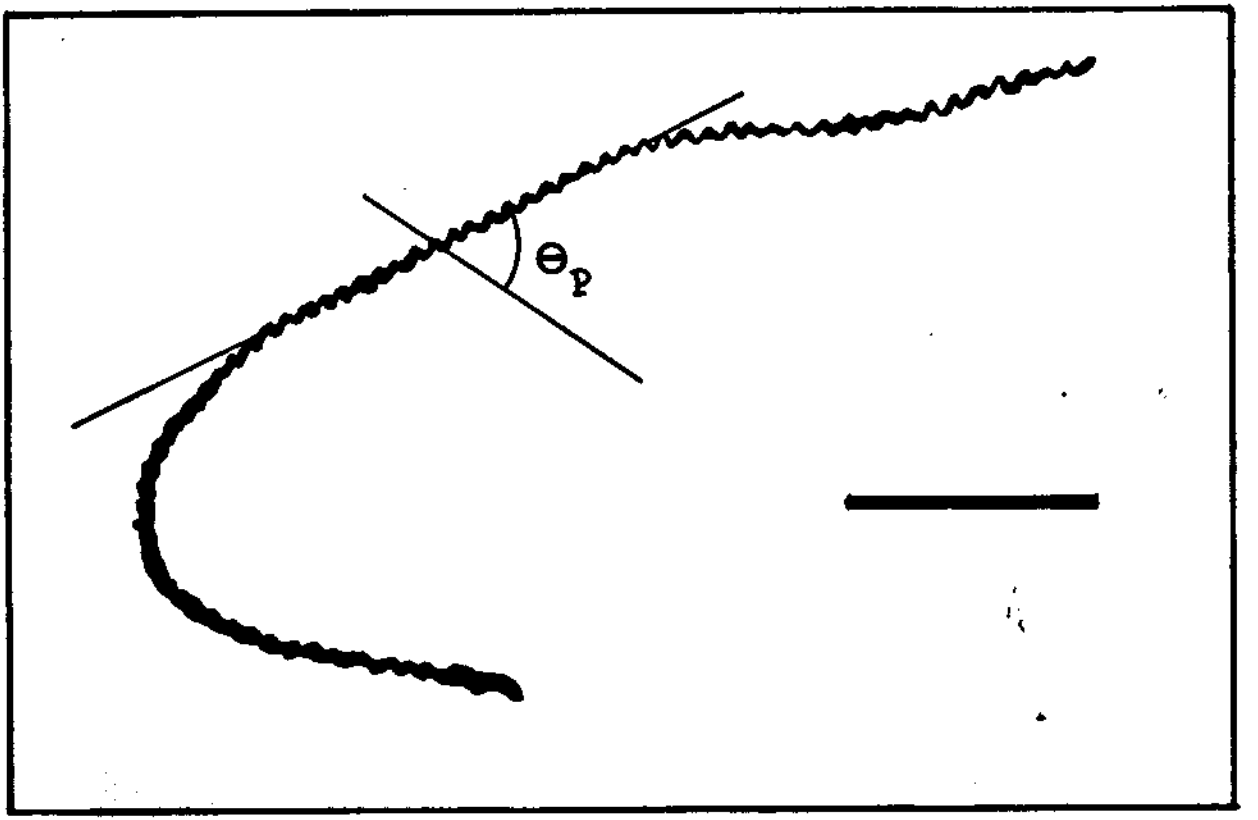
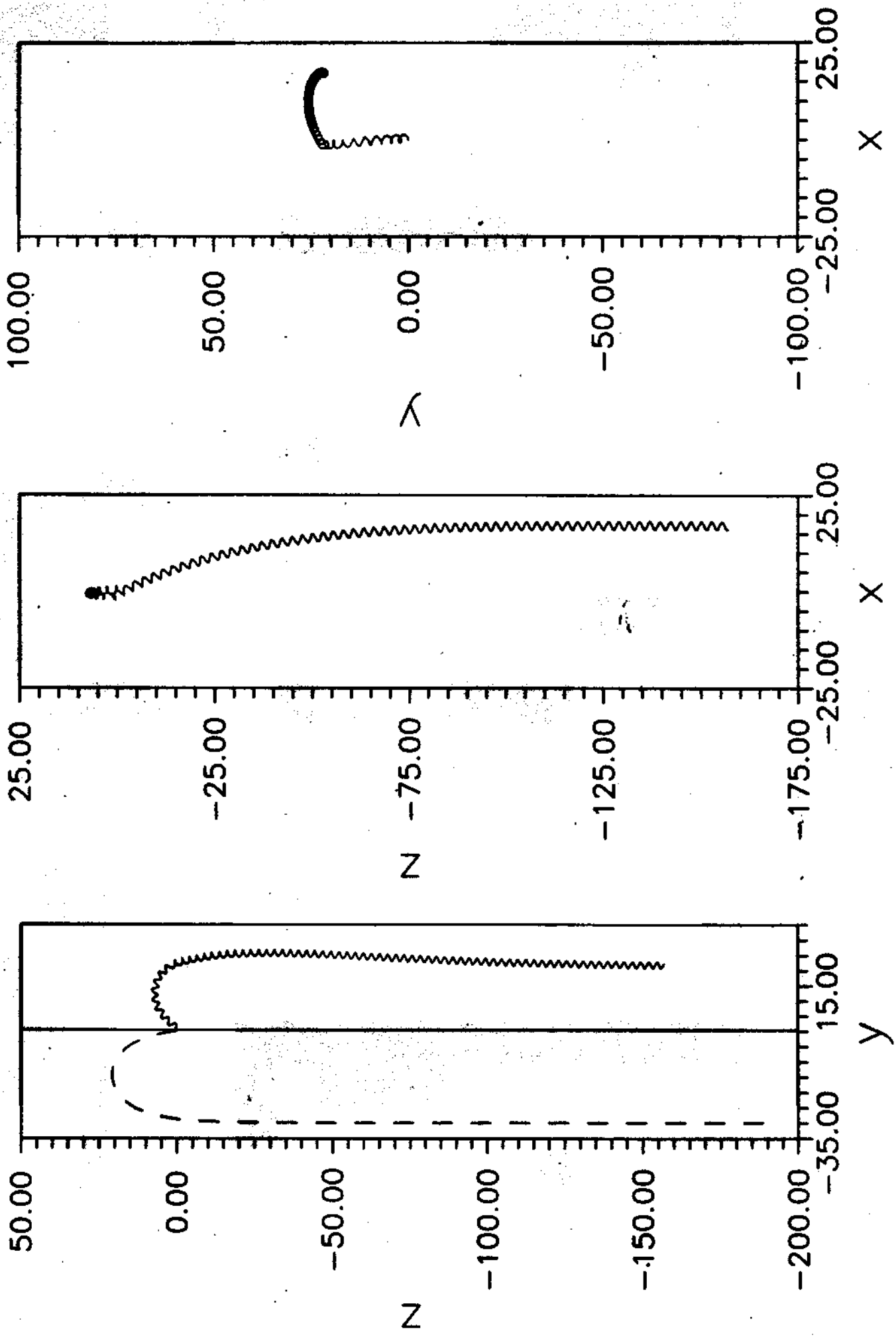


FIGURE 2b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25.00
-25.00
X
Y
25.00
