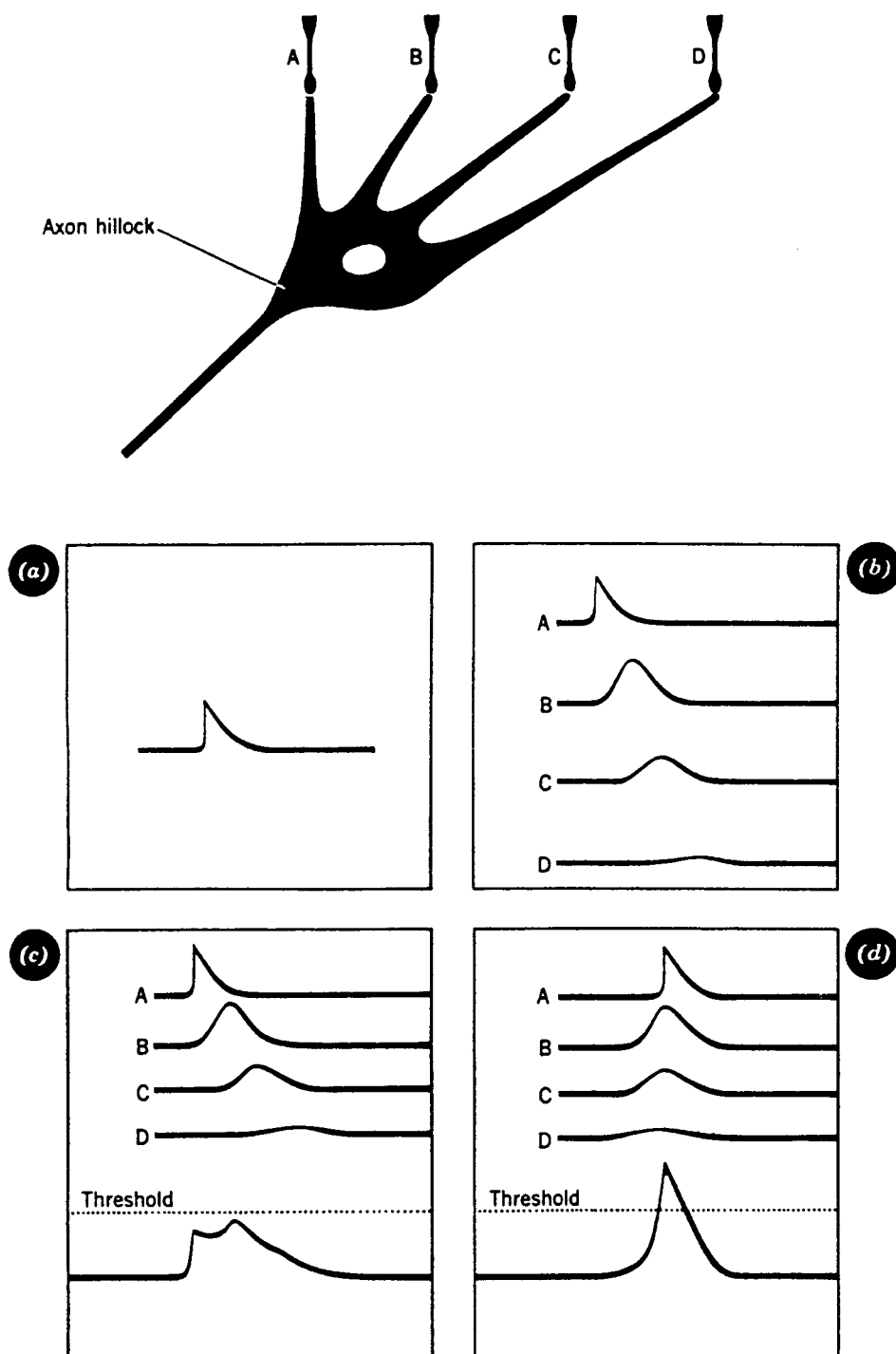


DENDRITIC PROCESSING). A highly simplified example (Figure 2) shows how the properties of nervous tissue just presented would indeed allow a simple neuron, by its very dendritic geometry, to compute some useful function (cf. Rall, 1964, p. 90). Consider a neuron with four dendrites, each receiving a single synapse from a visual receptor, so arranged that synapses A, B, C, and D (from left to right) are at increasing distances from the axon hillock. (This is not meant to be a model of a neuron in the retina of an actual organism; rather, it is designed to make vivid the potential richness of single neuron computations.) We assume that each receptor re-

