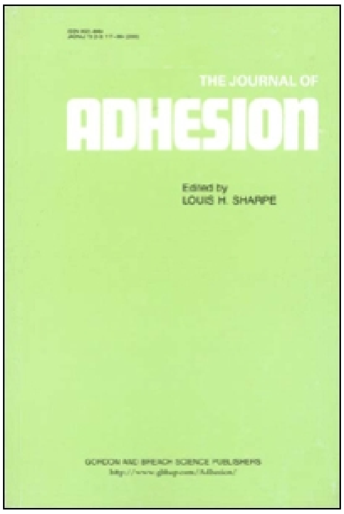

The Journal of Adhesion

Publication details, including instructions for authors and subscription information:
http://www.informaworld.com/smpp/title~content=t713453635

Capillary Driven Motion: The „Crawling“ Drop and a Possible Link with Phagocytosis

Martin E. R. Shanahan[a]
[a] Centre National de la Recherche Scientifique, Ecole Nationale Supérieure des Mines de Paris, EVRY, Cédex, France

To cite this Article Shanahan, Martin E. R.(1995) 'Capillary Driven Motion: The „Crawling“ Drop and a Possible Link with Phagocytosis', The Journal of Adhesion, 54: 1, 67 — 77
To link to this Article: DOI: 10.1080/00218469508014382
URL: http://dx.doi.org/10.1080/00218469508014382

J. Adhesion, 1995, Vol. 54, pp. 67–77
Reprints available directly from the publisher
Photocopying permitted by license only

Capillary Driven Motion: The "Crawling" Drop and a Possible Link with Phagocytosis*

MARTIN E. R. SHANAHAN

Centre National de la Recherche Scientifique, Ecole Nationale Supérieure des Mines de Paris, Centre des Matériaux P.M. Fourt, B.P. 87, 91003 EVRY Cédex, France

(Received April 19, 1994; in final form August 10, 1994)

A sessile drop at equilibrium on an ideal solid surface satisfies both Laplace's equation for the meniscus shape and Young's equation along the triple line. If, however, a single, small, energetic heterogeneity exists near the triple line, although meniscus equilibrium is assured, Young's equation is unsatisfied and a net force acts on the drop, causing it to "crawl" in order to engulf the inhomogeneity (of higher surface free energy). A dynamic energy balance between excess capillary energy and viscous dissipation governs the crawling motion. Similarities with phagocytosis are apparent, although the latter process generally occurs in a liquid medium without the presence of a solid substrate. The behaviour of a drop is, therefore, extended to that of a model cell suspended in a liquid medium. Although very much simplified, the system is modelled as an essentially spherical cell possessing a pseudopodium in contact with a small, spherical contaminant. By analogy with the crawling drop, a dynamic balance between excess interfacial free energy and viscous dissipation is established to estimate the time of engulfment, or phagocytosis, of the contaminant.

KEY WORDS Capillary motion; cell; crawling drop; engulfment; phagocytosis; surface tension.

INTRODUCTION

Classic treatments of sessile (or pendant) drops tend to consider the behaviour of perfectly axially symmetric systems (*e.g.* Refs. 1 and 2). Although, in the absence of gravity or other external force fields, the form of such drops is a spherical surface, inclusion of gravity leads to intractable mathematics even when axisymmetry is assumed. In everyday practice, the situation is, of course, more complicated. It is common knowledge that perfectly axisymmetric sessile drops are rarely encountered (unless experimental precautions are taken). For axial symmetry, the boundary condition of Young's equation[3] giving rise to a unique value of the equilibrium contact angle, θ_0, everywhere on the drop periphery is implicit. However, if contact angle is variable along the triple line for any of a number of reasons (presence of impurities, rugosity, local chemical heterogeneity, etc.), then meniscus shape will generally be complex and numerical methods[4] give the best hope for solving the corresponding

---

*One of a Collection of papers honoring James P. Wightman, who received the 13th Adhesive and Sealant Council Award at the ASC's 1993 Fall Convention in St. Louis, Missouri, USA, in October 1993.

