lished adenylate cyclase system. In hormone-dependent adenylate cyclase there is an assemblage of individual components–receptor, GTP-binding protein, and catalytic moiety—for signal transduction (*22, 23*). In contrast, the presence of dual activities—receptor binding and enzymic—on a single polypeptide chain indicates that this transmembrane protein contains both the information for signal recognition and its translation into a second messenger. It is possible that a third signal component (probably a lipid or an accessory protein) is needed to link these two activities functionally.

Note added in proof: Although the antibody to the 180-kD guanylate cyclase blocks guanylate cyclase activity, it does not inhibit the binding of ANF to the protein. This indicates that either the antibody is solely against the guanylate cyclase epitope of the protein or that there are two tightly coupled 180-kD proteins which are inseparable by the present techniques.

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26. These studies were carried out between 1982 and 1986 and constitute a portion of A.K.P.'s dissertation. We thank R. Nutt, Merck Sharp and Dohme Research Laboratories, for the sample of synthetic ANF; W. Y. Cheung, St. Jude Research Hospital, and M. Rodbell, National Institute of Environmental Health Sciences, for the critical review of the manuscript, and J. M. Sharma for editing the manuscript. Supported by NSF grant 8609867 and NIH grant NS23744.

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Technical Comments

Computing with Neural Networks

Hopfield and Tank (*1*) refer to "A new concept for understanding the dynamics of neural circuitry" using the equation (in a slightly different notation)

$$C_i\frac{du_i}{dt} = -\frac{1}{R_i}u_i + \sum_{j=1}^{n} T_{ij}f_j(u_j) + I_i \qquad (i = 1,\ldots, n) \qquad (1)$$

for the neuron state variables u_i. The concept is that the variables $u_i(t)$ approach equilibrium as $t \to \infty$ if the connections T_{ij} are symmetric ($T_{ij} = T_{ji}$). Hopfield and Tank also state that "a nonsymmetric circuit . . . has trajectories corresponding to complicated oscillatory behaviors . . . but as yet we lack the mathematical tools to manipulate and understand them at a computational level" (*1*, p. 629), and that "the symmetry of the networks is natural because, in simple associations, if A is associated with B, B is symmetrically associated with A" (*1*, p. 629).

Associations are often asymmetric, as in the asymmetric error distributions arising during list learning (*2*). Neural network models (*3*) explain these distributions when one uses Eq. 1 supplemented by an associative learning equation for the connections T_{ij}

$$\frac{dT_{ij}}{dt} = -AT_{ij} + Bu_if_j(u_j) \qquad (2)$$

Because of the nonlinear term $u_if_j(u_j)$ in Eq. 2, $T_{ij} \neq T_{ji}$.

Stability theorems (*4*) have been proved about neural networks which include and generalize Eqs. 1 and 2. Thus symmetry is not necessary to prove associative learning and memory storage by neural networks. Nor is symmetry needed to design stable neural networks for adaptive pattern recognition (*5*). Methods have also been developed (*6*) for analyzing the oscillatory behavior of neural circuits. We believe that the relation between symmetry and stability in neural networks is much more subtle and better understood than Hopfield and Tank (*1*) suggest.

Nonetheless, symmetry does help to analyze the system represented by Eq. 1. In fact, we (M.A.C. and S.G.) (*7*) independently discovered an energy function for neural networks "designed to transform and store a large variety of patterns. Our analysis includes systems which possess infinitely many equilibrium points" (*7*, p. 818), examples of which have been constructed (*8*). These networks are

$$\frac{du_i}{dt} = a_i(u_i)\left[b_i(u_i) - \sum_{j=1}^{n} c_{ij}d_j(u_j)\right] \qquad (i = 1, \ldots, n) \qquad (3)$$

Given symmetric connections ($c_{ij} = c_{ji}$), the energy function is

$$V = -\sum_{i=1}^{n}\int_0^{u_i} b_i(\xi_i)d_i'(\xi_i)d\xi_i + \frac{1}{2}\sum_{j,k=1}^{n} c_{jk}d_j(u_j)d_k(u_k) \qquad (4)$$

Along system trajectories

$$\frac{d}{dt}V = -\sum_{i=1}^{n} a_i(u_i)d_i'(u_i)\left[b_i(u_i) - \sum_{k=1}^{n} c_{ik}d_k(u_k)\right]^2 \qquad (5)$$

If $a_i(u_i) \geq 0$ and $d_i'(u_i) \geq 0$, then $\frac{d}{dt}V \leq 0$, which is the key property of an energy function. We (M.A.C. and S.G.) have noted that "the simpler additive neural networks . . . are also included in our analysis" (*7*, p. 819). The system represented by Eq. 3 reduces to the additive network (Eq. 1) when $a_i(u_i) = C_i^{-1}, b_i(u_i) = -1/R_i\ u_i + I_i$, $c_{ij} = -T_{ij}$ and $d_j(u_j) = f_j(u_j)$. Then

$$V = \sum_{i=1}^{n}\frac{1}{R_i}\int_0^{u_i}\xi_i f_i'(\xi_i)d\xi_i - \sum_{i=1}^{n} I_if_i(u_i) - \frac{1}{2}\sum_{j,k=1}^{n} T_{jk}f_j(u_j)f_k(u_k) \qquad (6)$$

which includes the energy functions used in (*1*). We (M.A.C. and S.G.) (*7*) also analyzed the more difficult and physiologically important cases where the cells obey membrane, or shunting, equations and the signal functions $d_j(u_j)$ may have output thresholds.

