INTRODUCTION

Cell locomotion attracts especial attention with regard to several major, indispensable features of eukaryotic existence, including the cell accumulation driven by chemotaxis and kinesis, in inflammatory processes and wound healing, in morphogenesis during tissue regeneration and development, and in tumor metastasis (Trinkaus, 1976). Similarly, cell shape changes are considered to underlie several key events in development and pathogenesis, such as the folding of epithelial sheets (Holtfreter, 1943, 1944; Kinnander and Gustafson, 1960; Karfunkel, 1974). In accord with the way most other fundamental cellular functions are generally viewed, cell locomotion is universally treated as a stochastic (Peterson and Noble, 1972; Potel and McKay, 1979; Tatsuka et al., 1989; Noble, 1990), chemical concentration-dependent (Devreotes and Zigmond, 1988; Fisher et al., 1989; Egelhoff and Spudich, 1991) process. The regulation of cell shape has been attributed to (unknown) properties of some elements of the cytoskeleton (e.g. see Bray et al., 1986).

Although cell locomotion has always been equated with a random, or Brownian, process, this view may have constrained the scope of locomotory analysis. Thus, in practice, the study of cell locomotion has been aimed predominantly at the quantification of scalar variables, such as locomotory speed, directional persistence, cell spread area, etc., which have been treated as phenomenological categories (Potel and McKay, 1979; Tatsuka et al., 1989; Noble, 1990; Dunn and Brown, 1990; Murray et al., 1992). Information about these parameters is usually obtained from time-lapse images of cells either by ubiquitous ‘dot-and-line’ methods, manually or with computer assistance to increase objectivity and collect sufficient amounts of data, or by image processing techniques capable of extracting more information. However, measurements of each of these parameters are subject to a paradox of validity in that the average of any temporal ensemble (e.g. cell speed per step) is of limited usefulness in representing the cell’s actual behaviour if its motion is random (Abercrombie and Heatysman, 1953). Accurate digital image analysis has fostered the search for more objective quantitative means to categorize dynamical cell form and movement in order to account for cell type-specific features, e.g. by fitting techniques (Dunn and Brown, 1989, 1990; Noble, 1990) or Fourier analysis to extract the spatial harmonics of the sinusoidal frequency information available.

SUMMARY

The dynamic periphery of unstimulated, preaggregation, hunger-stage Dictyostelium discoideum amoebae was investigated by time-lapse videomicroscopy and digital image processing. Circular maps (i.e. of each of 360 radii around the cell transformed upon Cartesian coordinates) were constructed around the centroid of individual cell images and analysed in time series. This novel technique generated spatiotemporal structures of various degrees of order in the maps, which resemble classical wave interference patterns. The patterns thus demonstrate that cell movement is not random and that cells are intrinsically vibrating bodies, transited by self-organized, superpositioned, harmonic modes of rotating oscillatory waves (ROWS). These waves appear to depend upon spatiotemporal oscillations in the physico-chemical reactions associated with actin polymerization, and they govern pseudopodial movements, cell shape and locomotion generally. ROWS in this case are unrelated to the cyclic-AMP-regulated oscillations, which characterize later, aggregative populations of Dictyostelium. However, the exposure of aggregation-stage cells to a pulse of the chemoattractant cyclic-AMP induces a characteristic sequence of changes in the global cellular concentration and spatiotemporal distribution of fibrillar (F-)actin. This reaction begins with what appears to be a phase resetting of ROWS and it may, therefore, underlie the cellular perception of and response to chemotactic signals. We also develop here an analytical mathematical description of ROWS, and use it to simulate cell movements accurately.

Key words: actin, cell oscillations, chemotaxis, digital image processing, mathematical modelling, rotating oscillatory waves, synergetics, video microscopy
in cell shape (Partin et al., 1989). Although such applications facilitate data collection and some comparisons between cells, they have not eliminated the validity paradox, deciphered the relationship between locomotory parameters or allowed deduction of the underlying locomotory and shape mechanism(s) at a theoretical level.