Laplace equation.[5] Nevertheless, it is possible to restrict the complexity of the problem. By assuming negligible effects due to gravity (small drops) and taking variability of the (small) peripheral contact angle to be due to weak, local perturbations, ε, to the average surface free energy of the solid, γ_{SV}, it is possible to obtain an analytic description of meniscus shape.[6] Although these perturbations are weak compared with the surface free energy of the liquid, $\gamma(|\varepsilon|/\gamma \ll 1)$, their distribution over the solid surface may be quite random. An interesting consequence of the analysis is that although Laplace's equation is satisfied on the meniscus, unless the field of heterogeneities, ε, is equilibrated, there remains a capillary imbalance and, thus, a net force acting on the drop at the triple line. The drop is not at equilibrium, despite meniscus stability, and the drop may "crawl" as a result.[7] An anology may be drawn with the phenomenon of phagocytosis of contaminants by a biological cell.[8] Nevertheless, a solid substrate is implicated in the process described, whereas an actual defence cell is more likely to be surrounded by a liquid medium, such as blood. In this article, we shall first briefly reconsider the special case of crawling of a sessile drop on an otherwise homogeneous solid surface presenting a single heterogeneity near the triple line. Following this, we shall attempt to extend the basic concepts to a "3-dimensional" model corresponding to a gross simplification of a phagocytic cell. The second part is very tentative and it is realised that many probably unrealistic assumptions about cell biology are made (necessarily, at this stage) but it is hoped that this naïve approach may inspire a few reflections as to some possible roles played by capillarity in biology.

A "CRAWLING" SESSILE DROP

We consider a small sessile drop of intrinsic radius of curvature, R, contact radius, r_0, and (small) contact angle, θ_0, on an essentially flat, smooth and homogeneous solid of surface free energy, γ_{SV} (see Fig. 1). Polar coordinates (r, ϕ) with the centre of the (unperturbed) contact circle as origin are adopted and the height of the meniscus above the solid surface is given by $h(r, \phi)$. The initially axisymmetric drop is perturbed by the presence of a small heterogeneity near its periphery, of surface free energy $(\gamma_{SV} + \varepsilon_0)$ and angular extent $\phi = \pm\chi$. This leads to a small protuberance, or "spur", being formed on the triple line, with corresponding modification to the meniscus shape. The actual form may be evaluated by minimisation of the free energy of the system and simplification using perturbation theory.[6] The reader is referred to

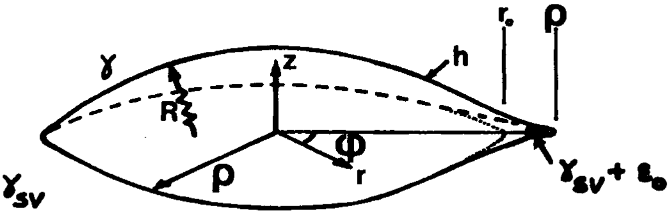

FIGURE 1 Sessile drop perturbed by surface heterogeneity, ε_0, near periphery and coordinate system.

the earlier article for explicit details, which are too lengthy to be presented here. Although a general distribution of surface heterogeneities may be treated, we are presently interested in the case of a unique inhomogeneity. Under these conditions, it may be shown that the actual shape of the triple line, $\rho(\phi)$, is given by:[6]

$$\rho(\phi) \sim r_0\left[1+\frac{\varepsilon_0}{\pi\gamma\theta_0^2}\left(-\chi+2\sum_{n=2}^{\infty}\frac{\sin n\chi}{n(n-1)}\cos n\phi\right)\right]. \tag{1}$$

