letter; (ii) about 30 to 60 minutes later, after receiving a typed version of their written or dictated letter and incorporating any proof-editing changes; and (iii) 2 weeks later. As predicted, novice dictators, just after composing, rated their two dictated letters as significantly poorer (3.8) than their two written letters (4.4) [F (1, 7) = 35.17; $P < .01$]. Subsequently they rated them as equivalent (stage 2: dictated = 4.6, written = 4.5, $P > .20$; stage 3: dictated = 4.1, written = 3.9, $P > .20$), as did outside judges (dictated = 3.6, written = 3.6). Experienced dictators, on the other hand, rated their written and dictated letters as equivalent at all stages. Written and dictated letters were similar in style. Judges performed only slightly better than chance when required to distinguish typed versions of dictated and written letters.

While dictation may fulfill some characteristics of a skill (*6*), it does not fulfill the most observable ones. Novices learned rapidly (in a few hours); problem-solving behaviors related to dictation per se were nearly absent after one training day; differences between the novice and experienced dictators were small; and differences between good and poor composers were larger than differences among composition methods. Composition, acquired with difficulty over years, appears to be the fundamental skill.

Our present understanding of composition includes more than a performance view. Performance theory (*7*) seeks to understand human behavior by identifying the skills, abilities, capacities, conditions, and cognitive mechanisms that limit and determine human behavior. This approach, while useful, is incomplete as a guide to understanding composition because it does not consider attitudes, tastes, motives, and feelings of authors. Our results suggest that both actual performance and perceived performance probably affect one's choice of method of composition in everyday life. A third class of reasons, which include secretarial variables and the sociology and organization of one's environment, need to be studied for a further understanding of compositional methods.

These results make several theoretical contributions. For example, the finding that planning time is two-thirds of composition time identifies the key process in composition, regardless of method or complexity. The conclusion that composition is the fundamental skill, and method of composition is secondary to it, contributes to the recent surge of interest in studying how experts do skilled tasks. The results demonstrate that composition can be studied successfully in the laboratory. They provide a context for investigating more specific cognitive issues in composition (*8*). At the same time, it is important to extend the present approach to longer documents, typewriting, use of computer text-editing terminals, interrupted environments (as offices are), discretionary tasks, and informal communications.

JOHN D. GOULD
STEPHEN J. BOIES
IBM Research Center, Box 218, Yorktown Heights, New York 10598

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3. People can write memorized material or transcribe printed material as fast as 40 WPM, and they can speak memorized material or read aloud printed material as fast as 200 WPM.
4. Experienced dictators, studied several months later, were rated on a 7-point scale: 1 = unacceptable; 3 = acceptable(−); 5 = acceptable(+); and 7 = excellent. Outside judges rated written letters 4.0 and dictated ones 4.5. An interim study suggested the value of using a 7-point scale.
5. Words per minute during generation were estimated by (i) dividing total composition time into 6-second intervals, (ii) classifying a 6-second interval as generation time if a participant wrote or spoke during it, and (iii) dividing the number of words in the composition by total generation time. We are now measuring generation time to 0.1 second accuracy, which gives about the same results.
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Particle Capture by a Pacific Brittle Star: Experimental Test of the Aerosol Suspension Feeding Model

Abstract. Ophiopholis aculeata, *a suspension feeding brittle star, is capable of removing artificial particles from seawater by some mechanism or mechanisms other than sieving; the animal can capture a finite proportion of particles in all size classes available from at least 30 to 360 micrometers in diameter. A marked shift in the size distribution of particles caught by the animal toward larger particle sizes agrees with predictions derived from aerosol filtration theory. Adhesion of particles to the tube feet is strongly dependent on the presence of fixed charged groups on the surface of the particles.*

In most studies of suspension feeding organisms it has been implicitly or explicitly assumed that the mechanism of feeding is that of a sieve. The suspension feeding organs of these animals usually consist of a regular array of structures (such as cilia, tube feet, and tentacles), and it has been assumed that the animals capture particles passing through their filter on the basis of the relative sizes of the particles and the spaces between the filtering structures. Animals operating as a sieve should capture 100 percent of particles larger than the spaces between the filtering structures; no particles smaller than these spaces should be captured.

Rubenstein and Koehl (*1*) recently pointed out that suspension feeding animals that have some form of adhesive (typically mucus) associated with their filtering structures are analogous to man-made aerosol filters and have the potential of capturing particles by a number of nonsieving mechanisms. I report here on particle capture experiments with a suspension feeding brittle star, *Ophiopholis aculeata* (*2*). The mechanism of particle capture by the brittle star in these experiments is clearly not that of a sieve; the experimental results agree qualitatively with predictions of the aerosol suspension feeding model.

