tors in pain in humans, and it has indicated that the sensory aspects of pain have been overemphasized in the past.

Our study suggests that SDT is a very useful and versatile tool for the evaluation of analgesic agents. The improved precision in measurement, and the increased information yielded by these methods, will permit investigators to evaluate human pain in the laboratory with more confidence than threshold methodology has warranted.

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On the Ascent of Sap

Plumb and Bridgman (*1*) suggest various ways of producing zero hydrostatic gradient in a vertical tube containing movable water. One way is by means of a series of semipermeable membranes separating solutions of increasing concentrations, another is by means of a tubing with an increasing density of wiggling molecular hairs affixed to the wall. If it were possible in a state of equilibrium to interfere with the hydrostatic gradient of water itself by means of captive molecules, a mere submersion of the system would create perpetual flow. In reality all such systems arrive at a hydrostatic gradient of pure water. This is borne out by direct experiments starting with Perrin's celebrated work on Brownian motion and, more recently, by measurements on gels, suspensions, and magnetic solutions (*2*). However, as contrary claims are commonly inferred for gels, counterions, secretory crypts, and so forth, the issue merits attention.

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2 October 1972

Scholander implies that it is impossible to interfere with the hydrostatic gradient of pure water by the constrained chemical activity gradient we have proposed (*1*) and asserts that if it were possible one could create a perpetual motion machine by submersion of the column in pure water. We show these tenets to be incorrect by the following thermodynamic analysis of the osmotic pressure effects.

Consider a vertical column, with a constrained activity gradient, the base of which is at elevation $z = 0$, and a reservoir of pure water, the surface of which is at elevation $z = 0$. The chemical potential of water in the reservoir is

$$\mu(z,P) = \mu^0 + Mgz + \bar{V}[P(z) - 1]$$

where P is the pressure in atmospheres, M the molecular weight, g the gravitational constant, and $\bar{V}$ the molar volume. If the pressure at $z = 0$ is 1 atm, the functional dependence of P on z is

$$P(z) = 1 - \frac{Mgz}{\bar{V}}$$

The chemical potential of water in the column is

$$\mu(z,h,P,\pi) = \mu^0 + Mgz + \bar{V}[P(h) - \pi(h) - 1]$$

where h is the distance from the base and π is the osmotic pressure. The functional dependence of π on h will be chosen as

$$\pi(h) = \frac{Mgh}{\bar{V}}$$

and, if the column is upright ($z = h$), the hydrostatic pressure is 1.0 atm throughout. If the column were rotated to a horizontal position the solvent would redistribute to produce a new thermodynamic equilibrium in which

$$P(h) = \frac{Mgh}{\bar{V}} + 1$$

Now specifically assume a 10-m column in which $\pi = 1.0$ atm at $h = 10$ m, and $\pi = 0.0$ atm at $h = 0$ m, such that $P = 1$ atm throughout when the column is vertical. If the column were placed horizontally the pressure would be 1.0 atm at $h = 0$ m and 2.0 atm at $h = 10$ m. If the horizontal column were submerged in the reservoir it would be at thermodynamic equilibrium with the reservoir. At the base end there is no hydrostatic or osmotic pressure differential. At $h = 10$ m the hydrostatic pressure differential is just the correct value to produce osmotic equilibrium. Thus, no flow would occur. A similar argument applies if the column is lowered vertically into the reservoir.

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15 January 1973

Plumb and Bridgman (*1*) have suggested that the ascent of sap in trees may be accomplished by two mechanisms which permit the hydrostatic pressure of the xylem sap to remain near ambient pressure at the highest part of the tree: (i) by a concentration gradient of filamentary monomolecular chains with one end attached to the xylem vessel wall and (ii) by solute injection.

If flagella-like molecules were projecting into the xylem sap and if they could lower the chemical potential of the sap, they would also lower the melting point of the sap. Recent experiments on winter-hardened conifer twigs indicate that the melting point of the xylem sap in situ is not lowered. Twigs were cooled to equilibrium in a calorimeter at several temperatures from $-0.8°$ to $-3.5°C$; then freezing was initiated. From the calorigrams, the rate and amount of water freezing at each temperature could be deduced. If the melting point of the xylem sap were lowered by those molecules postulated by Plumb and Bridgman to lower the chemical potential of the sap, then no sap would freeze at calorimeter temperatures above the computed melting point. In fact, it was found that sap did freeze above the computed melting point. The results showed that the chemical potential of the extracellular water in the xylem and the matrix of the cell wall was lowered by hydrostatic tension and not by any trapped osmotic substances which would have lowered the melting point. Thus, the first part of the Plumb and Bridgman thesis would not apply to the white fir or any of several conifers investigated.