Thus we consider the "new concept" in (*1*) to be a recent special case of an established neural network theory (*7, 8, 9*).

Hopfield and Tank also assert that "Unexpectedly, new computational properties resulted . . . from the use of nonlinear graded-response neurons instead of the two-state neurons of the earlier models" (*1*, p. 625). It has long been understood that two-state neuronal models differ computationally from graded-response models with sigmoid signal functions (*6, 8, 10*).

The application of neural network theory to technology would be expedited by further consideration of known results (*11*).

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Hopfield and Tank (*1*) present a neural model, a nonlinear feedback circuit, stating that it has a "natural" capacity for solving optimization problems. They amplify this idea with two examples: the traveling salesman problem (TSP) and the analog-to-digital converter.

It is recognized that neural functions and control mechanisms of most involuntary actions are optimized during evolution and ontogenesis. This, however, is not the same thing as solving abstract optimization problems. For instance, how good are human beings at solving the TSP? The main objection to this model is that the neuropsychological functions are not sufficiently localized and specified for this type of high-level semantic representation (*2*). In particular, there are two "unnatural" features in this approach. First is the special meaning attributed to each neuron, for example, in the TSP [figure 5 of (*1*)], "A given neuron ($V_{X,j}$) represents the hypothesis that city X is in position j in the solution." Although it is emphasized that the TSP is a nonbiological problem, the most important processes—formulation of the problem, generation of a circuit analogy, feeding of input information, and decoding of the outputs—are defined by the authors, not by the system. As a physical model, this network is therefore incomplete for simulating biological computation. On the other hand, a circuit is already known (*3*) in which a topographic order corresponding to a certain degree of semantical differentiation will be formed by self-organization.

The second "unnatural" feature of their approach is the dedicated architecture or connectivity between the "neurons" which must be tailored for every problem. The authors apply hindsight in designing the model: by conjecturing the form of the energy function corresponding to the system structure and parameter values or by computing them backward from the output state, they end up with the solution to the problem. This is especially apparent in the analog-to-digital converter example.

The authors also state that their network implements associative memory in a "natural" fashion. This was in fact the main result of their original work (*4*). Similarly, in their recent article the network interconnectivity is assumed a priori to be proportional to the correlation matrix of the wanted state vectors. If this network were to implement a genuine associative memory with a physical mechanism for both storage and recall, the network structure of (*4*) could be used (*5*), but the couplings should be formed adaptively, relating to the input and output signal values actually occurring all the time. Such a process then needs additional mathematical analysis (*5, 6*).

Depending on the nature of interconnectivity, the output state of such a feedback system may then relax to the linear range (*6*) or to saturation (*1, 3, 4, 7*). Learning or adaptive effects seem to take place in the former ("linearized") mode, while no learning appears to have been involved in (*1*) or (*4*).

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Hopfield and Tank (*1*) review the use of networks for computation. Many current investigations are based on Hopfield's observation (*2*) that the asymptotic behavior of the flow of activity in a neural network (*3*) can be described by a simple potential function (*4*). Some computational problems can be transformed into a more-or-less equivalent optimization problem by a so-called regularization procedure (*5*, *6*). Hopfield's potential function provides the link between this optimization problem and its solution in terms of neural network, since in the network the potential is automatically minimized (*1*); and by proper choice of the network parameters, notably the neuronal interconnections, one can produce any potential function which is a polynomial of a second order (*4*). A new result is that, approximately, any minimization problem can be broken down into two minimization problems for second-order functionals (*7*), and thus can be solved by an appropriately constructed neural network.

In particular for linear optimization problems this transformation into a second-order minimization problem (*8*) and the corresponding network solution appear to be very natural (*6*, *9*). In general it is, however, not at all clear under which conditions this transformation of the original problem into a network computation is reasonably economic (for example, in terms of the size of the network). In many cases a quite different, more economic network solution may present itself immediately (*10*).

From the point of view of economy it would be desirable to compare not only different network approaches with one another, but to compare network approaches to more conventional approaches to computation. Since these network approaches have a strong impact on analog computing and special-purpose machines—as opposed to their effect on the conventional von Neumann computer architecture—it is often difficult to compare the computational complexity of these new network procedures to that of more conventional computing approaches.