acts to the passage of a spot of light above its surface by yielding a generator potential which yields, in the postsynaptic membrane, the same time course of depolarization. This time course is propagated passively, and the farther it is propagated, the later and the lower is its peak. If four inputs reached A, B, C, and D simultaneously, their effect may be less than the threshold required to trigger a spike there. However, if an input reaches D before one reaches C, and so on, in such a way that the peaks of the four resultant time courses at the axon hillock coincide, the total effect could well exceed threshold. This, then, is a cell that, although very



**Figure 2.** An example, conceived by Wilfrid Rall, of the subtleties that can be revealed by neural modeling when dendritic properties (in this case, length-dependent conduction time) are taken into account. As shown in Part C, the effect of simultaneously activating all inputs may be subthreshold, yet the cell may respond when inputs traverse the cell from right to left (D). (From Arbib, M. A., 1989, *The Metaphorical Brain 2: Neural Networks and Beyond*, New York: Wiley-Interscience, p. 60. Reproduced with permission. Copyright © 1989 by John Wiley & Sons, Inc.)

simple, can detect direction of motion across its input. It responds only if the spot of light is moving from right to left, and if the velocity of that motion falls within certain limits. Our cell will not respond to a stationary object, or one moving from left to right, because the asymmetry of placement of the dendrites on the cell body yields a preference for one direction of motion over others (for a more realistic account of biological mechanisms, see DIRECTIONAL SELECTIVITY). This simple example illustrates that the *form* (i.e., the geometry) of the cell can have a great impact on the *function* of the cell, and we thus speak of *form-function* relations. When we note that neurons in the human brain may have 10,000 or more synapses upon them, we can understand that the range of functions of single neurons is indeed immense.

## Receptors and Effectors

On the "input side," receptors share with neurons the property of generating potentials, which are transmitted to various synapses upon neurons. However, the input surface of a receptor does not receive synapses from other neurons, but can transduce environmental energy into changes in membrane potential, which may then propagate either actively or passively. (Visual receptors do not generate spikes; touch receptors in the body and limbs use spike trains to send their message to the spinal cord.) For instance, the rods and cones of the eye contain various pigments that react chemically to light in different frequency bands, and these chemical reactions, in turn, lead to local potential changes, called generator potentials, in the membrane. If the light falling on an array of rods and cones is appropriately patterned, then their potential changes will induce interneuron changes to, in turn, fire certain ganglion cells (retinal output neurons whose axons course toward the brain). Properties of the light pattern will thus be signaled farther into the nervous system as trains of impulses (see RETINA).

At the receptors, increasing the intensity of stimulation will increase the generator potential. If we go to the first level of neurons that generate pulses, the axons "reset" each time they fire a pulse and then have to get back to a state where the threshold and the input potential meet. The higher the generator potential, the shorter the time until they meet again, and thus the higher the frequency of the pulse. Thus, at the "input" it is a useful first approximation to say that intensity or quantity of stimulation is coded in terms of pulse frequency (more stimulus  $\approx$  more spikes), whereas the quality or type of stimulus is coded by different lines carrying signals from different types of receptors. As we leave the periphery and move toward more "computational" cells, we no longer have such simple relationships, but rather interactions of inhibitory cells and excitatory cells, with each inhibitory input moving a cell away from, and each excitatory input moving it toward, threshold.