Specimens of *O. aculeata* were collected by hand from beneath cobbles in 10 to 20 m of water in the vicinity of Cantilever Pier, Friday Harbor, Washington; the animals were held in the seawater tables at Friday Harbor Laboratories with a continuous through circulation of fresh seawater. Suspension feeding experiments were conducted in a 40-liter (total volume) recirculating water tunnel (*3*); the return pipe of the water tunnel was submerged in flowing seawater to keep the tunnel at ambient seawater temperature. Given an appropriate substrate (*4*), the animals extended their arms and began suspension feeding within 15 to 30 minutes after introduction into the tunnel.

Suspension feeding in *O. aculeata* resembles the described behavior of other suspension feeding brittle stars (*5*, *6*).

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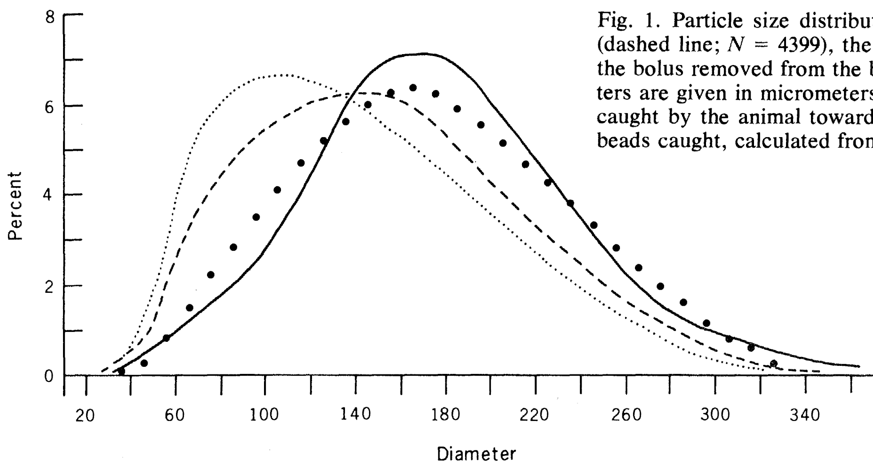

Fig. 1. Particle size distributions of Sephadex G-200 in the first water sample (dashed line; $N = 4399$), the second water sample (dotted line; $N = 3172$), and the bolus removed from the brittle star's arm (solid line; $N = 441$). Bead diameters are given in micrometers. Note the shift in the size distribution of particles caught by the animal toward larger particle sizes. (●) Predicted proportions of beads caught, calculated from the size distribution in the first water sample.

The arms and tube feet are held roughly perpendicular to the current flow and particles adhere to the mucus-covered tube feet. There was no evidence, from observation of particle capture or staining with toluidine blue, of a mucus web (*5*) between tube feet or spines. At 1- to 3-minute intervals, the most distal tube feet bent proximally and were wiped by the more proximal tube feet; this process continued down the arm, forming a bolus of particles embedded in mucus. As this bolus moved down the arm, each tube foot was wiped by its proximal neighbors and its load of captured particles added to the bolus. It has been previously demonstrated (*5*, *6*) that suspension feeding brittle stars do not show any active selection of particles captured at the level of the tube feet; each bolus of particles is tested by the oral tube feet and accepted or rejected as a whole.

In a typical experiment, the animal was introduced to the water tunnel with the water velocity fixed at approximately 4 cm/sec. After the animal had acclimated to conditions in the water tunnel for about 20 minutes, Sephadex beads were added (*7*) to the water. No attempt was made to approximate natural particle concentrations since the focus of this study was the mechanism of suspension feeding and not the ecology of *O. aculeata*.

All the Sephadex beads used in these experiments were denser than seawater, and it was necessary to "sweep" the bottom of the tunnel with water blown from a Pasteur pipette to keep the beads in suspension. When regularly done, this kept a constant and reproducible concentration of beads in the water column. Sweeping was continued until the animal was seen to be feeding and producing normal boluses.

After normal behavior had been established, the start of an experiment was signaled by the beginning of bolus formation by the distal tube feet, implying imminent cleaning of all the tube feet as the bolus moved down the arm. A 50-ml water sample was immediately siphoned from the water 5 cm downstream of the brittle star's arm to establish the particle concentration and size distribution in the water that would subsequently be filtered by the animal. The arm was photographed from the side and top to record the orientation of the arm and tube feet and to allow measurement of the expanded tube foot diameter and spaces between the tube feet in the undisturbed animal.

The animal was watched closely until a bolus of particles, representing particles captured since the preceding bolus, was formed; when the bolus approached the base of the arm, it was sucked up into a Pasteur pipette and stored (*8*). A second 50-ml water sample was then siphoned from the same region as the first. The beads in the water samples and the bolus stolen from the animal were allowed to settle to the bottom of their containers, pipetted into well slides, and photographed for subsequent counting (*9*).