-25.00
-75.00
-125.00
-175.00
25.00
-25.00
X
Z
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0.00
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15.00
-35.00
y
Z

FIGURE 3

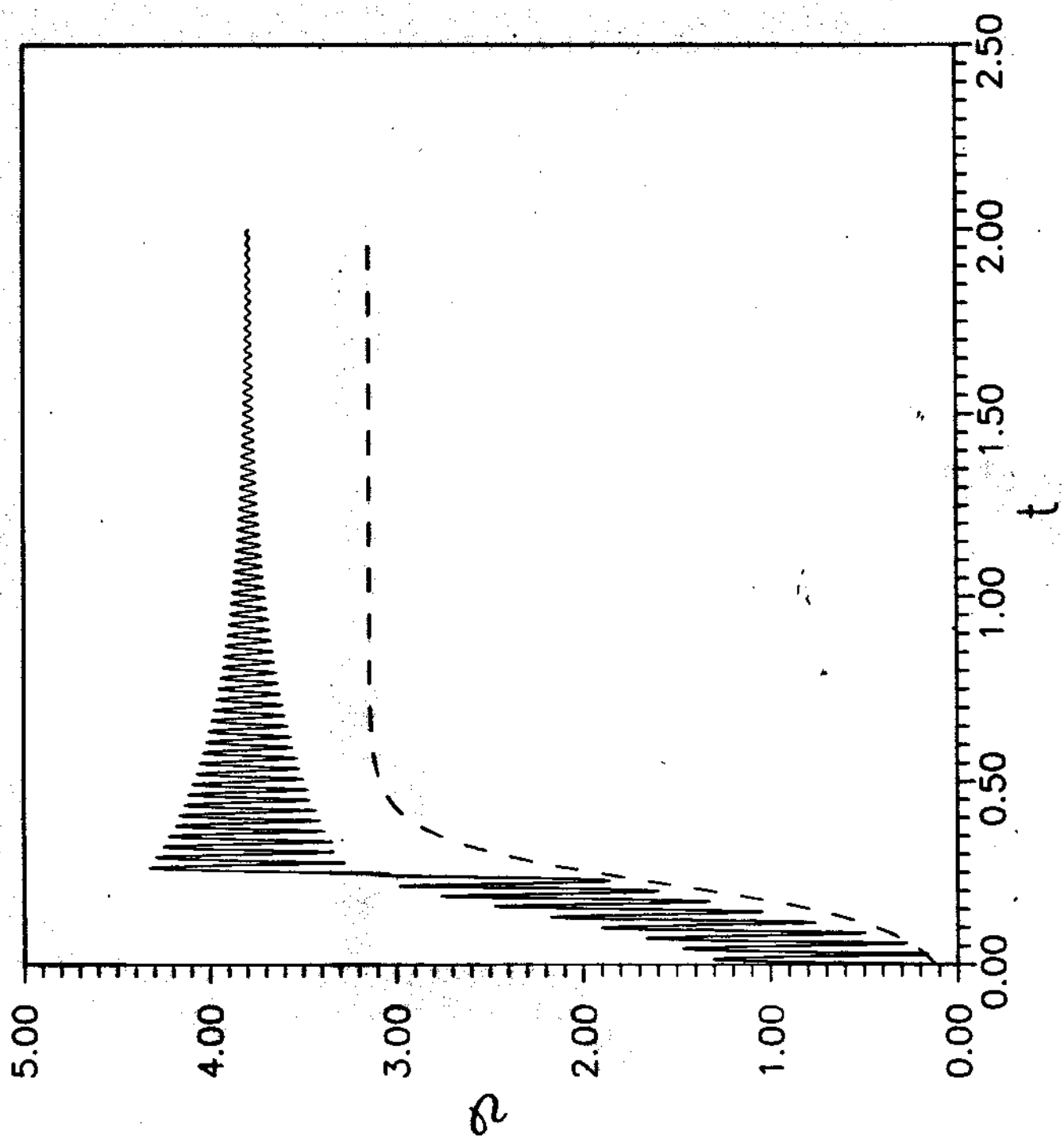


FIGURE 4a

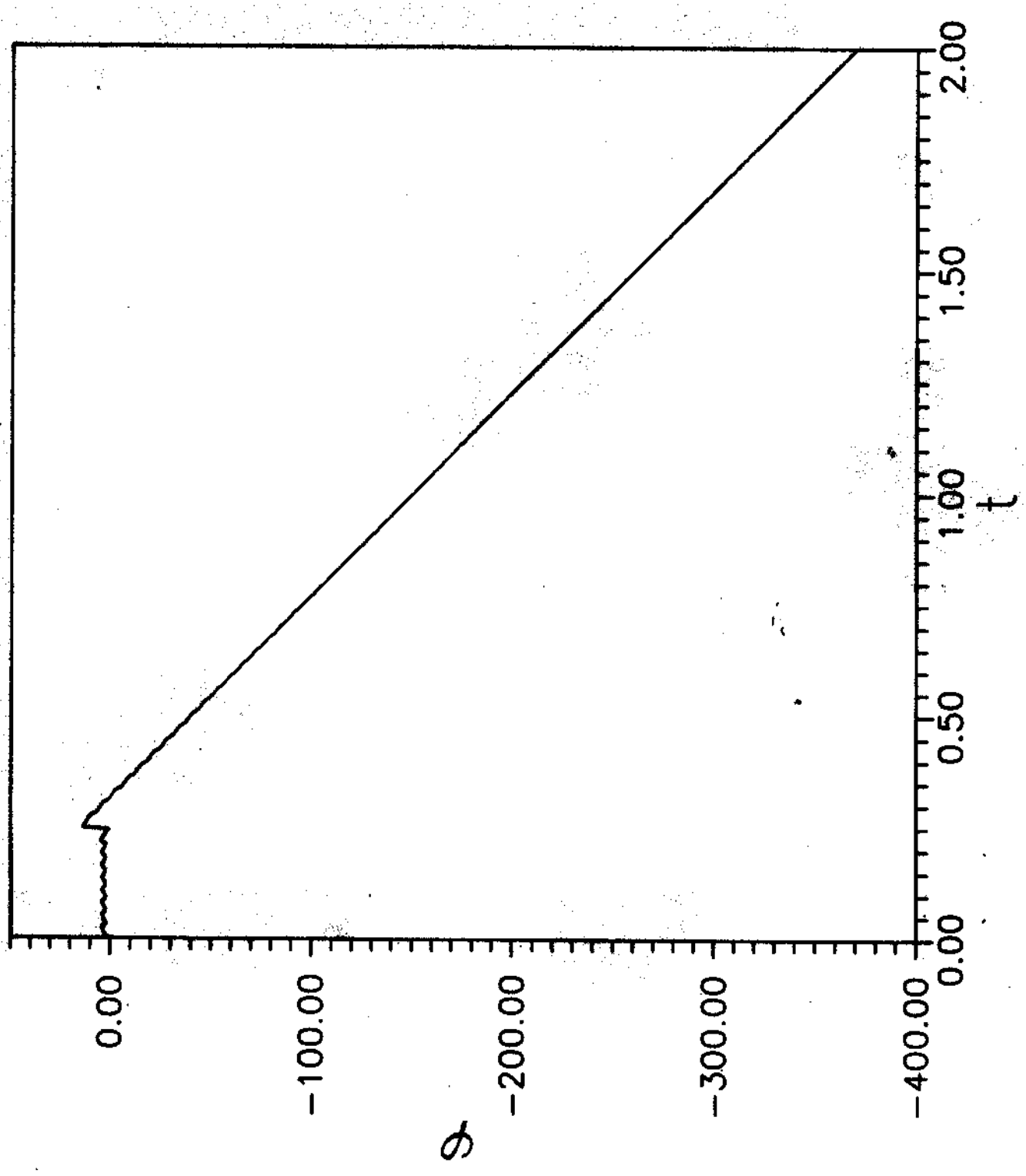


FIGURE 4b

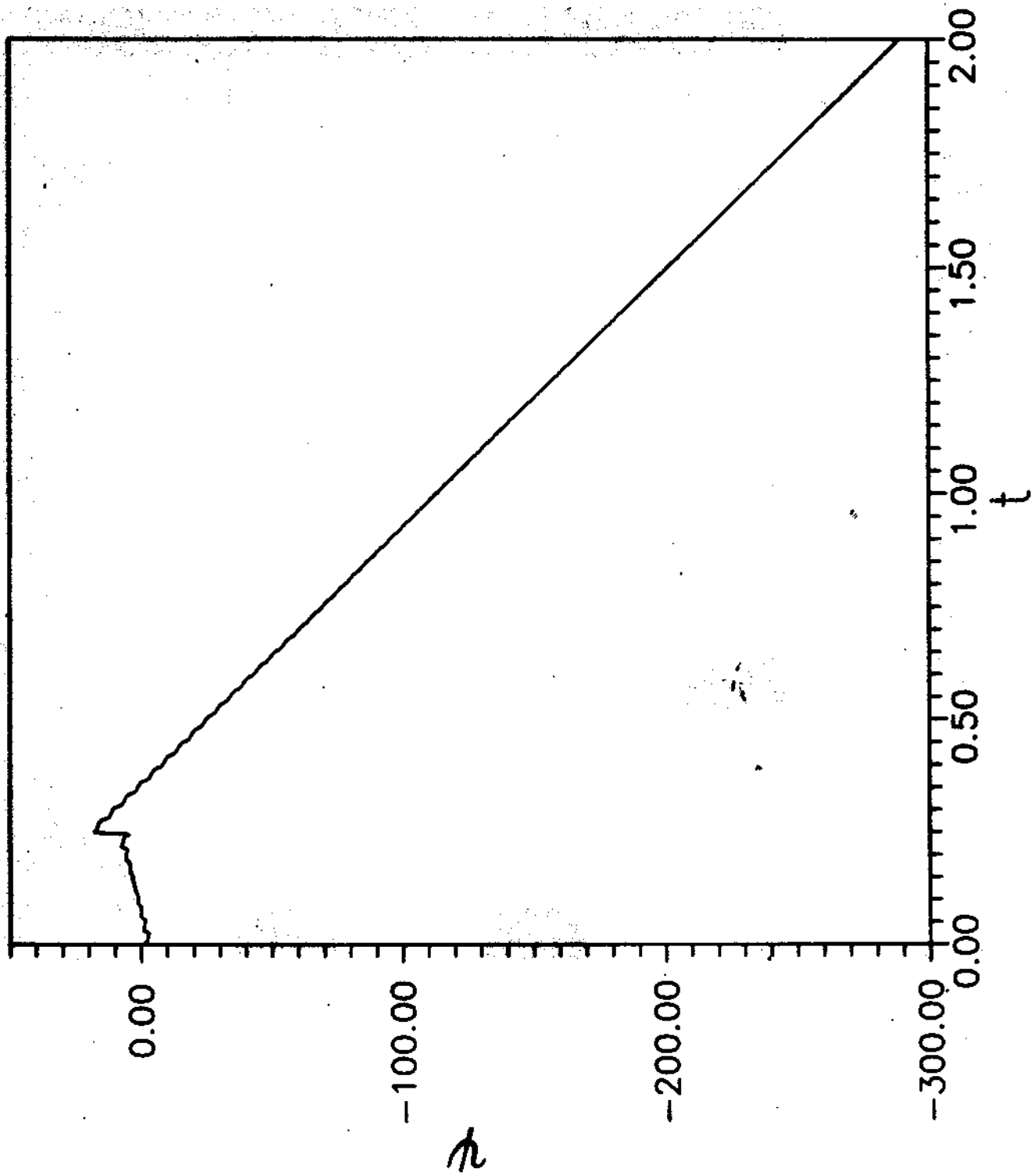