Time-lapse images of moving cells in vivo or in vitro commonly provide one of the most intriguing and enigmatic spectacles in biology. The observer is presented with bewildering, 4-dimensional impressions of cell surfaces and surface extensions in turmoil and of seemingly chaotic tracks, which, at present, only tempt qualitative, pictorial description. However, dynamic cell images are known to contain far more information than the current methods of observation and analysis are able to extract and exploit (Noble, 1990).

Nonlinear dynamics in many systems, e.g. bacterial locomotion (Schimz and Hildebrand, 1992), or rhythmic contractions of cytoplasm (Achenbach and Wohlfarth-Bottermann, 1981) and isolated actomyosin (Ezzel et al., 1983), offers an insight into some problems of cell locomotory behaviour (see Alt, 1985), but such systems remain peripheral to the core concepts of biology. It follows that cell behaviour will of necessity occasionally present theoretical puzzles when nonlinear behaviour does not correspond to conventional expectations. An interesting example of this disparity may be seen in eukaryotic cell chemotaxis, i.e. the oriented turning of individual motile cells in response to an oriented signal, which is usually attributed to the action of a 'chemotactic gradient' of attractant stimulant (Devreotes and Zigmond, 1988; Fisher et al., 1989; van Duijn and van Haastert, 1992). However, neither of the classical models of eukaryotic chemotaxis, neutrophil leukocytes (Vicker et al., 1986) and Dictyostelium amoebae (Vicker, 1990 and unpublished; Vicker et al., 1984), are able to perceive a spatial gradient or react tactically to it. Rather, these cells only respond tactically to an oriented temporal signal, such as a directed pulse of chemotactant. This circumstance has invited the hypothesis that intrinsic cellular biological time or, more precisely, some particular nonlinearity within the signal reception system, e.g. oscillatory behaviour, is necessary to determine signal perception and cell response (Vicker, 1989, 1990; Vicker et al., 1986).

In order to enquire about the mechanisms of cell locomotion, shape and pseudopodial dynamics, and the possible existence of a cellular oscillator, we investigated *Dictyostelium discoideum* (Vicker, 1984). This amoeba serves as a primary system in the study of morphogenesis (MacWilliams, 1984), chemotaxis (Beauchamp and McKay, 1979), and cytoskeletal structure and function (McRobbie and Newell, 1984; Rubino et al., 1984; Yumura et al., 1984; Newell, 1986; Condeelis et al., 1987, 1988; Egelhoff and Spudich, 1991; Schleicher and Noegel, 1992). The amoebae normally feed upon microorganisms by phagocytosis during their vegetative stage, but they begin metazoan development upon starvation. Within 6 hours, rhythmic cyclic AMP secretions emanating from a few ‘pacemaker’ cells slave taxis and other cellular activities within the neighboring cell population to oscillate with an initial period of about 8 minutes (Siegert and Weijer, 1989). These directed signals also induce the chemotactic aggregation of fields of cells into a small ‘slug’, which introduces the final stages of development (MacWilliams, 1984).

To eliminate this intercellular communication, we investigated isolated only isolated, starving, preaggregative-stage (precAMP-oscillation) cells, i.e. before cAMP-signalling oscillations begin.

**MATERIALS AND METHODS**

**Cell culture**

*D. discoideum* NC-4(H) (wild type) were grown on agar with *Escherichia coli* as nutrient for 48 hours at 21°C in the dark (Vicker et al., 1984; Sussman, 1987). The cells were then washed free of bacteria by three centrifugations in potassium phosphate buffer (KK2), pH 6.4. An axenic strain (AX-2) of cells was grown in H5L medium in shaken suspension (Sussman, 1987) for two days until a population density of $1 \times 10^6$ to $2 \times 10^6$ cells/ml was reached, then harvested and washed twice in KK2 buffer before use.