We may define a reduction in contact angle, $\Delta\theta(\phi)$, occurring as a result of the presence of the localised heterogeneity such that $\cos\theta(\phi)=\cos(\theta_0-\Delta\theta(\phi))$ and in the present case, it may be shown that:[6]

$$\Delta\theta(\phi) \sim \frac{1}{\gamma\theta_0}(\varepsilon(r_0,\phi)-2\varepsilon_0\chi\pi^{-1}\cos\phi), \tag{2}$$

where $\varepsilon(r_0,\phi)=\varepsilon_0$ for $|\phi|<\chi$ and $\varepsilon(r_0,\phi)=0$ elsewhere. The term in cos ϕ is a reflection of the fact that the drop is not in equilibrium with respect to the solid surface, although Laplace's equation for the meniscus is satisfied. The series representation of the form of the triple line, given by equation (1), is somewhat cumbersome. However, allowing for the fact that both ε_0 and χ are to be considered small, we may let $r_0 \to \infty$ mathematically and using a trigonometric identity for the cosine series, a much simpler form may be found. Defining δ as the deformation to the triple line, $\delta=\rho-r_0$, and letting x represent distance from the centre of the heterogeneity parallel to the undisturbed triple line, it may be shown that:[9]

$$\delta(x) \sim \frac{f}{\pi\gamma\theta_0^2}\left(-\tfrac{1}{2}+\ln\frac{r_0}{|x|}\right) \sim \frac{f}{\pi\gamma\theta_0^2}\ln\frac{r_0}{|x|}, \tag{3}$$

where f corresponds to the effective force exerted by ε_0 radially away from the centre of the drop. Although some fine detail has been lost in equation (3) (indeed it is only valid for $|x|\gtrsim r_0\chi$), it is much simpler than equation (1) and corresponds to a form previously found directly for the deformation to an initially straight triple line[10] and later confirmed experimentally.[11]

Using a similar procedure, the length of the spur, $\delta(0)$, may also be obtained:[9]

$$\delta(0) \sim \frac{f}{\pi\gamma\theta_0^2}\left(\tfrac{1}{2}+\ln\frac{2r_0}{w}\right) \sim \frac{f}{\pi\gamma\theta_0^2}\ln\frac{2r_0}{w}, \tag{4}$$

where $w \sim 2r_0\chi$(the width of the inhomogeneity).

Although the meniscus is at equilibrium, there is a force, f, acting on the drop as a whole. This force, although of no consequence for an "infinite" drop, *i.e.*, when the triple line is strictly straight and corresponds to the limit of a very large mass of liquid, will lead to motion in the case of a finite drop. Its value is a function of spur length and can be found either directly from equation (4):

$$f \sim \pi\gamma\theta_0^2 l^{-1}\delta(0), \tag{5}$$

where $l=\ln(2r_0/w)$, or by making use of equation (2). (The second term in brackets of equation (2) amounts to a modulation and leads to a capillary imbalance. By integrating the unbalanced Young equation around the drop periphery, the net force may be obtained. Reference 7 gives more explicit details.)

Henceforth we may define $f(t)$ and $\delta(t)$, respectively, as the force acting on the drop and the length of the spur, *i.e.* $\delta(0)$ in equations (4) and (5), both now taken as a function of time. Force $f(t)$ causes drop motion and in so doing, work $f(t)\ U$ (per unit time) is expended where U is overall drop speed (*i.e.* speed of the centre of gravity of the essentially spherical drop parallel to the solid surface in the direction of the perturbation). This work is dissipated by viscous resistance in the liquid. Two simplifying assumptions are adopted in the calculation of this dissipation. Firstly, since the intrinsic contact angle, θ_0, is taken to be small, we use the lubrication approximation for the shear movement within the liquid.[12] This amounts to ignoring any components of liquid velocity normal to the solid surface. Boundary conditions of no liquid slip at the solid surface and no tangential stress at the liquid/vapour interface are used. Secondly, the intrinsic contact angle and the basic spherical cap shape are assumed not to change during lateral motion, or "crawling". The velocity profile may then be written as:

$$u(z) \sim \frac{3U}{2h^2}(2hz - z^2), \tag{6}$$

where, we recall, h is the height of the meniscus above the solid, and z is normal distance from the plane of the solid. Height, h, is given by:

$$h \sim \frac{1}{2R}(r_0^2 - x^2 - y^2), \tag{7}$$

where x and y are distances from the drop centre in the plane of the solid, respectively perpendicular to, and parallel to, the direction of drop motion (see Fig. 2). The situation is more complex than that for radial flow[12] and dissipation will arise from both velocity gradients $(\partial u/\partial z)$ and $(\partial u/\partial x)$. (Only the former term is present in radial flow.) Employing equations (6) and (7), it may be shown that the viscous

