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### Countercurrent Streaming in Liquid Surfaces and Its Relevance to Protoplasmic Movements

**Abstract.** Movements of surface films counter to the interior stream are brought about by film pressure generated by surface tension gradients. In a similar process, the formation of new interfaces during protoplasmic syntheses could sustain gradients of interfacial tension with resulting protoplasmic movements.

Biologists are familiar with movements of contiguous protoplasmic constituents in opposite directions (1). Some simple but fascinating hydrodynamic systems that produce similar effects and may have a general bearing on protoplasmic movements are presented in this report.

If a propulsive mechanism is assumed at some region along the longitudinal axis of a closed, fluid-filled system, a flow pattern like that depicted in Fig. 1(a) follows from the continuity equation. Similar flow patterns, "fountain streaming," have been observed in amebas (2). Such patterns of flow can also occur in essentially open systems. The surface forces that are responsible can produce an amazing diversity of phenomena but have received little recent notice in connection with biological problems.

Working models are produced by allowing a stream of water from a nozzle to flow down an inclined plane into a vessel. As long as the stream flows without obstruction and runs off the bottom edge of the plane, the flow remains essentially unidirectional (Fig. 1, b). However, when fluid accumulates in a pool at the edge, or when the stream emerges directly into the water

in the vessel, separation of flow and backflow of the peripheral surfaces occurs. A countercurrent circulation with sharp boundaries of flow separation is initiated (Fig. 1, c). Peripheral surface film is transferred centrally by convergence at the upper boundaries of the vortices. Central surface film either reenters the peripheral streams at the region of emergence over the static body of water, or returns after traveling out over the water. A large portion of the surface can become involved in the circulation.

These surface movements are readily visualized with powdered charcoal. Particles at the surface are seen to flow in opposite directions along adjacent paths, as indicated in rough schematic outline in Fig. 1 (c, d, e, f, g). If an outer loop (or a network) is created at the periphery, surface film travels out into the loop and rejoins the main circulation upstream (Fig. 1, f). But the loop stream itself travels in the opposite direction and joins the mainstream downstream. When particulate matter moving downstream in the interior is viewed through the countermoving surface film, also carrying particulate matter, particles moving in opposite directions seem to be threading their way between one another. The same impression is gained on microscopic examination of countermoving particulate matter in protoplasm, where depth of focus permits simultaneous viewing of particles both at and between interfaces.

If a stream is confined between two plates, the vortical circulations are limited to the menisci but are greatly

accentuated. Even at relatively high flow rates, countermoving peripheral surface film travels from distant regions to the nozzle. Surface particles transfer to the interior at points where the meniscal film is broken. Sometimes they become trapped between the counterflowing surface films, where they spin like tops.

These effects occur over a wide range of flow rates and also take place on horizontal surfaces. A leisurely countercurrent streaming has been set up in a narrow, almost horizontal, stream 15 inches long; convergence of peripheral surface film into the mainstream tends to occur in regions where an appreciable velocity gradient is created by narrowing of the stream, or obstructions cause the peripheral flow to deviate centrally.

These phenomena do not depend on the presence of particulate matter or gas-liquid interfaces. Vortical surface circulations occur to some degree even in double glass-distilled water, on the surface of which camphor will "dance" actively; bits of dust reveal the existence of the circulations. Patterns of movement in water are influenced by rate of flow, extent of the wetted area, obstructions (Fig. 1, f), and other factors. The lower the surface tension and slower the flow, the greater the distance over which countercurrent streaming occurs.

It seems clear that the forces responsible for counter movement of surface film in these systems are transmitted longitudinally within the film. Since this cannot take place in the surface of pure water (3), the phenomenon

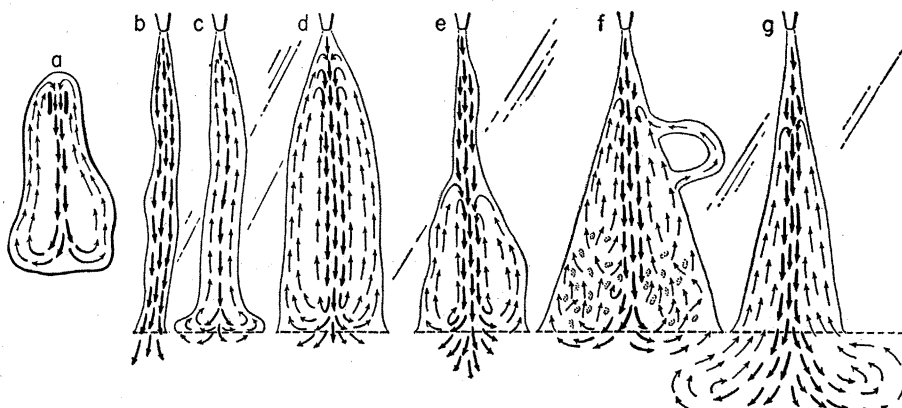


Fig. 1. Models of countercurrent streaming. In b, c, d, e, f, and g the dashed base line represents the edge of the inclined plane and (in c, d, e, f, and g) the water level in the vessel. The pattern of e occurs either at a greater flow rate or smaller surface tension gradient than that of d. A speck of detergent, by lowering the surface tension and increasing the surface tension gradient, converts the circulation of e to that of d.

is dependent upon the presence of ubiquitous surfactants. This can be shown by aspirating all existing surface film from a system in which countercurrent streaming is occurring; the circulations cease and are not re-established until the clean surface has aged for some time or surfactants are introduced.