**Scanning electron microscopy**

Washed NC-4 cells in KK2 were plated onto KK2-buffered agar for 16 hours at 6°C: a standard method allowing development to the early aggregative stage (Sussman, 1987). The cells were then washed and plated onto regenerated cellulose (Schleicher & Schüll, Dassel) for incubation at 21°C for 60 minutes before SEM preparation (Condeelis et al., 1987) and critical point drying.

**Digital image processing**

Growing AX-2 or NC-4 cells were harvested, washed and 1-5 cells in 2 µl KK2 were spread between a glass slide and coverslip separated by a ring of one parafilm sheet ~50 µm thick, leaving a band of air around the droplet. After about 15 minutes, images were acquired at 21°C with a CCD-500 video camera, a Zeiss Standard microscope (Oberkochen) with a ×20, 0.25 NA, F-LD phase-contrast objective, and were digitized at minimal illumination by an AT computer with coprocessor and an FG-100-AT-1024 video digitizer (Imaging Technology; Woburn, MA, USA) using a tracking program written by F. Siegert (Siegert and Weijer, 1989). A cell image analysis program (T. Killich) processed and transformed the raw, grey scale images, on a scale of 256, to binary (i.e. black and white) images by suitable processing techniques (Weiss et al., 1988; Tatsuka et al., 1989). Thus, cell centroids were determined at each 3-second time step for each image by averaging all the grey levels along the x direction and all those in the y direction of a 50x50 pixel box, which contained the cell image. Binary images were created by low-pass filtering, histogram equalization, linear and exponential scaling and threshold cut-off to transform all grey levels above a particular threshold to black (cells) and those below to white (background).

**Circular mapping**

To ‘open’ cells for circular (radial) mapping, the cell contour was followed to ascertain cell centroid-to-edge radii starting at a defined angle. Rare concave edge regions produced three, and occasionally more, radii at one angle, and were treated for analysis by subtracting the innermost cell-free space (e.g. the space between the outer edge of the main cell body and the inner edge of a curving cell process such as a pseudopod) to obtain one absolute radius at the relevant angle. This produced little or no distortion of the results.

**Actin staining**

After growth, NC-4 cells were plated upon KK2-agar for 16 hours
at 6°C until sensitivity developed to cyclic 3′,5′-AMP (cAMP). Cells were resuspended and washed twice in KK$_2$ before $2.5 \times 10^5$ cells were plated on washed glass coverslips. After 5 minutes, cAMP (Serva, Heidelberg) in KK$_2$ was quickly added to a concentration of 0.5 µM and cells were fixed for 2 hours in 3.7% formaldehyde after the times indicated. After two washings in KK$_2$, excess fluid was removed and 50 µl of 1 µg/ml phalloidin-FITC (Sigma, Diesenhof) in KK$_2$ was added for 30 minutes at 37°C (Hall et al., 1988). Cells were washed twice then mounted in KK$_2$, pH 6.0, containing 90% glycerol and 2.5% NaN$_3$ before recording on Kodak TMY-400 film using a Zeiss Standard fluorescence microscope with filter combination blue-violet H 436.

**Fig. 1.** Scanning electron microscope (SEM) views of 3 migrating *Dictyostelium* NC-4 cells upon a regenerated cellulose surface. Bar, 10 µm.

**Fig. 2.** Binary transformations of optical video images of the time-lapse sequences of 4 cells with 30 seconds between images. Time progresses from top to bottom. Bar, 10 µm.
RESULTS AND DISCUSSION

Dynamical patterns of cell shape and locomotion

At first sight, isolated Dictyostelium cells express what seems to be completely incoherent sequences of movement. Occasionally, however, intervals appear showing a nearly repetitive repertoire of form changes. In particular, cell paths often zig-zag and a pseudopodial ‘bud’ pair at one (Fig. 1A) or both poles (Fig. 1C) arises, which may be best seen in scanning electron micrographs. For locomotory analysis of these dynamical features, sequential cell video-images were subjected to binary (i.e. black and white only) transformation (Fig. 2A-D) and circular mapping (Fig. 3). Maps of polar cells demonstrate two maxima, one for each pole.