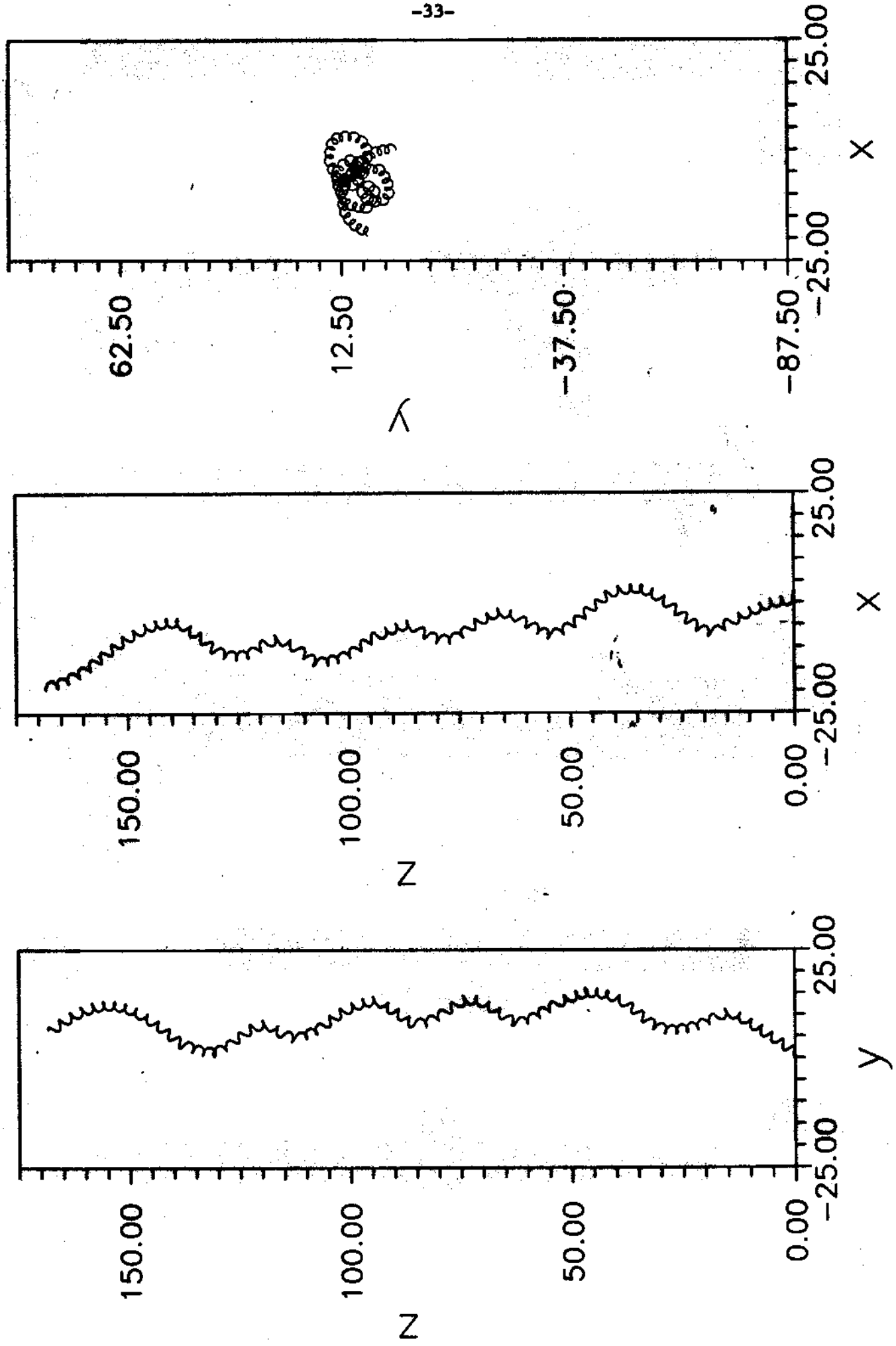


FIGURE 4c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X
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50.00
