flight. A wind-angle change in the appropriate direction would then restore activity of A fibers and increase that of B fibers. Figure 2C shows an example of just such behavior. More precise testing of this scheme has not proved fruitful due to the apparent closeness of the threshold levels of units of like size and to neuronal noise in the system. These findings argue, however, that wind-angle change has a common effect on all the follower cells in this population. It seems reasonable that wind-angle inputs may produce their effects at some common premotor point rather than at each of the 12 separate motoneurons.

MAIJA HINKLE
JEFFREY M. CAMHI
Section of Neurobiology and Behavior, Cornell University, Ithaca, New York 14850

References and Notes

1. J. M. Camhi, *J. Exp. Biol.* **52**, 519 (1970); *ibid.* p. 533.
2. P. L. Miller, *ibid.* **37**, 264 (1960).
3. J. M. Cambi and M. Hinkle, *Science* **175**, 550 (1972).
4. Simultaneous drive of a motoneuron by two different oscillators has been observed in crickets [D. Bentley, *J. Insect Physiol.* **15**, 677 (1969)].
5. P. L. Miller, *J. Exp. Biol.* **37**, 224 (1960).
6. It was sometimes necessary to stimulate bursting in the isolated ganglion by perfusion of the saline with CO$_2$. The CO$_2$ receptors in this ganglion have indirectly been shown to stimulate a local ventilatory oscillator (*5*).
7. The justification for scaling axon diameters by spike height (*3*), relies upon histological examination and measurements of spike-conduction velocity.
8. W. J. Davis, *J. Neurophysiol.* **34**, 274 (1971).
9. This generalization holds primarily for the larger B fibers and even then is not absolute.
10. Motoneuron size is an important and sometimes major determinant of the firing properties of vertebrate motoneurons [see E. Henneman, G. Somjen, D. O. Carpenter, *J. Neurophys.* **28**, 560 (1965)] and some crayfish motoneurons (*8*). The size principle is generally interpreted in terms of an inverse relation between postsynaptic cell size and the cell's input resistance [B. Katz and S. Thesleff, *J. Physiol. London* **137**, 267 (1957); see also (*8*). Since in our experiments axon diameter rather than dendrite diameter is correlated with cell physiology, this suggests a correlation, within each cell, of the diameter of the axon with that of the dendrites, the presumed synaptic loci. We are unable to rule out alternative correlations between axon diameter and presynaptic properties or some dendrite property other than diameter, although dendrite diameter seems the simplest possibility.
11. D. M. Wilson, *J. Exp. Biol.* **38**, 491 (1961).
12. The frequency of the flight oscillator in the absence of input from stretch receptors, one located on each wing, is about half the normal wingbeat frequency of the intact locust (17 per second). Each of the four stretch receptors elevates this frequency in about equal increments [D. M. Wilson and E. Gettrup, *J. Exp. Biol.* **40**, 171 (1963)]. Thus input from only the forewing stretch receptors, in a greatly adapted condition [E. Gettrup, *ibid.*, p. 323; H. Pabst and S. Schwartzkopff, *Z. Vergl. Physiol.* **45**, 369 (1962)] could be expected to produce a flight motor frequency of about the observed 10 per second.
13. A. C. Neville, *J. Exp. Biol.* **40**, 123 (1963).
14. This is an elaboration of model presented to explain bursting in lobster swimmeret motoneurons (*8*).
15. By level of synaptic drive we mean the magnitude of some synaptic event just prior to the step influenced by individual motoneuron properties. Specifically, if dendrite size is the factor causing individual motoneuron differences, then level could be taken to mean strength of synaptic current.
16. One deviation from perfect compliance with the model is that during prolonged flights, the smallest two or three B fibers are often silent. Another factor is that during simultaneous flight and ventilatory oscillator activity, the flight interburst intervals often show no activity (Fig. 2B) rather than the low activity predicted by Fig. 3C. This silence, which may reflect inhibition from antagonistic elements of the flight motor, will be discussed (M. Hinkle and J. M. Camhi, in preparation).
17. Supported by NIH grant NS-09083 to J.M.C. We thank W. J. Davis and G. Wyse for their helpful comments and C. Monroe for technical assistance.

22 October 1971; revised 26 November 1971 ■

Sieving Behavior of a Series Membrane System

The purpose of this technical comment is to clarify a recent report by Bresler *et al.* (*1*). The illustrative example that Bresler *et al.* presented is carefully qualified, but, as it stands, it could be misleading. We shall show here that it is correct to require a removal mechanism in the steady state, but that it is erroneous to conclude that only the first membrane in an array generally determines the array's sieving characteristics. We shall also show that the arguments in (*1*) do not call into serious question present-day concepts of the interactions involved in membrane separations.