Typical cell behaviour is depicted in three representa-

Fig. 3. A typical circular map of one cell, the first image in Fig. 2A. The radial amplitude of extensions from centroid to cell edge are indicated on the ordinate, and the pericellular angles around the centroid are recorded on the abscissa, i.e. a polar-to-Cartesian transformation.

Fig. 4. (a,d) Circular maps of two AX-2 cells recorded for 1500 seconds at 3-second intervals are arranged with time ascending along the ordinate and with extensions originating at pericellular angles indicated on the abscissa. Increasing cell centroid-to-edge radii correspond to black-to-white grey levels, respectively. Cells extending one pseudopod produce two radial maxima about 180° apart, because the centroid becomes positioned between each cell pole. (b,e) 200-image excerpts (white lines) of the circular maps are depicted as stacked 2-D cell outlines viewed from one perspective. Thus, the cell outline (the peripheral ring of the cell outline from the binary image) at every time interval was laid upon the outline from the preceding interval and the whole ‘cylinder’ was turned and ‘photographed’ from a particular angle. The pseudocolours deep-to-light blue and salmon-orange tones represent increasing cell radii. (c,f) Two 100-image, circular maps produced as 3-D ‘landscapes’ in which increasing cell radii on the z axis are represented in the pseudocolours blue, green, brown, red and white. The sequence mapped in (f) lies between 600 and 900 seconds of (d) and that in (c) between 2400 and 2700 seconds of the cell described in (a), being similar to 0 to 300 seconds of this cell. Compare the original binary cell shapes in Fig. 2A and D with (c) and (f), respectively, here.
Cell shape and movement are not random

arranged by time, and they record the amplitudes, directions and durations of cell projections, particularly pseudopodia and cell ‘tails’, as ascending parallel white stripes. The cells generate intervals of both highly ordered and less-ordered patterns, lasting various times from seconds to minutes. Qualitatively similar patterns were demonstrated by more than 15 AX-2 and NC-4 cells locomoting for 25-100 minutes. No differences were detected between cell types, cells starved for 0-420 minutes, or cells in low-Ca\(^{2+}\)-containing water, which virtually inhibited locomotion, but not pseudopodial activity (van Duijn and van

Fig. 5. A diagram modelling cell shape at a given, arbitrary time step. The sine function: 
\[ q = h_m \sin(3\psi), \]
with \( h_m = 0.4 \), gives the shaded regions perpendicular to the \( x, y \) plane. A central symmetrical projection from the point ‘l’ onto the \( x, y \) plane generates the shape function \( Q \) producing a ‘cell’ outline overlayed upon the basal circle of radius \( r \). \( \psi \) is the angle between \( r \) and the \( x \) axis. See text for further explanation.

Fig. 6. The dynamics of cell shape as simulated by temporal changes in 4 ‘cell’ outlines generated by the superposition of periodic functions. In each figure, two superimposed, rotating waves generate the shape changes, reproduced on the left for consecutive time intervals, and the stacked and circular maps, middle and right, respectively. Increasing cell radii are represented by the colours blue, dark blue, green, yellow, brown, red, white and light blue. Also given are the parameters \( m \), mode number; \( a \), rate of rotation; \( t \), time and \( h \), centrifugal amplitude. \( \psi \) is the angle around the cell. Standing (stationary) wave (A-C) and travelling wave (D) patterns are depicted. The maps (A-D) correspond to cellular patterns presented in Figs 2A,4C; Figs 2B,4A (600 to 900 seconds); Fig. 2C; and Figs 2D,4F, respectively.
Haastert, 1992). Spatiotemporal, schlieren patterns of ‘honeycombs’ (lower Fig. 4A) and diagonal ‘zebra stripes’ (mid- Fig. 4D), alternating with more complex patterns, are discernible within the maps. Although both pseudopodial buds of an anterior pair become active contemporaneously; side branches arise, because extension is invariably aborted in one bud, which remains stuck in place as the cell passes it (e.g. Figs 1B, 2C). Therefore, such extensions appear to migrate around the cell (left or right on the map). Rounder, stationary cells produce an essentially horizontal pattern. The more ordered regions of these maps from 600-second excerpts may be inspected as stacked 2-D cell outlines to show periodic ‘chain link’ (Fig. 4B) or helical (Fig. 4E) patterns, respectively; 300-second segments of these two frequent patterns may be displayed as 3-D ‘landscapes’ (Fig. 4C,F). These simple patterns are interdispersed between structures of higher complexity and seem to evolve out of one another.