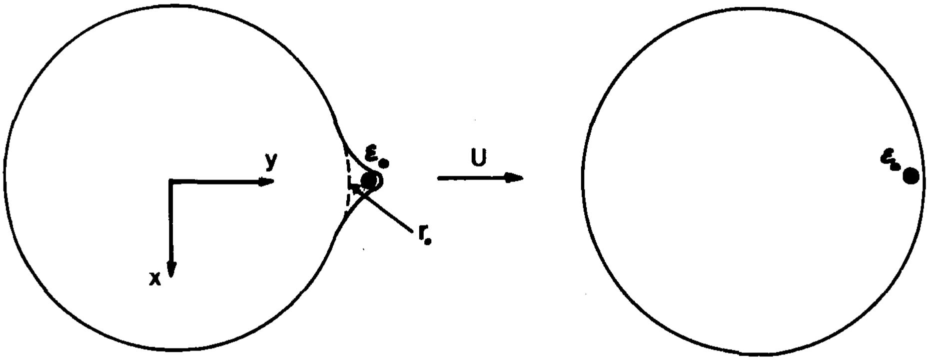

FIGURE 2 Plan view of drop with surface heterogeneity, ε_0, near periphery causing triple line deformation and after motion to engulf the heterogeneity.

dissipation (per second), $T\dot{S}$, in the drop of volume, V, is given by:

$$T\dot{S} \sim \eta \int_V \left[\left(\frac{\partial u}{\partial z}\right)^2 + \left(\frac{\partial u}{\partial x}\right)^2\right] dV \sim 3\pi\eta U^2 r_0 L\left(\frac{2}{\theta_0}+\frac{\theta_0}{10}\right), \tag{8}$$

where η is viscosity and $L \sim \ln(r_0\theta_0^2/b)$, b being a molecular distance. L represents a cut-off to the simplified flow field adopted.[13] We note that the dissipation due to gradient $(\partial u/\partial z)$ is inversely proportional to θ_0, due to thinning of the liquid bulk, whereas the second term is directly proportional to contact angle, reflecting its resulting from variability in drop height.

We may equate relation (8) to $f(t)$ U, using equation (5). This represents a dynamic energy balance. Realising that the speed of the drop as a whole, U, is equivalent to the rate of disappearance of the spur, $(-d\delta(t)/dt)$, we obtain the following differential equation:

$$\frac{-d\delta(t)}{dt} = \gamma\theta_0^2\,\delta(t)\Big/\left[3\eta r_0 Ll\left(\frac{2}{\theta_0}+\frac{\theta_0}{10}\right)\right], \tag{9}$$

whose solution is:

$$\delta(t) = \delta(0)\exp(-t/\tau), \tag{10}$$

where the time constant is given by:

$$\tau = \frac{3\eta r_0 Ll}{\gamma\theta_0^2}\left(\frac{2}{\theta_0}+\frac{\theta_0}{10}\right). \tag{11}$$

We can thus see that the drop "crawls" to its equilibrium position at an exponentially-decreasing speed. Final equilibrium is obtained when the heterogeneity has been engulfed by the drop and Young's equation is satisifed everywhere on the triple line. This capillary-driven motion can be pictured as a form of phagocytosis. In practical, everyday conditions, the behaviour described above may be observed in the sporadic motion of a small rain drop rolling down a window pane. Although the overall tendency is gravity controlled in this case, small changes in speed and direction are caused by local heterogeneities such as spots of grease or dirt.