The long-standing problem of realizing an associative memory that can be addressed by arbitrary parts of a (stored) pattern—often referred to as the problem of pattern matching for content-addressable memories—has also been considered in the framework of these networks (*11–13*). In this particular case it seems possible to compare the network solution to more conventional pattern-matching approaches (*14*) in terms of their computational complexity, that is, the number of operations needed in the retrieval of a stored pattern from a (sufficiently large) part of it (*15–17*). Such a comparison may seem to favor the conventional approaches because of the common conviction that a network of n neuron-like elements (or nodes) can only store less than n patterns reliably (*2*, *16*). However, the immense possibilities provided by appropriate coding of the patterns to be stored have been widely overlooked. In fact, a proper coding of the patterns to be stored into sparse 0-1-sequences (that is, sequences containing mostly zeroes) makes it possible to store effectively (*18*) much more than n patterns in a network of n (neuron-like) elements (*19*). More exactly, if z patterns, each containing x bits of information, have to be stored, one can use a network of $n = 2\sqrt{x \cdot z}$ elements, provided that the patterns are coded into 0-1-sequences of length n that contain all the same low number ($k \approx \sqrt{x}$) of ones (*20*). In the retrieval one would conventionally need $b \cdot z$ comparisons ($1 < b \leq x$), whereas the network performs only less than $k \cdot n \approx 2x\sqrt{z}$ simple counting operations.

Therefore, if z (the number of patterns to be stored) is large compared to x (the information content of one pattern), a situation that is quite typical for the usual applications, then the network method is computationally simpler than conventional methods, and also the number of patterns that can be stored (z) is considerably larger than the number of network elements (n), which is in clear contradiction to Hopfield's estimate (*2*) $z \approx 0.15\ n$. But this associative memory network only works so well if the patterns are coded sparsely [the probability of a nonzero element in a codeword should be $k/n \approx 1/(2\sqrt{z})$, whereas usually, for instance in the spin-glass literature, it is assumed to be about 1/2]. Consequently the next step in the network approach to memory should be the investigation of sparse-coding techniques.

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3. Some authors consider the same equations as a so-called spin-glass model. The relation between neural networks and physical spin-glass models is explained, for example, by W. Kinzel [*Z. Phys. B* **60**, 205 (1985)]. Spin-glass models were first related to optimization problems by S. Kirkpatrick, C. D. Gelatt, and M. P. Vecchi [*Science* **220**, 671 (1983)].
4. The function is given by $H\ (x_1, \ldots, x_n) = -(1/2)\sum_{ij} c_{ij}x_ix_j + \sum_i x_i\theta_i$, where $(x_1, \ldots, x_n)$ is the vector of neural activities, $c_{ij} = c_{ji}$ is the symmetric matrix of connection-strengths between neurons, and $(\theta_1, \ldots, \theta_n)$ are the neural thresholds. Note that $H(x_1, \ldots, x_n)$ is the general second-order polynomial functional, although the connectivity matrix c_{ij} has to be symmetric for the potential-function formalism.
5. The idea probably goes back to A. N. Tikhonov [*Soviet Math. Dokl.* **4**, 1035 (1963)].
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7. I have shown [G. Palm, *Biol. Cybern.* **34**, 49 (1979)] that any functional $S(x_1, \ldots, x_n)$ can be approximated as $S = \sum_i a_1 \exp(L_i x)$, where the L_i are linear functionals of the vector $x = (x_1, \ldots, x_n)$. The problem $S^2(x)$ = min! can be reduced to the two problems (i) $S^2(y) = \sum_{ij} a_ia_jy_iy_j$ = min! and ln $y_i = L_i x\ (i = 1, 2, \ldots)$, solve for x! Both problems can be solved by network methods [compare methods in (*4*), (*6*), and (*9*)].
8. That is, an optimization problem where the functional to be minimized is a second-order polynomial, such as the function H in (*4*).
9. D. W. Tank and J. J. Hopfield, *IEEE Trans. Circuits Syst.* **CAS-33**, 533 (1986). If the problem is simply to solve a system of linear equations as in the second problem in (*7*), then the regularization leads to the classical pseudo-inverse of a matrix [compare also (*11*)].
10. For example, in the traveling salesman problem, compare J. J. Hopfield and D. W. Tank, *Biol. Cybern.* **52**, 141 (1985).
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18. That is, with very low error probability in the recall.
19. This is already obvious from (*12*), but see also (*15*) and (*17*).
20. G. Palm, in *Brain Theory*, G. Palm and A. Aertsen, Eds. (Springer Verlag, Berlin, 1986), pp. 211–228.

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Response: The intellectual thrust of our article (*1*) was to show the neurobiologist how a conceptual framework and methodology could be used to understand how a class of model neural circuits solve specific computational problems. In addition, we used examples of model circuit computation to illustrate the general problems neurobiologists face in understanding computation in biological neural circuits.

The use of Liapunov functions in stability analysis is widespread in physics and engineering. An energy function (Liapunov function) applicable to the task of mapping specific problems onto neural networks with symmetrical connections was first proposed by Hopfield in 1982 (*2*). The importance of this energy function is that it can be used with a theory and methodology which together provide an understanding of how specific problems could be solved by these networks. This is a central idea in the work we reviewed (*1*), and it distinguishes this work from that cited by Carpenter, Cohen, and Grossberg. As discussed in (*1*), the methodology and conceptual framework together with this function were first used to understand the mapping of associative memory onto a model neural circuit having discrete, stochastic (*2*), or continuous (*3*) response. The approach was determined to be of general use when it was used to map more conventional combinatorial optimization problems onto similar neural networks