The significance of these more ordered segments of the 2-D patterns is particularly striking, because they present, analogous to chemical wave patterns in other systems (e.g. see Jakubith et al., 1990), the explicit, classical patterns of travelling waves (Fig. 4F), produced by continuous cell turning, and standing (stationary) waves (Fig. 4C), produced by periodically shifted movements. Therefore, these patterns indicate that the corresponding cell movements are determined (non-random) and are essentially of a wave nature.

**An analytical model of cell movement**

To cast these observations into a general or mathematical form, we formulated a basal circular or elliptical surface (depending on the basal cell form) with associated boundary conditions, and reduced the 3-D experimental problem to a circularly closed, 1-D line (Fig. 5). The 3-D cell is projected onto a 2-D surface and the ‘cell’ boundary becomes a closed line, with temporally altering geometry. This cellular problem is analogous to that of α-electroencephalograph (α-EEG) patterns, which consist of oscillations of left- and right-hand waves rotating like a sector about a disk, as characterized by maps of temporal changes in local amplitudes as a function of the corresponding angles and radii. The synergetic methods employed to analyse these maps (Fuchs et al., 1988; Bestehorn et al., 1989) were able to exploit the complete spatiotemporal information available in the system. However, by applying the qualitative synergetic arguments of these authors, we may still describe the dynamics of the geometrical changes affecting the cell periphery, although they are the only data we possess, by the temporal superimposition of very few spatial modes. Thus, rather than examining the amplitude used in the α-EEG problem, we chose vector lengths in the direction ψ (the angle around the cell) terminating on the cell edge. For rotating waves we may write:

\[ q_{rot} = h_m \sin(m \psi + a t) ; \quad m = 0, 1, 2, ..., \]  

in which \( m \) is the mode number, \( a \) the rate of rotation, \( h_m \) the centrifugal amplitude, \( t \) is time and \( \psi \) is the angle between \( r \) and the \( x \) axis; whereas oscillations in themselves may be described by the function:

\[ q_{osc} = h_m \sin(m \psi) \sin(t) ; \quad m = 0, 1, 2, ..., \]  

or by superimposition of positively and negatively rotating functions of \( q_{rot} \) with \( a^0 \) and \( a^\circ \), respectively. Both functions \( q_{rot} \) and \( q_{osc} \) may be combined to give:

\[ q = h_m \sin(m \psi + a t) \sin(t) ; \quad m = 0, 1, 2, ..., \]  

which describes oscillating waves rotating about a circle. These descriptions may be complemented with the function:

\[ Q(\psi,t) = r(\psi,t) + q(\psi,t) \]  

to produce 3-D landscape maps. \( r(\psi,t) \) is the vector length from the cell centroid to a point on the basal circle or ellipse. The superposition of \( q \)-functions, with \( m = 0, 1, 2, 3 \) and/or \( 4 \), results in a reasonable, qualitative description of the temporal changes of the cell outline given the additional derivation \( q(\psi,t) \), i.e. distance, of the actual point on the outline from the basal circle (or ellipse) of radius \( r \).