In the steady state, all concentrations and all fluxes in the system are defined to be constant in time. The steady-state concentrations within any compartment and the steady-state fluxes between any pair of compartments are determined by the properties of the separating membranes and the boundary conditions of the problem. For series membrane systems, the steady-state fluxes through each membrane are the same and, like the compositions in the internal compartments, have values determined by the properties of all the membranes in the system, the applied hydrostatic pressure difference, and the composition of the ambient baths.

No conceptual difficulty is encountered in trying to understand the constancy of the composition of the solutions in the internal compartments, since the fluxes of solute and solvent entering the compartment are the same as those of the solute and solvent leaving the compartment. In a sieving experiment, there is also no difficulty in understanding the constancy of the concentration of filtrate, C_s^B; it is made up of what has passed through the membrane assembly. Thus

$$C_s^B = J_s/J_v$$

where J_s and J_v are the solute and volume fluxes, respectively, each constant in time.

If the volume of the filtrand compartment, V_A, is infinite, its composition can remain at the steady-state value, C_s^A, indefinitely; otherwise, it will become richer in solute with the passage of time. Hence, the use of steady-state concentrations in describing flow through a series of membranes implies either that V_A is so large that C_s^A is substantially unchanged during the period of time in which the steady-state description is proposed to apply, or that the accumulating solute is removed from the filtrand in some unspecified fashion. This is the "removal" of which Bresler *et al.* write. Since the solute is, in this sense, removed from the filtrand, and inasmuch as all material passing through the first membrane in the series passes through to the filtrate (J_s and J_v are the same for each membrane), the statement that "all effective sieving still occurs at the first membrane" is merely a rephrasing of the assumptions implicit in the definition of the steady state.

It is incorrect to deduce, however, that the sieving behavior of a series membrane system is determined by the structure of the first membrane alone. It is as reasonable to try to pour water through a funnel faster than it can discharge fluid and then to deduce from the site of the overflow that the principal resistance to flow through a funnel is at the wide end. The site of a cause is not a priori the site of its effect. Consider, for example, the case of a membrane M with a nonzero rejection coefficient, located downstream of another membrane N. There is no accumulation of solute between the two; rejection is always from the filtrand. Yet the overall sieving characteristics of the system, including the concentration of the filtrate and the rate at which solute must be removed from the filtrand to hold its concentration at C_s^A depend on the properties of M as well as those of N. The *reductio ad absurdum* is

$$R_M = 1, R_N = 0$$

The relative influence of the first and succeeding membranes in a series array on the sieving behavior of that array depends on, among other things, the flow rate through the array. If the membrane flow equations, which can be derived from the frictional representation of membrane transport, are applied to a series array, it is seen that J_s/J_v becomes *independent* of the second and subsequent membranes only if J_v is *infinite*. The example of Bresler *et al.* can therefore be correct only in this limit. Since the downstream membranes do influence J_s/J_v when J_v is finite, the example in (*1*) does not cast any doubt on the concept that internal interactions in membranes [modeled in (*1*), we assume, by rejection coefficients R_2 and R_3] are important to sieving. Even at driving pressures such that J_s/J_v is nearly independent of the downstream membranes, J_v and hence J_s are not independent of the downstream membranes, since J_v depends on all the membranes, through their respective flow conductivities. Thus the *rate* of rejection, that is, the rate of removal of solute from the filtrand alluded to above, which is equal to $(J_vC_s^A - J_s)$, *always* depends on the properties of the entire array.

Similarly, J_s/J_v becomes *independent* of the concentration downstream of a membrane only when J_v is *infinite*. For finite flows, equation 2 of Bresler *et al.* is strictly false. This serious limitation is hedged by relaxing the "simplifying" assumptions of the illustrative example, and it is finally conceded that the properties of the several membranes interact to give an overall rejection coefficient for the system. The example is supposedly saved by the claim that "the foregoing results still hold in a formal mathematical sense." Equation 2 of (*1*) may indeed be regarded as a definition of a set of R's in terms of J's and C's, but, except for R_3 (which is bounded by filtrate with a composition corresponding to the fluxes through the last membrane), the R's so defined are without clear relation to the true rejection coefficients of each membrane.