Another set of observations render the second part of their thesis untenable. Stems of mangrove twigs of three genera (*Rhizophora, Laguncularia, Avicennia*) were cut off under water and joined to a potometer containing distilled water. The steady-state transpiratory influx of water was determined. Then the distilled water was replaced by 3.0 osmolar NaCl solution. The steady-state influx of the 3.0 osmolar NaCl solution lasting for several hours was not less than for distilled water in all three genera. The fact that the influx was never reversed, stopped, or even diminished by the NaCl solution suggests that injection of solute into the xylem conduits of transpiring plants would have no effect on water movement. As long as the solute is free to disperse toward the evaporating surface there is no way it can affect water movement in these potometer experiments for many hours. Likewise, as long as solutes injected into the xylem conduits are free to disperse in either direction from the site of injection, there is no way they can affect water movement. Of course, should enough solute accumulate at the evaporating surfaces to lower the vapor pressure significantly, then transpiration should diminish, but never increase.

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Measurement of freezing point depression should, in principle, provide a means of deciding if the chemical activity of the xylem water varies with height. However, the freezing point depression is quite small for concentrations of solute which will produce considerable osmotic pressure. The approach would be further complicated by the difficulties of assuring thermodynamic equilibrium in a heterogeneous system such as a twig and measuring the heat of fusion of water over the background of the heat capacity of the other components.

On the basis of the information presented, we doubt that the experiments could have detected a depression of freezing point caused by a sol or other modifier of the chemical activity of water. White fir trees grow to a maximum height of about 38 m. The freezing point depression corresponding to an osmotic pressure of 3.8 atm is only 0.29°C. "Initiating freezing" at temperatures lower than − 0.29°C would give no information about the presence of a solution with a freezing point depression of less than 0.29°C. That solution would already have been frozen or, if not, it would be supercooled and subsequent experimental observations of the temperature at which it freezes would have no thermodynamic significance.

The comparison of the steady-state influx of water and of a solution of NaCl to twigs joined to a potometer is interesting. The rate-controlling step in the experiment described is most probably evaporation at the leaves rather than transport through the twig, and we would expect the same steady-state behavior with pure water and with salt solution up to the point where solute accumulation affects the rate-controlling step. However, we would expect that a transient decrease in rate could be detected for a short time after the water reservoir is replaced by the salt solution while osmotic equilibrium is being established.

R. C. PLUMB, W. B. BRIDGMAN

15 January 1973

Plumb and Bridgman (*1*), in discussing their gel gradient theory, concentrate on the hydrostatic gradient of water activity in trees and credit it with a central role in sap ascent. Many others are not so sure. One may give the total potential depression at a certain point in the plant as a sum of independent terms representing soil, hydrostatic, and flux characteristics of the system (*2*):

$$(-)\psi_{\mathrm{W}} = (-)\psi_{\mathrm{S}} + (-)\psi_{\mathrm{g}} - \sum_{\mathrm{S}}^{\mathrm{P}} f_i r_i$$

where ψ_w is the total water potential; ψ_s is the soil water potential; ψ_g is the hydrostatic potential (0.1 atm/m); and the last term, friction potential, represents the sum of products from partial fluxes f_i and partial resistances r_i along the branched conduit from soil **S** to point **P** in the plant.

Soil and friction both may become by far more momentous than hydrostatic gradients: Soil water potentials have long been known to range from about 0 atm at field capacity to −15 atm at "permanent wilting point," whereas frictional gradients in transpiring conifer branches may be as high as 1 atm/m (*2, 3*). Moreover, soil water content and transpiration fluxes may change very rapidly, whereas standing gel gradients in trees could balance, if anything, only the minor hydrostatic potential drop (0.1 atm/m), since the gel content of fully developed tracheids and vessels could not be adjusted to these changes. We could perhaps maintain the Plumb-Bridgman mechanism as a factor preventing negative pressures in nontranspiring trees rooted in water-saturated soil. Since neither the extremely specialized case nor the comparatively minor hydrostatic tensions deserve such an exception, we might as well uphold the cohesion theory, which readily explains all the experimental data.

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Other authorities (*1*) state that under conditions of maximum flow the pressure gradient in the xylem is only about 50 percent greater than in a static column of pure water, indicating that the problem which our theory addresses is perhaps the major one.