The results of one experiment with Sephadex G-200-120 are shown in Fig. 1. Note the shift in the particle size distribution toward smaller sizes from the first to the second water sample. Because the photographs and water sample had to be taken in the 1 to 3 minutes before formation of the next bolus, it was impossible to continue sweeping particles off the bottom. The shift in Fig. 1 is the result of preferential settling of the larger beads (with higher settling velocities) during the period when sweeping had to be discontinued.

If these animals captured particles by a sieving mechanism, no beads smaller in diameter than the spaces between the tube feet should be captured. In this animal, the spaces between the tube feet had a mean width of 442 ± 50 μm (mean $\pm$ standard deviation) (*10*); if it were filtering as a sieve, the animal should catch none of these particles (maximum diameter, 360 μm). The solid line in Fig. 1 represents the particle size distribution of the beads in the bolus stolen from the brittle star's arm; the animal caught a finite proportion of all beads present, including those with diameters as small as 30 μm.

Of the five potential aerosol filtration mechanisms (*11*), three are likely to be of relevance for this experiment—direct interception, inertial impaction, and gravitational deposition. Actual efficiency of filtration should be a function of the relevant dimensionless parameter (*11*); in all three cases the efficiency of filtration should increase with larger particles. The distribution of particle sizes for

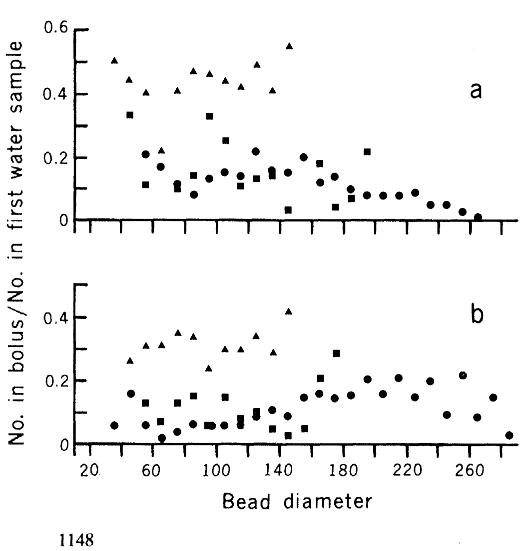

Fig. 2. Effect of surface charge of particles on capture efficiency. Points plotted represent the ratio of particles caught to particles in the ambient water sample for a particular size class and bead type. (a) Sephadex G-200 (●), G-25 (■), and SP-C25 (▲), and (b) Sephadex G-200 (●), G-25 (■), and Q-25 (▲) presented simultaneously for filtration. In seawater, Sephadex SP-C25 has a net negative surface charge, Q-25 has a net positive surface charge, and G-200 and G-25 are both electrically neutral. Sephadex G-25, SP-C25, and Q-25 all have approximately the same density. Note the increased capture of charged (▲) over neutral (●, ■) beads.

beads in the bolus was markedly shifted toward the larger particle sizes. The mean particle size for the first water sample was 156 ± 61 μm; for the second water sample, 143 ± 60 μm; and for the bolus removed from the animal, 178 ± 60 μm (*12*). This result cannot be explained as an artifact due to passive changes in the beads available for filtration; settling of particles from the water column would preferentially remove the larger beads, leaving only the smaller ones available for capture by the brittle star.

Since the direct interception parameter is an order of magnitude larger than the parameters for the other filtration mechanisms (*11*), it is valid to assume that direct interception is the predominant filtration mechanism in this experiment. It is then possible to predict what the size distribution of caught particles should be (*13*), given the original particle size distributions in the water and the diameter of the tube feet (mean, 217 ± 22 μm) (*10*). The results of these calculations are plotted in Fig. 1; the agreement between theory and experiment is impressive. The predicted mean size of particles captured is 173 ± 59 μm, which is not significantly different from the mean particle size in the bolus, 178 μm.