SIMPLE MODEL OF "CELL"

The apparent analogy between capillary-driven motion as described above and phagocytosis has been deemed worthy of further investigation. Clearly the structure of a biological cell is exceedingly complex and its operation is poorly understood. However, we shall assume, in the case of a phagocytic cell, that at least part of its capturing mechanism depends on capillary phenomena. In our much-simplified model, we take the cell to be a membrane (spherical at equilibrium, if such a state can exist) which contains a liquid, the system being in suspension in a second liquid (probably less viscous). Typically, cell dimensions will be of the order of a few microns. The behaviour of the membrane in contact with a contaminant will be complex, but it would seem that it can break when needed, in order to engulf a foreign body, and then reconstitute itself.[14] (We are not aware of the time scale of this process, and it may be that this corresponds to the rate-determining step in biological phagocytosis.) Despite oversimplification of the process, this behaviour leads us to assimilate the membrane to a liquid meniscus. However, whilst a liquid has a simple surface tension, γ, the equivalent parameter for the cellular membrane is a "composite" tension, $\Gamma = \gamma_1 + \gamma_2 + T$, where γ_1 and γ_2 represent the two interfacial tensions between the membrane and its contents and the membrane and the exterior and T is a potential mechanical tension in the cell wall, if such exists.[15] It is quite plausible that T may be varied in reality by chemical means but, for present purposes, we shall consider Γ to be constant.

The "contaminant" to be phagocytized will be modelled by a small sphere of radius a. Viruses have typical dimensions in the range 0.02–0.25 μm and it is thus reasonable to take the "phagocyte" to be much larger than its "prey".

In the following, we shall treat the system as though initial contact between the cell and the contaminant has already been established. Indeed the mechanism(s) by which a phagocyte searches out its prey would seem to be exceedingly complex, and probably involve(s) following a sort of "chemical trail".[16] Chemical receptors are involved and the cell wall must have a propensity for forming pseudopodia, or protrusions.[17] Despite these complications, we shall consider the system from a naïve point of view. We take the cell to remain essentially spherical, of radius R, with a small pseudopodium, or protuberance, of length s, extending to engulf the contaminant at its extremity (see Fig. 3). The distance separating the centres of the spheres (cell and prey) is equal to $R + s$($N.B.$ $R \gg a$). We shall ignore the time necessary for the membrane to break and recombine around the contaminant although, as stated above, this may correspond to the rate-determining step in reality. Our starting point is that shown schematically in Figure 3.

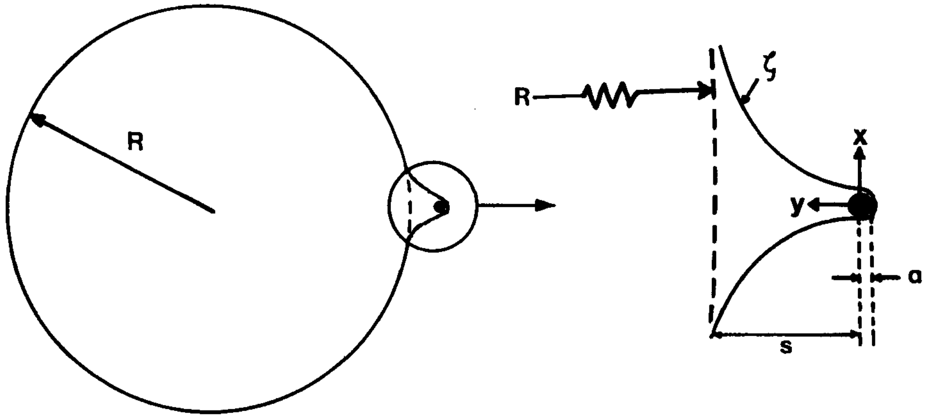

FIGURE 3 Simple model of essentially spherical phagocytic cell with pseudopodium contacting small contaminant.

ATTRACTION OF THE CONTAMINANT

With the scenario described above, the pseudopodium being small compared with the cell, Laplace pressure effects will be weak and, in this state of quasi-equilibrium, the form of the local meniscus will be essentially that of the surface of revolution of a catenary:

$$\zeta \sim a\cosh\left(\frac{y}{a}\right);\ 0 \lesssim y \lesssim s, \tag{12}$$

with y denoted as in Figure 3.

