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A LAYERED NETWORK MODEL OF SENSORY CORTEX

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ABSTRACT

An integrated computational approach to modeling sensory systems which couples realistic layered neural models of sensory cortex and midbrain nuclei to detailed models of the sense organs (e.g., retina or cochlea) is described. The approach is applied to the auditory system. Through an exercise of the model, it is shown that spatial location of sounds may be a natural consequence of the way cochlear response is mapped onto the cortex.

INTRODUCTION

"I am the set of neural firings taking place in your brain as you read the set of letters in this sentence and think of me."

(D Hofstadter, Metamagical Themas)

Neurobiological systems embody solutions to many difficult problems such as associative memory, learning, pattern recognition, motor coordination, vision and language. It appears they do this via massive parallel processing within and between specialized structures. The mammalian brain is a marvel of coordinated specialization. There are separate areas for each sense modality, with massive intercommunication between areas. There are topographic maps, many specialized neuron types, and quasi-regular small scale structure (columns and layers) which vary from area to area to accommodate local needs, and plasticity

in connections between neurons. Feedback occurs on many levels. This complexity is apparently necessary for the kind of multi-mode processing that brains perform but it's not clear how much of this structure is necessary to perform isolated tasks such as vision or speech recognition, nor do we know if nature's solutions are optimal. (See Chapter 8 of Oster & Wilson (1978), for example, for an interesting discussion of optimization in biology.)

Regardless of whether the brain represents the optimal structure for cognitive processes, it is the only successful one we know of. By analyzing it and modeling it, we may learn the principals on which it operates, and presumably be able to apply these principals to computer technology.

Our knowledge of neural systems originates with experimental studies. Experimental data should lead to conceptual models, ultimately to computational theories, which can be implemented through well-defined algorithms (Marr, 1982). These provide a tool for high-level information processing whose worth can be evaluated explicitly. If one is interested in their biological or psychological validity, model predictions can be tested with further biological measurements. This usually leads to new theories and algorithms.

No comprehensive computational theory of the brain has been established at present, although some interesting work in this direction is developing (Pellionisz, 1984). There is a great deal of data on the hardware the brain uses; namely, its anatomy and its physiology. There is also some understanding of the algorithms (transformations) that the brain employs on sensory input. The fuzziest area of our knowledge of the brain concerns exactly what the brain is computing and why.

Models of cognitive processing are at present highly idealized and simplified. Nevertheless, they show the rich behavior that neural systems are capable of.

In the area of learning and pattern recognition, a fruitful theoretical approach has been the study of neural networks. Much of the work in this field has focused on the mathematical properties of nets with varying degrees of realism (Clark, Rafelski & Winston, 1985). Recently, the minimum energy theory (Hopfield, 1982) has led to a breakthrough in the ability of networks to perform cognitive functions. Capacity has increased as structure increases from symmetric neural connections (Ackerly, Hinton & Sejnowski, 1985) to nonsymmetric (Lapedes & Farber, 1985) to high-order correlation (Chen, et al., 1986) models. Another viewpoint that promises to be very powerful is the application (Hogg & Huberman, 1984; 1985) of concepts from dynamical systems theory to neural networks.

These studies (1) generally look at neural nets in isolation; that is, without simulating the kind of sensory input that real neural systems operate on; (2) do not attempt to implement the actual structure of parts of the nervous system, such as cortex, that presumably are necessary for recognition, memory, etc. One recent study (Krone, et al., 1986) does incorporate some of the detail of mammalian cortex, but still makes many simplifications with regard to neuron types and their connectivity. Also, no plasticity was allowed in synaptic strengths (an important process, as shown, e.g., by Buhmann & Schulten (1986)); and the processing of sensory data that occurs in subcortex structures was omitted. (Even so, several interesting features were seen in that model's behavior.)