Care should be taken not to interpret this agreement as sufficient justification for direct application of the theoretical efficiency equations to suspension feeding animals. A basic assumption underlying all efficiency equations in aerosol filtration theory is that adhesion is 100 percent efficient (*14*); that is, all particles that touch a fiber adhere. Staining reactions with methylene-blue chloride and acid fuchsine indicate that the mucus coating of the tube feet of *O. aculeata* is an acid mucopolysaccharide. In seawater the mucus should have negatively charged groups fixed to the molecule, and one would expect differential adhesion of positively, negatively, and neutrally charged surfaces to the tube feet. Figure 2 represents two experiments where three kinds of beads, two with no net charge and a third with either a positive or a negative surface charge, were simultaneously suspended in the water in the tunnel. The points plotted in Fig. 2 represent the ratio of the number of beads in a particular size class in the bolus to the number of beads of the same type and size class in the water sample. This analysis, although crude, shows that beads with a net surface charge, regardless of the sign of the charge, are three times as likely to appear in the bolus as beads that are electrically neutral. The increased adhesion of positively charged beads was expected because of the fixed negative charges on the mucus, but the increased adhesion of negatively charged beads was not. It may be due to divalent cation–mediated adhesion, such as that postulated to account for the adhesion of the negatively charged bacterial glycocalyx to negatively charged surfaces (*15*); in seawater adequate numbers of Ca^{2+} and Mg^{2+} ions should be present. Natural particles in the oceans almost universally possess a net surface charge (*16*); a mechanism that promoted adhesion of any charged particle, regardless of the sign of the charge, would undoubtedly be of selective value to a suspension feeding animal.

These experimental results support the prediction of aerosol filtration theory that, for this filtration situation, larger particles should be captured more efficiently than smaller particles. These results are in contrast to the results expected if sieving were the only filtration mechanism available to these brittle stars—given the relative sizes of the beads and the spaces between the tube feet, no particle capture should have occurred for any of the beads available. Thus, there is probably not just one filtration mechanism available to suspension feeding animals, but six—sieving, direct interception, inertial impaction, gravitational deposition, diffusive deposition, and (perhaps) electrostatic attraction. However, care should be taken not to apply uncritically equations derived from standard aerosol filtration theory to suspension feeding animals since a basic assumption, 100 percent adhesion of all particles, may be violated.

The results reported here imply a large number of niche dimensions along which suspension feeding animals may differentiate—diameter and spacing of fibers in the filter, flow velocity through the filter, and characteristics of the adhesive in the filter, with their effects on the size, density, and charge of the particles captured (*11*). Further studies may lead to the prediction of the filtering characteristics of a particular animal from flow velocities and the morphology of the filtering organs alone, and to an understanding of how competition is minimized between suspension feeding animals.

MICHAEL LABARBERA*

Department of Zoology,
University of Florida, Gainesville 32611

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8. The volume of ambient water taken up with the bolus was always less than 0.5 ml. Contamination of the bolus with beads suspended in the water was negligible.
9. All photographs of samples were made with flat-field objectives. The beads were measured by projecting the negatives with a photographic enlarger; measurements were made in 10-μm size classes from 20 to 360 μm. Histograms of the percentage of the total sample in each size class were drawn and fitted by a smoothed curve. The goodness of fit of the curve was estimated by a chi-square test; the figured curves fit the original histograms at better than the 99 percent significance level for each curve.
10. These morphological measurements were made on photographs of undisturbed animals taken with a MicroNikkor lens set on maximum magnification. The diameter of the tube feet includes their surface papillae.
11. The aerosol filtration model (*1*) postulates five potential mechanisms besides sieving for particle capture. In a medium with such a high concentration of mobile charge carriers as seawater, long-distance electrostatic effects are unlikely, and I have discounted the importance of the electrostatic attraction mechanism. However, very-short-range electrostatic interactions may be of major importance (see text). The relative importance of the other four mechanisms may be evaluated by using various dimensionless parameters. The numerically largest parameter indicates the most important mechanism for a particular situation, although the magnitude of the parameter does not necessarily indicate the magnitude of the mechanism. For the experiments reported here, the dimensionless parameters are $N_{RF} = d_p/d_f \approx 10^0$ to 10^1 (direct interception); $N_{If} = 2(V_0/d_f)(v_g/g) \approx 10^{-2}$ to 10^{-4} (inertial impaction); $N_{Gf} = v_{g?}V_0 \approx 10^{-2}$ to 10^{-4} (gravitational deposition), and $N_{Mf} = (kT/d_p)(3\pi\mu V_0 d_f)^{-1} \approx 10^{-9}$ to 10^{-10} (diffusive deposition), where d_f stands for fiber diameter; d_p, particle diameter; g, acceleration due to gravity; k, Boltzmann's constant; T, absolute temperature; v_g, settling velocity of the particle; V_0, ambient fluid velocity; and μ, viscosity of the fluid.
12. All means are significantly different at the 0.02 percent confidence level (one-tailed t-test).
13. Efficiency = $(1 + N_{Rf}) - (1 + N_{Rf})^{-1}$ [J. Pich, in *Aerosol Science*, C. N. Davies, Ed. (Academic Press, New York, 1966), p. 223].
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* Present address: Department of Anatomy, University of Chicago, Chicago, Ill. 60637.

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