Several observations indicate that surface film is subject to a surface pressure originating downstream: (i) separation of flow is maintained at slow speeds over long distances; (ii) countercurrent streaming does not begin until the stream flows into a static body of water; (iii) the entire surface film of a loop travels counter to the flow in the interior; and (iv) when relatively rapid flow from the nozzle is cut off (or slowed), the film circulating at some distance downstream (Fig. 1, *e*) spreads to the upstream limits like an expanding monolayer.

A film pressure develops because of inequalities in surface tension in different regions of the system. Interfacial tension is high at the freshly formed surface near the nozzle but becomes progressively lower as surfactants accumulate during the downstream flow. As the surface tension decreases, the film pressure increases, providing motive force for the backflow. Experimental manipulations that destroy the gradient also stop the vortical circulations.

Resemblances between countercurrent streaming and protoplasmic movements suggest that the same forces operate in both. Since the cell is essentially a bag of interfaces, in which new surfaces are often produced at a great rate, these forces could play a major role. Continuous production of interfaces as a result of protoplasmic syntheses probably leads to sustained gradients of interfacial tension at many points within the cell. Acting in consort, these gradients could give rise to the observed multifarious streaming movements. Local changes in interfacial tension also might account for such phenomena as the gyrating contortions of mitochondria which are, so to speak, "struggling to put forth new interfaces." Since on this basis energy for movement would be an additional debt to be met by energy of formation of membranes (taking into account both synthesis and structural ordering), correlation of extent of protoplasmic movements with amount of synthetic activity suggests itself.

Energy of formation of membranes might be transformed into energy of movement by at least three processes: (i) movement of existing films of low interfacial tension (at old interfaces) along gradients of interfacial tension at new interfaces; (ii) gross hydrodynamic flow of protoplasm into spaces between newly separating membranes (possibly responsible for nuclear rotation); and (iii) osmotic movement of water out of channels between membranes as a result of gradients set up by attraction of water molecules away from new interfaces. The metabolites of smallest intrinsic free surface energy, which accumulate concomitantly by positive adsorption, probably provide building blocks for further membrane formation. Thus one consequence of membrane formation might be the assemblage of the next generation of building blocks.

Counter movement of surface film caused by film pressure gradients also could explain the otherwise enigmatic phenomenon of filament streaming (4) in the long slender reticulopodia of *Allogromia*; on this basis filament streaming is interpreted as follows. When a reticulopodium is being extended, a filament of protoplasm flows outward but its surface film (and adhering particulate matter) flows inward to the cell body. When it is being withdrawn, the central protoplasm flows inward but the surface film flows outward. Surface film reaching the outer tip of the filament converges into the interior, carrying particulate matter inward to the cell body. In this way, feeding could be carried out both in the processes of extending and withdrawing reticulopodia—the animal simply "moves its mouths." The complex movements observed in networks of anastomosing reticulopodia are understandable on the same basis. They can be simulated in models by forming a network of peripheral loops.

A remarkable demonstration of countercurrent streaming can be carried out in the domestic closet bowl. When water begins to rise after a flushing, pencil sharpener filings are deposited on its surface. Many centers of countercurrent streaming are set up around the surface of the bowl (5).

*Note added in proof.* It now has been shown that the relatively high dynamic surface tension of the stream is primarily a consequence of its motion. The phenomenon is particularly pronounced in aqueous solutions of surfactants flowing in thin sheets. The entire

surface film actually spreads upstream; the apparent failure to do so in the center is an illusion, based upon transverse velocity gradients in the stream. The surface tension of dynamic fluids has been treated theoretically by Stuke [*Z. Electrochem.* **63**, 140 (1959)].

Forces at nonequilibrium interfaces also can give rise to vigorous longlasting interior circulations in fixed fluid bodies. Some papers describing the possible significance of these processes for protoplasmic contractility and transport of cytoplasmic matrix are in preparation.

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#### References and Notes

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### New Biological Effect of the Gases of the Helium Group

**Abstract.** The mold *Neurospora crassa* ATCC 5297a was grown in gaseous environments of helium, neon, argon, krypton, xenon, or nitrogen containing approximately 5 percent oxygen. A close correlation of the growth rate *R* (in millimeters per hour at 30°C) with the molecular weight *MW* of the chemically inert gas was observed. This correlation is described by the empirical equation:  $R = 3.88 - 0.1785 (MW)^{1/2}$ .

Although ordinarily they do not enter chemical reactions, the gases of the helium group, if present in sufficiently high concentration, are capable of eliciting physiological responses in a number of higher biological systems (1). Very little information, however, is available concerning the responses of simple life forms to the presence of noble gases. In order to make a quantitative assessment of the environmental influence of these gases on a well-characterized biological model system, an exploratory study was carried out with the fungus *Neurospora crassa*.

A helium-tight incubator capable of confining an experimental gas mixture for a minimum of 2 weeks without significant loss was designed and con-