The goal of the project described in this paper is to build a biologically valid model of a sensory system, which integrates what is known both structurally and physiologically at several levels, from the peripheral sense organ to the midbrain nuclei to the cortex. Despite the complexity of these systems,

there is a great deal of data available at each level to permit a fairly realistic model for some sensory systems (vision, hearing, and olfaction), although simplifications in scale must be made especially at the cortex level to remain within present computer memory and speed limits. Attractive features of such a model are that it: 1) includes more structure (and presumably more processing capacity) than previous models, 2) provides each subsystem with the kind of input that the biological counterpart receives (to understand what the brain is doing requires a clear description of the data it operates on), 3) emphasizes the dynamic or time dimension, 4) provides a means of testing theories about sensory perception. In the remainder of this article, the structure of the cortex and subcortical nuclei are discussed in the context of a particular sensory system, the auditory. A computational model is presented, and results of an application of the model are shown.

LAYERED NEURAL SYSTEMS

A great deal of experimental work over the last hundred years has slowly revealed the intricacies of the structure of the mammalian brain. Input from the periphery reaches the brain either through the spinal cord or special cranial nerves. These neural signals pass through a variety of midbrain nuclei (large groups of neurons) before they finally reach the cortex (outer surface of the brain). The cortex is actually a collection of fairly well-defined cortical regions (Fig. 1) each of which is dedicated to a specific cognitive function, such as visual processing. Massive communication occurs between most of these regions.

Although our knowledge of the cortex is still incomplete, many features are well established. The cortex consists of several (generally six) layers of neurons (see Fig. 2), each layer having a characteristic composition of specific neuron types (Truex & Carpenter, 1969). (The nuclei of the lower brain are also layered structures.) The number and thickness of layers varies in different regions of the brain (Fig. 3), presumably reflecting differences in function. The upper layers of the cortex are fairly recent in the evolutionary development of the mammalian brain. These layers are especially rich with neurons in man. Neural activity follows a generally vertical pattern; signals from the periphery enter mainly in layer 4, pass to the upper layers and then to the lowest layers, and then back up. Neurons in the upper layers also project to other cortical areas and neurons in the lower layers also project to subcortical nuclei. In addition to the layered structure a vertical columnar organization has been established through physiological measurements. These columns are roughly 0.5 mm in diameter and contain several thousand cells. Cells within a column

generally exhibit the same sensitivity to sensory stimuli. Considerable lateral interaction between columns is now known (Imig & Morel, 1983) to occur.

Neurons are very complex structures. Neurons receive input on their dendrites, a collection of branch-like processes which radiate from the soma (body) of the neuron for many microns to millimeters. Input signals from other neurons travel down the dendritic branches, decaying as they travel towards the soma where they are summed. If the membrane potential is raised sufficiently, an action potential will travel down the neuron's axon. Axons can extend for considerable distances, up to millimeters in the cortex, to meters in the periphery. Axonal projections frequently branch, sending collaterals to several layers. Transmission from one neuron to another occurs at synaptic junctions via chemical transmission (in almost all cases). A large number of transmitter molecules have been identified. Some transmitters produce an inhibitory effect on the receiving neuron, while others are excitatory; the nature of the effect depends on the type of receptors on the receiving neuron. Each neuron usually receives input from many (up to thousands) of other neurons; each neuron typically transmits to many neurons.

The neurons found in the cortex layers come in a great variety of forms. Roughly, nine or ten types of cortical neurons have been identified with many subtypes recognized. Cortical neurons are not arranged haphazardly. Certain neuron types are found in certain layers and not others. Some neurons, such as basket cells, synapse only on one or two types of neurons. Axonal projections are fairly specific as to the layers they reach. Two commonly found cortical neurons are shown in Figs. 4 and 5.

STRUCTURE OF THE AUDITORY SYSTEM

The sensory system considered in this paper is the auditory. The comprehension of sound and speech begins with transduction of sound waves into transient motions of the basilar membrane of the cochlea in the inner ear (Figs. 6, 7, and 8). Displacements of the basilar membrane lead to discharge of hair cells in the organ of Corti and generation of action potentials in auditory nerve fibers. A particular frequency will cause peak displacement at a characteristic location along the basilar membrane. The dynamics of the organ of Corti is still a subject of great interest (Hudspeth, 1985). Details of cochlear structure and function are given by Pickles (1982).

The auditory nerve bundle feeds into several nuclei in the lower brain and midbrain regions before the cortex is reached (Fig. 9). Some of these nuclei use auditory input to initiate behavior such as head turning and other reflex actions. Others serve to sharpen auditory input and to integrate input from each ear. Fibers from all these nuclei converge onto the auditory cortex. More details are given in the review article of Imig and Morel (1983).