To discuss the "output side," we must first note that a muscle is made up of many thousands of muscle fibers. The motor neurons that control the muscle fibers lie in the spinal cord or the brainstem, whence their axons may have to travel vast distances (by neuronal standards) before synapsing upon the muscle fibers. The smallest functional entity on the output side is thus the *motor unit*, which consists of a motor neuron cell body, its axon, and the group of muscle fibers the axon influences.

A muscle fiber is like a neuron to the extent that it receives its input via a synapse from a motor neuron. However, the response of the muscle fiber to the spread of depolarization is to contract. Thus, the motor neurons which synapse upon the muscle fibers can determine, by the pattern of their impulses, the extent to which the whole muscle comprised of those fibers contracts, and can thus control movement. (Similar remarks apply to those cells that secrete various chemicals into the bloodstream or gut, or those that secrete sweat or tears.)

Synaptic activation at the *motor end-plate* (i.e., the synapse of a motor neuron upon a muscle fiber) yields a brief "twitch" of the muscle fiber. A low repetition rate of action potentials arriving at a motor end-plate causes a train of twitches, in each of which the mechanical response lasts longer than the action potential stimulus. As the frequency of excitation increases, a second action potential will arrive while the mechanical effect of the prior stimulus still persists. This causes a mechanical summation or fusion of contractions. Up to a point, the degree of summation increases as the stimulus interval becomes shorter, although the summation effect decreases as the interval between the stimuli approaches the refractory period of the muscle, and maximum tension occurs. This limiting response is called a *tetanus*. To increase the tension exerted by a muscle, it is then necessary to recruit more and more fibers to contract. For more delicate motions, such as those involving the fingers of primates, each motor neuron may control only a few muscle fibers. In other locations, such as the shoulder, one motor neuron alone may control thousands of muscle fibers. As descending signals in the spinal cord command a muscle to contract more and more, they do this by causing motor neurons with larger and larger thresholds to start firing. The result is that fairly small fibers are brought in first, and then larger and larger fibers are recruited. The result, known as Henneman's Size Principle, is that at any stage, the increment of activation obtained by recruiting the next group of motor units involves about the same percentage of extra force being applied, aiding smoothness of movement (see MOTOR NEURON RECRUITMENT).

Since there is no command that a neuron may send to a muscle fiber that will cause it to lengthen—all the neuron can do is stop sending it commands to contract—the muscles of an animal are usually arranged in pairs. The contraction of one member of the pair will then act around a pivot to cause the expansion of the other member of the pair. Thus, one set of muscles *extends* the elbow joint, while another set *flexes* the elbow joint. To extend the elbow joint, we do not signal the *flexors* to lengthen, we just stop signaling them to contract, and then they will be automatically lengthened as the *extensor* muscles contract. For convenience, we often label one set of muscles as the "prime mover" or *agonist*, and the opposing set as the *antagonist*. However, in such joints as the shoulder, which are not limited to one degree of freedom, many muscles, rather than an agonist-antagonist pair, participate. Most real movements involve many joints. For example, the wrist must be fixed, holding the hand in a position bent backward with respect to the forearm, for the hand to grip with its maximum power. *Synergists* are muscles that act together with the main muscles involved. A large group of muscles work together when one raises something with one's finger. If more force is required, wrist muscles may also be called in; if still more force is required, arm muscles may be used. In any case, muscles all over the body are involved in maintaining posture.

## Neural Models

Before presenting more realistic models of the neuron (see PERSPECTIVE ON NEURON MODEL COMPLEXITY; SINGLE-CELL MODELS), we focus on the work of McCulloch and Pitts (1943), which combined neurophysiology and mathematical logic, using the all-or-none property of neuron firing to model the neuron as a binary discrete-time element. They showed how excitation, inhibition, and threshold might be used to construct a wide variety of "neurons." It was the first model to tie the study of neural nets squarely to the idea of computation in its modern sense. The basic idea is to divide time into units comparable to a refractory period so that, in each time period, at most one spike can be generated at the axon hillock of a given neuron. The McCulloch-Pitts neuron (Figure 3A) thus operates on a discrete-time scale,  $t = 0, 1, 2, 3, \dots$ , where the