The excess of free energy of the pseudopodium with respect to the situation where the small sphere of radius, a, is completely "ingested" by the phagocyte (again spherical with no protrusion) is given by:

$$E \sim \pi\Gamma\left\{2\int_0^s \zeta\left(1+\zeta'^2\right)^{1/2} dy - \zeta^2(s)\right\}$$

$$\sim \frac{\pi\Gamma a^2}{2}\left[\frac{2s}{a} - 1 - e^{-2s/a}\right], \tag{13}$$

where ζ' represents $d\zeta/dy$.

As the sphere is attracted towards the bulk cell, distance, s, diminishes and excess free energy is released at a rate given by:

$$\frac{dE}{dt} \sim -\pi\Gamma a(1+e^{-2s/a})v, \tag{14}$$

where v is the speed of approach ($v = -ds/dt$).

This motion will create a flow field within the liquid inside the pseudopodium (and outside, but this effect is neglected since overall shear will be less and viscosity is assumed to be smaller). We consider that the liquid within the cell is incompressible, to a first approximation. As a result, the liquid immediately ahead of the moving contaminant will be swept aside towards the local cell wall. In addition, as the membrane retracts towards the cell's main body, it will tend to take liquid with it, assuming negligible interfacial slippage. The system may be viewed schematically rather as a table tennis ball balanced on the top of a fountain. We, therefore, model the behaviour approximately as Poiseuille flow, $u(x)$ (parabolic). With boundary conditions of $u(0)=0$ and $u(\zeta)=v.\cos\,[\tan^{-1}\,d\zeta/dy]$ and using the fact that the average speed of the liquid towards the cell is v, we obtain the velocity profile:

$$u(x) \sim \frac{12}{\zeta^2}\left[\frac{u(\zeta)}{3} - \frac{v}{2}\right].[x^2 - \zeta x] + \frac{u(\zeta)x}{\zeta}, \tag{15}$$

where $u(\zeta) = v/\cosh(y/a)$ (see Fig. 4). Viscous dissipation is then given by:

$$\dot{D} \sim 2\pi\eta\int_0^\zeta\int_0^s\left(\frac{\partial u}{\partial x}\right)^2 x\,dx\,dy \sim 12\pi\eta v^2 s, \tag{16}$$

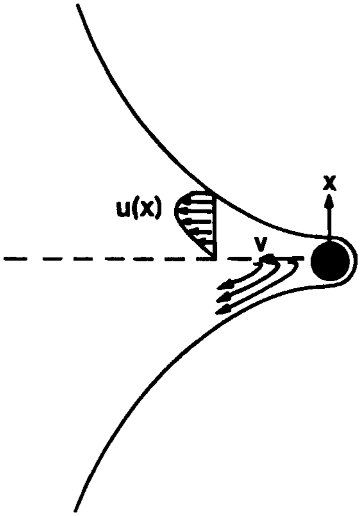

FIGURE 4 Assumed Poiseuille (parabolic) flow field during attraction of spherical contaminant towards main cell.

where, as before, η is liquid viscosity. Dynamic equilibrium corresponds to:

$$\frac{dE}{dt}+\dot{D}\sim 0, \tag{17}$$

and using relations (14) and (16), we obtain:

$$s\sim\left(s_0^2-\frac{av^*t}{6}\right)^{1/2}, \tag{18}$$

where s_0 is pseudopodium length at the outset, *i.e.* for $t=0$, and v^* is a characteristic speed given by Γ/η. The speed of approach increases as s decreases.