In the auditory system, the cortex surface is organized into several tonotopic maps. In a tonotopic map, a particular point on the cochlear basilar membrane (representing a particular frequency) maps to a specific strip of tissue in the auditory cortex. At least four are known in the cat brain (Fig. 10); two are very specific maps, the other two are diffuse. This multiplicity of frequency maps also appears in various nuclei of the medial geniculate body. The tonotopic map is conserved throughout the auditory system, but mappings onto isofrequency strips are both divergent and convergent (Fig. 11). Association fibers connect isofrequency curves from each map onto the corresponding isofrequency curves in the other maps. Along an isofrequency

curve, each ear is represented by alternating clusters of neurons. It is believed (Merzenich, Jenkins & Middlebrooks, 1984) that this second dimension of the auditory cortex map is used with the frequency map to accomplish spatial localization of sound.

Little is known about processing of auditory data at higher levels of the brain, except that neural activity extends outward from the primary auditory area to associational areas and is integrated with other sense modalities. There is of course a strong interaction with the speech generation areas (Wernicke and Broca). Most of the experimental work has used cats, with some measurements in owls and monkeys. Recently, the human auditory cortex has become accessible via the magnetoencephalographic (MEG) technique.

THE MODEL

A three-part mathematical model of the auditory system has been developed. It includes a hydromechanical model of the cochlea with hair cell innervation for studying transduction of sound into basilar membrane motion and then into neural signals. This model is similar to others (Allen, 1977; Holmes, 1982) that have been studied, but attempts to treat the temporal dimension more realistically. Output from this portion of the auditory model can be and is being compared to auditory nerve recordings. The second portion applies layered neural networks to simulate auditory processing in nuclei such as the dorsal cochlear nucleus. Several of these nuclei have a relatively simple structure (two or three layers with feed forward only) and, based on recent studies, (Shamma, 1985 a, b) use lateral inhibition to sharpen the auditory signal train. The medial geniculate nucleus (MGN) has a more complex structure involving feedback within itself and with the cortex to which it projects. The third part of

the model attempts to simulate neural activity in the auditory cortex, including feedback to the midbrain nuclei. Because of the extremely large number of neurons and interconnections between neurons in the brain, only a very small portion of the cortex (roughly a few square millimeters) can be modeled in great detail, and even then certain aspects such as connection to other cortex areas will be difficult or impossible on present computers. Alternatively, a coarser-grained model can be used to approximate an "average" structure of larger cortex regions. Even these crude models may contain enough structure to have cortex-like dynamics. The emphasis in this paper is on the application of this third part of the model to auditory processing.

A general neural network model is used to simulate cortex-like structures. The model, a computer code called LCM, operates in discrete time (a continuous time version is under development). It allows a variable number of layers, number of neurons and neuron types. The composition of each layer is determined by the user. For each layer, the types of neurons are specified, as well as the spatial density (number/unit area) for each type, radii of influence (distance over which a neuron's axonal projections and dendrites extend in each direction in each layer), refractory periods and the excitatory or inhibitory character of each type. The effect of electrotonic transport from the point of synaptic junction to the cell body is included via space constants. Neurons can send axonal projections into multiple layers and dendrites can extend beyond a single layer. Within radii of influence, actual connections between neurons are determined on a probabilistic basis. Two or three-dimensional structures can be created. Input stimuli to a network can be simple or time-dependent and can be fed in as a topographic map and in a "dual" manner to simulate input from multiple sources, e.g., binaural input. Special routines are used to simulate peripheral sensory organs - the retina for vision and the cochlea for hearing,

with options to present realistic stimuli, such as a bar moving across the retinal field, or a word's sound train entering the cochlea. Super networks can be created which consist of layered neural networks that communicate with one another. In this way, different sense modalities can be coupled, and thalamic nuclei and cortex can communicate in both directions. The state of each neuron at each time step is determined by summing inputs from all other neurons, subtracting its threshold value and then, if the neuron is not in a refractory state, using the Fermi probability to calculate whether the neuron fires an action potential. It is assumed that plasticity in connectivity is governed by a differential Hebbian rule (Kosco, 1986) in which connection strength depends on previous activity (increases with use, decreases with disuse), with the restrictions that the sign (excitatory or inhibitory) of a connection cannot change and that connection strength is bounded.