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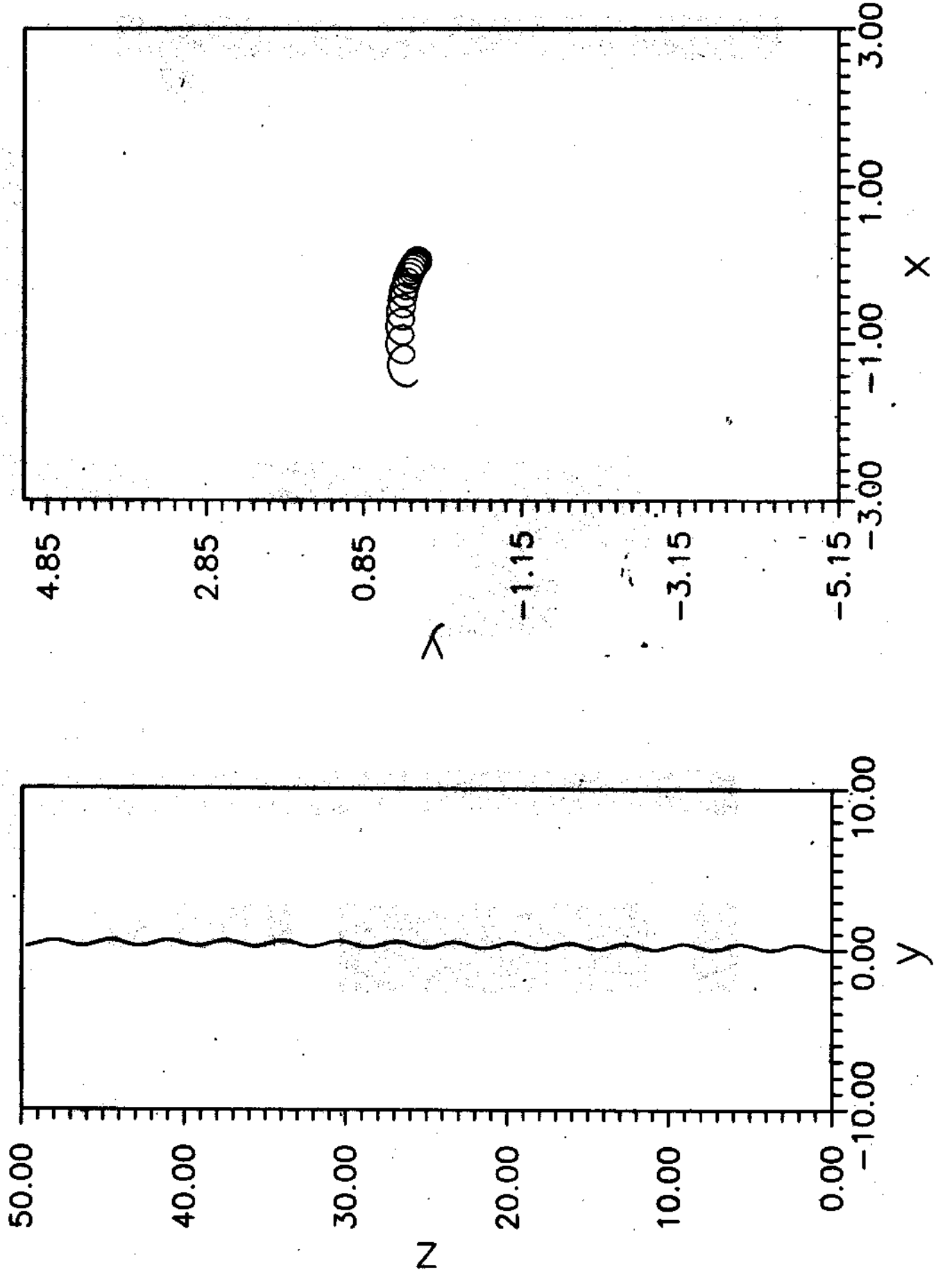
Z
25.00
y
-25.00
150.00
100.00
50.00
0.00
Z

FIGURE 5