FINAL "INGESTION" OF THE CONTAMINANT

Equation (18) will be approximately valid until $s\sim 2a$ and then a somewhat complex transition will occur before the final stage shown schematically in Figure 5. Towards the end of the "ingestion" process, the small spherical contaminant will be partially inside the bulk cell but a bump will still be present on the membrane. Distance s is now negative. Ignoring the thickness of the membrane, the excess free energy, E, due to distorsion, and playing the role of "motor" for final engulfment of the particle, is given by:

$$E\sim\Gamma(A-S)\sim\pi\Gamma a^2(2-2\cos\alpha-\sin^2\alpha), \tag{19}$$

where A and S are, respectively, the surface area of the bump in the cell wall and the equivalent area without the perturbation, and α is the angle shown in Figure 5. Using the fact that $s=\sim-a\cos\alpha$, we obtain the rate of free energy loss as

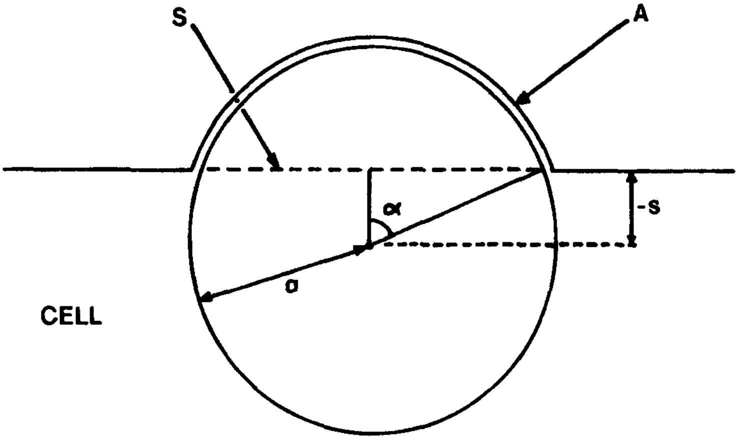

FIGURE 5 Final part of absorption of spherical contaminant into main cell.

(*cf.* equation (14)):

$$\frac{dE}{dt} \sim -2\pi\Gamma(a+s)v. \tag{20}$$

(Clearly, in this regime, we may not neglect a compared with s.)

Given that more than half of the small sphere is now inside the cell, we assume that viscous drag, F, may be described by (modified) Stoke's law:

$$F = N\pi\eta a v, \tag{21}$$

where N would be equal to 6 if the particle were entirely surrounded by liquid, but is probably greater in these conditions. The dynamic energy balance becomes (*cf.* equation (17)):

$$\frac{dE}{dt} + Fv \sim 0. \tag{22}$$

Using equations (20) and (21), we obtain:

$$s \sim -a\left\{1 - \exp\left[-\frac{2v^*}{Na}(t-t')\right]\right\}, \tag{23}$$

where t' represents the time at which $s = 0$. Finally, the contaminant becomes entirely engulfed by the phagocyte, this last step being represented by a classic law of exponential decay (*cf.* equation (10)). The final state, in this simple model, is the cell having regained its spherical shape, but with a (slightly) increased radius. The particle is completely inside and the process of "digestion" can commence.

DISCUSSION AND CONCLUSION

Although the initial treatment of "crawling" of a sessile drop should be close to real behaviour, the extension to phagocytic behaviour involves enormous simplifications and clearly considerable work would be required to refine the description. Nevertheless, a basis to a possibly important mechanism involved in cell behaviour has been proposed. Whilst admitting that our model is almost certainly far from reality, let us make a few comments on it. From equations (18) and (23) we can see that ingestion speed is directly related to the ratio $\Gamma/\eta(=v^*)$, where $\Gamma = \gamma_1 + \gamma_2 + T$. Now, we have no data available concerning phagocytes, but those obtained by Evans[18] for erythrocytes (red blood cells) suggest that the interfacial tensions, γ_1 and γ_2, would be very small, of the order of $10^{-6}\,\mathrm{Nm}^{-1}$, whilst the intrinsic tension, T, of the *deformed* membrane (not at equilbrium) could, in certain cases, reach 5 to $10 \times 10^{-3}\,\mathrm{Nm}^{-1}$. Similarly, we have no data concerning the average viscosity of the components within the cells, but if we assume a value of 10^{-2} Pas, we obtain a value of v^* of the order of $10^{-4}\,\mathrm{ms}^{-1}$ for $T = 0$ and $10^{-1}\,\mathrm{ms}^{-1}$ with $T = 10^{-3}\,\mathrm{Nm}^{-1}$. For an initial separation distance between the cell and the particle, s_0, of 100 nm and a radius, a, of 20 nm, the approach time will be of the order of 10^{-1}s for $T = 0$ and 10^{-4}s with $T = 10^{-3}\,\mathrm{Nm}^{-1}$. Very probably, T may be controlled chemically and, as a consequence, the cell may "adjust" the speed of attraction according to its needs. With the values adopted above and taking a value of 10 for N, the time constant in equation (23) ($= \mathrm{Na}/2v^*$) is of the order of 10^{-3}s without T and 10^{-6}s with T. (Comparing with drop crawling (equation (10)), we take $\gamma \sim 3 \times 10^{-2}\,\mathrm{Nm}^{-1}$, $\theta_0 \sim 0.1$ rad, $r_0 \sim 1$ mm, $w \sim 10\,\mu\mathrm{m}$, $L \sim 8$ and the same viscosity, and find a time constant, τ, of *ca.* 90 s.) These values are very small, but then the overall scale is microscopic. Not only is the scale reduced but, in the case of the crawling drop, the entire liquid mass, or "cell", moves with respect to the solid, whereas, in the present case, it is only the pseudopodium which retracts, leaving the bulk cell essentially immobile.