In summary, we agree with Bresler *et al.* that a removal mechanism is essential to steady-state sieving by a membrane system and that removal is only from the filtrand, but we contend that the separation characteristics, measured by parameters such as the rejection coefficient, depend on all the membranes in the system and their internal interactions with solute and solvent. We do not regard any of these observations as being profound or original, but we believe that their clear presentation is essential to a balanced picture of the fundamental aspects of membrane transport.

M. H. FRIEDMAN, R. L. MCCALLY
Johns Hopkins University
Applied Physics Laboratory,
Silver Spring, Maryland 20910

Reference and Note

1. E. H. Bresler, R. P. Wendt, E. A. Mason, *Science* **172**, 858 (1971).
2. Supported in part by the National Institute of Neurological Diseases and Stroke, National Institutes of Health, under grant NS 07226.

15 June 1971; revised 12 November 1971

Friedman and McCally agree with our major point (*1*) that effective steady-state sieving can occur only when a removal mechanism coexists with the rejection mechanism, but they purport to find us in error on two other important points. The first is in our example of a series array of membranes, for which we contend that the sieving properties of the whole array are determined by the rejection coefficient of the first membrane only. Second, they claim to show that we do not call into serious question present-day concepts of the interactions involved in membrane separations.

Regarding the first point, Friedman and McCally apparently have in mind an analogy with a water funnel, which does indeed make our result seem to defy common sense, as would a similar analogy with series resistors. But these are false analogies; we made no claim that the hydraulic conductivity of a series array of membranes is determined by that of the first membrane alone. This is clearly absurd. What we did claim was that, subject to certain simplifying but realizable conditions, the *sieving* properties of the array are determined by those properties intrinsic to the first membrane. Our reasoning is clearly, although perhaps tersely, set forth in our report (*1*) in the form of equations 2, 3, and 4, and need not be repeated here. The flaw in Friedman and McCally's argument is their implicit assumption that the steady-state concentration in a well-stirred compartment is equal to the concentration of filtrate entering it. This is not the case; for instance, the entering filtrate can be less concentrated than the overall solution of that compartment, the deficit being made up by the rejection of solute by the subsequent membrane back into the well-stirred compartment. Thus the compartments will each attain a concentration at steady state given by our equation 4, and this concentration will in general *not* be equal to (J_s/J_v) (which is indeed the same for every membrane in the series). Moreover these concentrations will attain steady-state values which very nearly cancel out the effect of the downstream membrane on the overall sieving behavior of the array.

The remaining objection on the first point seems to be that our result can be valid only in the limit of infinite J_v. Although this might be true in a strict mathematical sense, it is our contention that there is a physically reasonable set of conditions, encompassing a wide range of flow rates and concentrations, for which an excellent approximation is that the intrinsic rejection behavior of each membrane remains *essentially* unchanged by virtue of its being placed in a series array. In particular, when the pressure difference across each membrane element is large as compared to the osmotic pressure (that is, $\Delta P \gg \Delta\pi$) and when all solutions are dilute enough and volume flow is fast enough so that back-diffusion contributes a negligible fraction to the total solute moving through the system, then the sieving behavior (R) of a membrane depends on the structure of the membrane and the qualitative nature of the solution, and not on the concentrations of what is upstream or downstream from it. The mere fact that R values, measured under the above conditions, are used to characterize the behavior of membranes attests to this fact.

It is true that J_V and J_S *individually* depend on all the membranes in an array; here the hydraulic analogy is correct. However, it does not thereby follow that the ratio J_S/J_V must have a similar dependence; here the hydraulic analogy is fallacious.

The case chosen by Friedman and McCally for an attempted *reductio ad absurdum* argument, in which an impermeable membrane M ($R_M = 1$) is placed downstream from a completely permeable membrane N ($R_N = 0$) is one that explicitly violates such conditions. For this case our equation 4 would predict that no steady state is possible, the compartment concentration continuously increasing toward infinity. Actually, however, back-diffusion must finally take over as a removal mechanism, and an unusual type of steady state results where convection of solute into the compartment is exactly counterbalanced by back-diffusion outward through the same membrane. Under this set of conditions the overall steady-state sieving characteristics will, of course, be those intrinsic to membrane M rather than membrane N.