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-3.15
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Y
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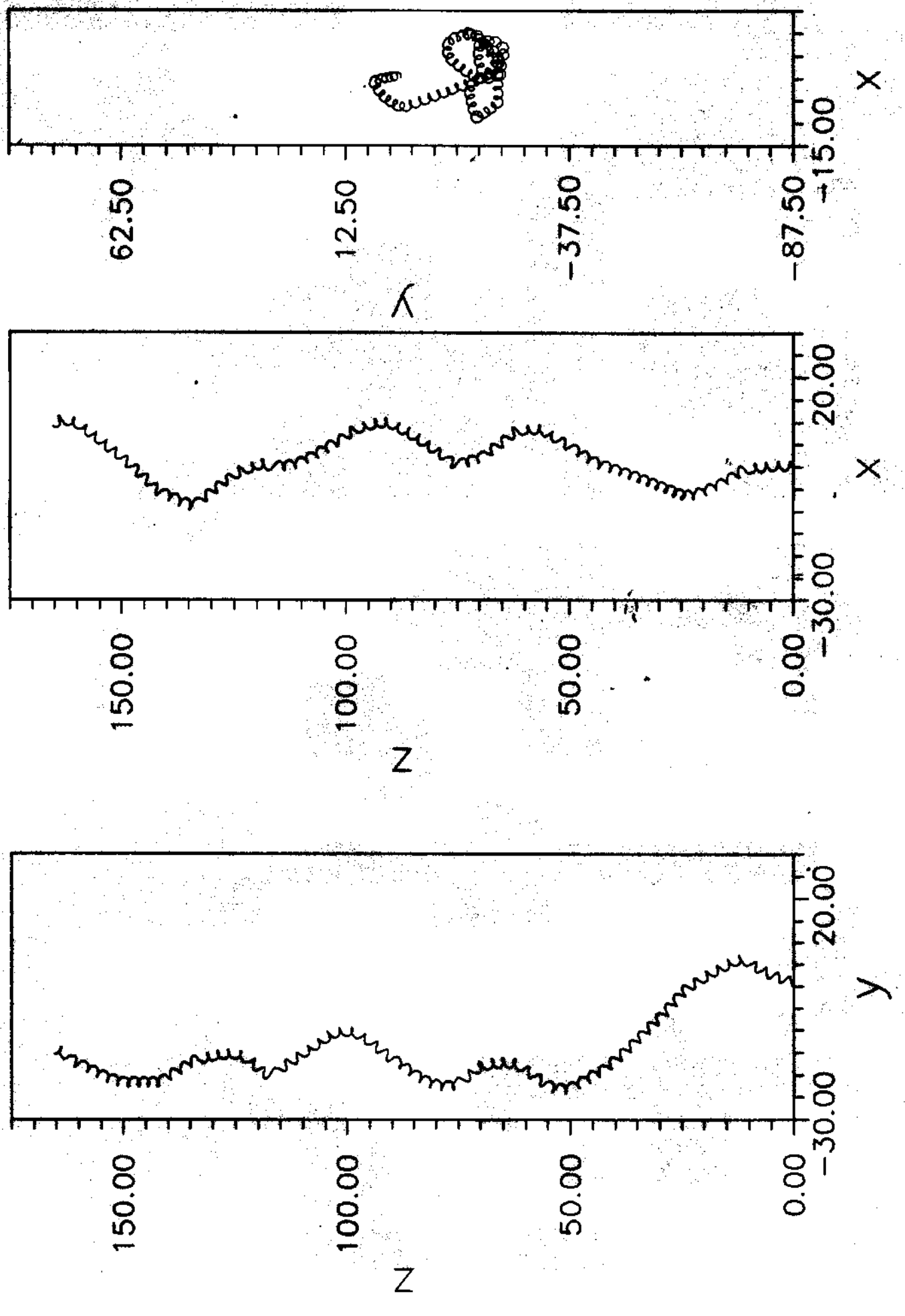