These orders of magnitude are probably debatable. Apart from a lack of confirmed data concerning viscosity and surface properties, we have not taken into account the true mechanical nature of the membrane. Amongst other complications in the real, biological situation, it is quite likely that the cell wall will be at least to some extent viscoelastic, in which case the relaxation time (s) of the membrane would also be implicated in this complex problem (and could indeed govern the overall time of attraction). Nevertheless, for all its simplicity, we hope that this approach to phagocytosis may inspire biophysicists and biochemists to consider possible roles of capillary-driven motion in cell behaviour.

At a far more modest level, the model presented could be modified in order to explain the retraction of "isthmuses" of liquid after the separation of pendant drops (*e.g.* dripping taps or wet paint dripping from a ceiling!).

References

1. J. F. Padday, *Philos. Trans. R. Soc. London, Ser. A*, **269**, 265 (1971).
2. S. Hartland and R. W. Hartley, *Axisymmetric Fluid-Liquid Interfaces* (Elsevier, Amsterdam, 1976).
3. T. Young, *Phil. Trans. R. Soc. London*, **95**, 65 (1805).

4. R. A. Brown, F. M. Orr and L. E. Scriven, *J. Colloid Interface Sci.*, **73**, 76 (1980).
5. P. S. Laplace, *Mécanique Céleste, Suppl. au X livre* (Coureier, Paris, 1805).
6. M. E. R. Shanahan, *J. Phys. D: Appl. Phys.*, **22**, 1128 (1989).
7. M. E. R. Shanahan, *J. Phys. D: Appl. Phys.*, **23**, 321 (1990).
8. G. Kaplan, *Scand. J. Immunol.*, **6**, 797 (1977).
9. M. E. R. Shanahan, *J. Phys. D: Appl. Phys.*, **23**, 703 (1990).
10. J. F. Joanny and P. G. de Gennes, *J. Chem. Phys.*, **81**, 552 (1984).
11. G. D. Nadkarni and S. Garoff, *Europhys. Letters*, **20**, 523 (1992).
12. P. G. de Gennes, *Rev. Mod. Phys.*, **57**, 827 (1985).
13. P. G. de Gennes, X. Hua, P. Levinson, *J. Fluid Mech.*, **212**, 55 (1990).
14. E. D. Korn and R. A. Weisman, *J. Cell. Biol.*, **34**, 219 (1967).
15. M. E. R. Shanahan, *J. Adhesion*, **18**, 247 (1985).
16. G. D. F. Jackson, Private communication (1994).
17. C. J. van Oss, R. J. Good and A. W. Neumann, *Electroanal. Chem. Interfac. Electrochem.*, **37**, 387 (1972).
18. E. Evans, *Biophys. J.*, **30**, 265 (1980).