Finally, we do believe that we have called into question certain present-day concepts relating to steady-state sieving. There are two views relating to this process which differ from one another in a quite fundamental way. According to the first view, sieving is regarded as taking place by an exclusion process: there is a dispersion of pore sizes with uniform particle sizes, or a dispersion of particle sizes with uniform pore sizes, or oddly shaped particles or pores (or both) so that some sort of lock-and-key arrangement involving proper orientation is required in order for solute to cross the membrane. According to the second view, the interior of the membrane is an extended convoluted surface that may interact through the thickness of the membrane more strongly with one species passing through it than with another. We question the validity of this second view for the steady state, since it implies that more of one species than another is continually accumulating in the membrane as long as sieving goes on, unless some mechanism (as yet undefined, to our knowledge) acts to discharge the accumulating solute back into the feed solution. Incidentally, we did not propose the series array model as a valid model of a sieving membrane with the membranes after the first serving as analogs for frictional interactions, but rather to illustrate that a removal mechanism must be present to remove solute from the site at which it is accumulating in order for effective sieving to occur. With this in mind, let us analyze a simple presumed frictional model for sieving in the form of a capillary, the walls of which retard the passage of solute more strongly than solvent. When a flow of solution is generated in this capillary, relatively less solute than solvent emerges. This hypothesis implies continual accumulation of solute within the capillary unless in the steady state some mechanism is available which either (i) transports solute from inside the capillary back into the feed solution or (ii) prevents a portion of the solute from entering the capillary. For the first possibility one might attempt to postulate a concentration gradient. But since the solution entering the capillary has a higher concentration than that emerging, the orientation of a presumed gradient is the opposite of what is required. For the second possibility we must ask ourselves what force could be present at the capillary entrance that could be transmitted from frictional events inside the capillary to the solute molecules but not to the solvent molecules (both electrically neutral). This possibility would appear to require either some action at a distance or some contact force involving such enormous concentrations of solute that the molecules in the capillary are in virtual direct contact with one another. The first mechanism is unknown, and the second seems highly implausible. Thus sieving on the basis of continuous point-to-point interaction with the interior of a membrane does not seem possible in the steady state, but can only be a transient phenomenon, as in the example of chromatography, and will disappear as the interaction sites become saturated. In fact, a main point of our report, which seems somehow to have become lost, was that this particular attempt to visualize the nature of sieving in concrete physical terms cannot be valid in a steady state. The use of the constraint of the steady state is not a trivial exercise in semantics (although the conclusions appear obvious in retrospect), but rather is a powerful tool that can be used in a very simple way to test theoretical models of the sieving process.

E. H. Bresler
Veterans Administration Hospital and
Tulane University School of Medicine, New Orleans, Louisiana 70140

E. A. Mason
Brown University,
Providence, Rhode Island 02912

R. P. Wendt
Loyola University,
New Orleans, Louisiana 70118

Reference

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18 October 1971; revised 27 December 1971 ■

Boconó Fault, Venezuelan Andes

Preliminary study of glacial stratigraphy in the valley of Rio Santo Domingo, State of Mérida, Venezuela, leads us to comment on the conclusion reached by Schubert and Sifontes (1) that right-lateral, strike-slip movement along the Boconó fault has averaged 0.66 cm/year during the last 10,700 years.

The width of the area mapped by Schubert and Sifontes adjacent to the fault [figure 1 in (1); compare Fig. 1] is not sufficient either to establish the crest of the lateral moraine or to project its apparent curvature into the fault zone. This can be demonstrated on their map by restoring the two segments of the Victoria lateral moraine to the prefault configuration; the fault apparently cuts the moraine at a point of abrupt change in curvature, an unlikely coincidence. Furthermore, projection of the *north* side of the Victoria moraine across the fault zone would yield a significantly larger measure of apparent displacement. The citation of the computed average of 66 m (1, p. 68) to two significant figures implies an accuracy unlikely to be achieved by the method used and thus represents no improvement on the previous estimate of 80 to 100 m (2).

The terraces within the Zerpa lateral moraine described by Schubert and Sifontes (1, p. 68) at 20 to 25 m and at 6 to 10 m above the bed of the creek (see Fig. 1) were deposited within the morainal loop in the Zerpa valley at times when the stream draining the valley crossed the moraine at altitudes higher than the modern outlet. The outlet was lowered at least twice, either by faulting or by erosion, preserving the terraces as traces of two higher long profiles. The higher terrace, which is well developed upstream of the fault, ends near the point where the fault cuts across the morainal loop; the lower terrace is downthrown by 50 to 100 cm north of the fault. We do not dispute that incision ultimately was responsible for preserving the two terraces, but it seems probable that vertical movement on the fault induced the incision. Displacement occurred at least twice after emplacement of the moraine; in each case, the sense of