By introducing appropriate parameters into the functions, we obtained various patterns virtually identical to those typically demonstrated by *Dictyostelium*. Four oscillatory sequences depicting ‘cell’ outline shapes, cylindrical stacked outlines and 3-D maps (Fig. 6) clearly simulate the characteristic patterns of rotating waves and oscillations. The travelling waves (cf. Figs 6D to 4F, which are based on Fig. 2D) and standing (stationary) waves (cf. Figs 6A-C to 4C, which are based on Fig. 2A-C) simulated here are comparable to the patterns generated by cells. The periodically shifted movements apparent in the standing wave patterns arise because consecutive cell extensions are phase shifted, e.g. by 90°C in mode 2 (e.g. Figs 2A, 4A 0-300 seconds, 5A). Cell shapes express modes analogous to those mechanically generated in bounded vibratory systems, such as a stretched membrane: larger modes reflect smaller features. These results demonstrate that cells are intrinsically vibrating bodies, transited by self-organized, superpositioned, harmonic modes of rotating oscillatory waves (ROWS). It should be noted that in a system like a motile cell, its own edge, or boundary, is a volatile product of its own (ROWS) activity. The alternating activity of pseudopodial pairs induces *Dictyostelium* cells, like neutrophils (Nossal and Zigmond, 1976), to describe sinuous courses (M. G. Vicker, unpublished observations). Cell adhesion and the anterior microtubule organizing center (Rubino et al., 1984) might influence these wave dynamics and, thus, cell shape and trajectories. In biological reality, both the rate of wave rotation \( a \) and the wave amplitude \( h_m \) are functions of \( t \), \( a = a(t) \) and \( h_m = h_m(t) \), rather than constants (Plath et al., unpublished data). These concepts are currently being applied to the analysis of actual cell movements and to the extraction of these parameters from them. Nevertheless, the simplifying mathematical description developed here depicts in synergetic terms the essential elements of cell shape and movement.

**Actin response to cyclic AMP**

Pseudopodial activity is an expression of actin polymerization (McRobbie and Newell, 1984; Rubino et al., 1984; Yumura et al., 1984; Newell, 1986; Hall et al., 1988; Condeelis et al., 1988), which is stimulated by chemotactic cAMP-pulse signals in aggregation-stage cells to produce a characteristic quadriphasic, adaptive reaction. Significantly, this reaction is specific to the temporal signal, being
Cell shape and movement are not random absent in static cAMP spatial gradients and isotropic concentrations. Within 10 seconds after a cAMP pulse, the intensity of F-actin staining increases dramatically and is redistributed as a nearly homogeneous, pericellular ring (sphere), pseudopodia wither and cells round (Fig. 7). By 20 seconds, staining decreases to a minimum, but transiently reappears within 1-2 minutes; these events have been confirmed by quantitative fluorimetry (data not shown and McRobbie and Newell, 1984; Hall et al., 1988).

Thus, the first 20 seconds of the response to cAMP extinguishes ROWS, and cell projections, by inducing actin polymerization as a uniform, subcortical ring (sphere). This appears to constitute a phase resetting (Winfree, 1990) of ROWS, whereby all modes and their inter-relationships become reduced to mode 0, i.e. to a fundamental, feature-less structure. This event may be required for chemotaxis, because it offers an explanation of how an oriented temporal signal might induce a fairly accurately oriented pseudopodal projection. This point might seem curious, because although the chemotactic signal traverses the entire cell within a short, finite time (Vicker, unpublished; Vicker et al., 1984), with undiminished intensity, it nevertheless selectively elicits pseudopodia in only one direction (Swanson and Taylor, 1982). ROWS presumably originate in physicochemical reactions associated with actin polymerization and, therefore, it seems likely that they might reorganize pseudopodia first at the initial site of cAMP temporal signal impact and phase resetting. This point requires investigation, because it suggests that the dominance of this first post-signal pseudopod depends alone on its superior competition for G-actin, which becomes increasingly available as F-actin decay proceeds at all other points around the cell (Fig. 8). This proximal F-actin accumulation would tend to accelerate the decrease in the G-actin concentration at distal regions of the cell. The possible contributions of actin, cell surface tension and morphogenetic instability to cell shape have been theoretically considered (Alt, 1990; Lewis and Murray, 1992). It is possible to speculate that wave activity depends on the dynamic spatial distribution of factors associated with actin polymerization, e.g. nucleation site, G-actin and/or Ca$^{2+}$ concentration. Actin self-organization may alone determine the spatial modes of the cell. The accumulations of polymerizing actin that induce local pseudopod development will result in a depletion of the actin monomer (G-actin) concentration elsewhere within the cell. The rate by which G-actin becomes newly available for other competing sites of actin polymerization and pseudopod formation depends on the conditional (local) stoichiometry of F-actin disassembly. Spatiotemporal oscillations and waves of polymerization and pseudopod formation may rest on this feedback system.