y
50.00
40.00
30.00
20.00
10.00
0.00
Z

FIGURE 6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0.00
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X
Z
150.00
100.00
50.00
0.00
-30.00
20.00
y
Z

FIGURE 7

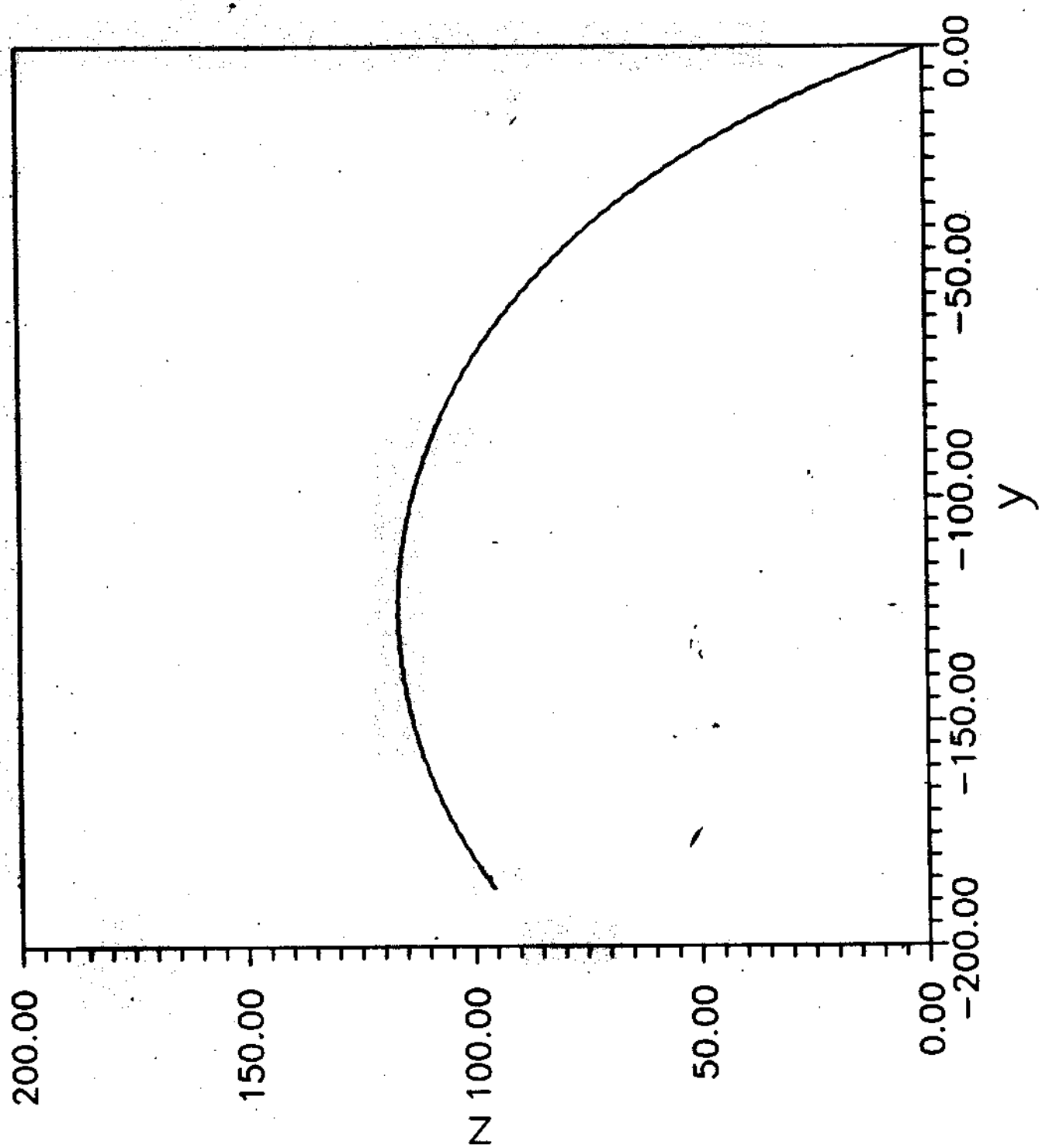

FIGURE 8

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