When gradients in excess of the physiological values are imposed on the xylem the conductivity decreases markedly (*2*); the shutdown is probably due to closure of bordered pits.

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15 January 1973

The report by Plumb and Bridgman (*1*) appears to be inconsistent with the quantitative physiochemical basis for constructing such a theory (*2*). We would like to make two points of criticism.

1) The authors "suggest that the xylem conduit contains a filamentous gel-like structure having a concentration gradient sufficient to support the column without pressure gradients." There is no evidence that the hairlike gel structures the authors refer to extend across the lumen. The volume of the fibrils would have to be a small fraction of the flowing liquid in order not to impede the flow by frictional resistance. "The xylem of a tree at 100 m of height would contain about 10 percent of this gel," or about 10 g of dry gel per 100 ml of total water in the xylem. These fibrils will be in essential equilibrium with the water flowing past them and have a water content of about 90 percent (in order to have a water potential of about 10 atm). This would impede the water flows, which have been observed at 75 cm/min. Lower gel concentrations in dry matter per total volume of water would not provide the activity gradient required by the authors' hypothesis.

2) They suggest that, "the transport of water is hydrodynamic and not diffusion controlled." Experiments have shown that the actual flow rates are several orders of magnitude too large to be accounted for by diffusion. The authors then propose a mechanism of a "dynamic balance of the gravitational potential with an activity gradient," and this statement appears to contradict the one above. First, if there is an activity gradient, the flow must proceed because there is a concentration gradient (induced by temperature or pressure gradients) which must be relaxed by diffusional processes. Second, the thermodynamic description of a system involving a mixture in a uniform gravitational field (we assume that a 100-m change in elevation will not significantly change the local acceleration of gravity) with two phases present (a water phase and a gel phase) is controlled by the total potential for mass flow between the phases (*3*). Therefore, the activity defined by the authors is related to the adsorption and desorption of water by the gel at a particular elevation in the tree. This steady state (or equilibrium) does not involve the motion of the fluid through the xylem.

These points, which can be discussed in more detail, lead us to reject the hypothesis proposed by these authors.

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A reasonably complete discussion of the thermodynamics of columns of liquids bearing a constrained chemical activity gradient appears in the *Journal of Physical Chemistry* (*1*). We do not feel that the abridged discussion in *Science* (*2*) constitutes an adequate basis for a discussion of the validity of the thermodynamic analysis of the columns.

It is possible that the alternative theory we have proposed may be shown to be unrealistic and unacceptable on the grounds that the substance imposing the chemical activity gradient would introduce too high an impedance to flow. However, cell wall and cortical gel effects on water structure are not well understood at this time. It has been established by microscopic observation that gels and sols near cell walls play a role in cytoplasmic streaming in plants (*3*) and in amoeba locomotion (*4*). The physical chemistry of the mechanisms by which these motile systems operate is not known. Until these phenomena are better understood we prefer to withhold judgment on an argument which assumes a particular concentration, volume, and mode of action for the gel structure. Some recent nuclear magnetic resonance spectroscopic measurements (*5*) are pertinent. They indicate that agar (the major component of which is agarose, a polysaccharide similar to that which we proposed) imprints a structure on all the water in a gel, not just on the water molecules adjoining the macromolecular chains.

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22 January 1973

On Habituation in the Cochlear Nucleus

Humphrey and Buchwald (*1*) recorded neural response decrements in the cochlear nucleus of decerebrate cats during a series of tonal or white noise stimulations. These decrements were interpreted as evidence of neuronal habituation. Simplified mammalian preparations that exhibit true habituation would aid in understanding the plasticity of the mammalian central nervous system (CNS). Neural plasticity that can be shown to develop under controlled procedures with a time course of minutes or tens of minutes may form the basis for explanations of the information storage capabilities of the CNS. For these reasons, we wish to question several methodological points in Humphrey and Buchwald's report.

We contest the intended implications in their statement, "Thus the development of cochlear nucleus response decrements in the absence of changes in the microphonic potential indicated that receptor adaptation was not responsible for the phenomenon." On the contrary, the cochlear microphonic (CM) potential recorded from the round window (or anywhere near the cochlea) in a healthy preparation will not diminish in amplitude under continuous stimulation (*2, 3*). The cochlear microphonic potential is literally a microphonic potential, and reflects the transformation of the mechanical disturbance at the hair-