Oscillatory waves in cell behaviour and morphogenesis

Our results indicate the non-random, determined nature of G-F-actin/pseudopodial activity, cell shape dynamics and locomotion and may provide a basis for their comprehensive analysis. Actin’s evolutionarily conserved function due to intracellular signals from the plasma membrane. The G- to F-actin evolution would reverse in the absence of G-actin, and also in the original direction of polymerization. However, the second phase of polymerization would be restricted to the proximal site of signal impact due to G-actin diffusion, and F-actin’s intrinsic autocatalytic properties and competition for G-actin. This local, transient wave would generate an oriented pseudopod. The time after signal passage is indicated under the cell. The dots indicate G-actin (monomer); and the mesh F-actin in the cortex and developing pseudopod. Between 25 and 30 seconds the figure is meant to show a G-actin gradient developing across the cell.
implies that ROWS are not restricted to *Dictyostelium*, but might be a fundamental determinant of cellular activity, e.g. in white blood cell oscillations (Haston and Shields, 1984; Murray et al., 1992). We interpret the actin ‘rings’ that appear at a few ‘corners’ of freshly stimulated fibroblasts (Hedberg et al., 1993, e.g. Figs 1i, 4b) as dorsoventrally flattened, expanding spherical wave fronts of actin polymerization and depolymerization. These waves appear to become locally extinguished upon collision with other rings or the cell boundary. Such properties are common to chemical waves (Jakubith et al., 1990). Several morphological and pathological examples of cell locomotion, such as contractions at wounds and gastrulation, are heralded by intense pulsatile motion of hitherto quiescent cells (e.g. see Lash, 1955; Kinnander and Gustafson, 1960). It is possible that these movements are determined by ROWS. Similarly, ROWS might be involved in temporal signal perception (like that in chemotaxis), which appears responsible for the many prominent oscillatory features especially during early morphogenesis (Vicker, 1993, and unpublished). At least some of these movements may have a chemotactic basis. During particular phases of chemotaxis, the amplitudes of some cellular properties, such as intercellular adhesion, are also regulated by the oscillatory signal. Yet, cells might also be able to communicate with their neighbours by a ROWS-based mechanism directly, as is possibly shown by: (a) the ability of cells to transmit mechanical stresses through their cytoskeleton (Wang et al., 1993); and (b) the chain reaction of induced surface projections (‘nudging’), which occurs in vitro and presumably also as part of epiboly in *Fundulus* embryos (Tickle and Trinkaus, 1976). We note with interest that the cylindrical map structures generated by ROWS are often reminiscent of the lateral periodic differentiation in regenerating or apically growing systems, such as leaf positions in plants. The standing wave patterns in the examples presented here demonstrate periods varying from <1 minute to several minutes, which are thus much shorter than those characterizing the cAMP oscillator in these cells (Siegert and Weijer, 1989). In addition to the variability of frequencies, intervals of relatively ordered patterns are interrupted by intervals of cell rounding or highly complex patterns, and the order of subsequent intervals is not readily evident. Such behaviour is unlikely to be due to either a simple oscillator or a random process and, therefore, escapes meaningful interpretation by methods such as Fourier analysis. One possible explanation of this behaviour may be apparent, i.e. because of its similarity to deterministic chaos. At present, we are using the wave model to extract and analyse the parameters of wave speed and mode number in moving cells. Future work will involve investigations of the signal field effects, elaboration of the time dependence of the model’s coefficients, and determination of the Ljapunov exponents and the dimensions of the underlying processes.

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