To demonstrate the LCM model, a six-layer, two-dimensional simulation of cortex containing the neuron types (Imig & Morel, 1983; Pickles, 1982, Gilbert, 1983; Kolb & Whishaw, 1985; Shepherd, 1979) described in Tables I-III was constructed. It has been assumed that neuron types in the auditory areas are approximately the same as those found in other cortex areas. Input stimuli are directed into layer 4. The flow of neural activity is then up into layers 2 and 3 (and 1), then down to layers 5 and 6. Activity flows from layers 5 and 6 back up to 4 and the upper layers, creating an iterated loop. Pyramidal cells in layers 2, 3, and 6 are assumed to represent output units. Input vectors were constructed to represent approximately the frequency and temporal patterns seen for words and syllables in auditory nerve recordings (Sinex & Geisler, 1984) in animals and voice spectrographs in humans.

Figures 12 and 13 show connectivity for two neurons obtained on one simulation involving 600 neurons. In Fig. 12, a particular pyramidal cell in layer 6

(indicated by "x") receives input from many neurons in layer 5 (remember the long range of pyramidal cell axons in layer 5 shown in Fig. 5) as well as pyramidal cells in layers 2 and 3. Apical dendrites extend into layer 1 where they receive input from the horizontal cells. Figure 13 shows neurons which connect to a layer 2 pyramidal cell. Note the essentially vertical structure. The set of neurons connecting to each neuron will vary even within the same neuron type because of the randomness factor used in determining connections.

An input stimulus was directed into layer 4. This stimulus had a repeat rate of 20 msec and components at 4 frequencies corresponding to locations at $x = 183-267$, $x = 333-333$, $x = 450-500$, and $x = 670-750$ in Fig. 14. Figure 14 shows contours of activity in the cortex model at 100 msec. The x-axis represents distance along the cortex in the direction of increasing frequency (topographic map). The y-direction represents vertical position, i.e., $y = 0$ is the bottom of the deepest layer, while $y = 6000 \mu\text{m}$ represents the top of the cortex. The columnar nature of the activity is immediately apparent. In addition, activity is segregated vertically into three regions - high activity in the upper layers (layers 2 and 3), moderate to high activity in the lower layers (5 and 6), and low or inhibitory activity in layer 4 (about $y = 2000$ in Fig. 14). At later times (several hundred msec), layer 4 is strongly inhibited, as though the cortex were trying to turn off or ignore a constant input signal. Total activity shows a definite decrease around 50-60 msec after introduction of the input signal. This may represent the time required for the cortex model's processing to be effected. The overall pattern of behavior is very much like that proposed by Edelman and Finkel (1984).

Activity in individual neurons varies greatly. Figures 15 and 16 show spike trains from two model pyramidal cells. For one, the input triggers a rapid burst of activity for 50 msec followed by a silent period until a little

over 100 msec, with renewed activity thereafter. For the other, not much activity occurs until after 50 msec, and activity varies. Connection strength can also show interesting behavior. In Fig. 17, the total strength of all connections to a particular pyramidal cell oscillates in time in a sawtooth fashion. Another neuron (Fig. 18) shows a more erratic evolution. These small fluctuations in connectivity strength allow the model cortex to modulate its activity on the basis of past experience.

A method of characterizing the behavior of a layered network with the structure described is required. The overall activity of the system can be plotted. Activity vs. time of individual neurons, and connection strength between any two neurons can be generated. Contour plots of activity on any vertical or horizontal plane through the system can also be generated. These output forms can be compared to physiological measurements to validate the model as well as to visualize the global or local behavior vs. time of the net. However, to get a handle on what the model is doing, to quantify its capacity for learning or discriminating, some additional functional is needed. The concept of iterated maps may provide the needed metric.

Table I Distribution of dendrites and axons of primary excitatory neurons

Neuron Type	Layer Containing Cell Body	Layers for Apical Dend.	Layers for Basal Dend.	Layers for Axonal Proj.
Pyramidal	2	1	2	2,3,5,6
Pyramidal	3	1	3	2,3,5,6
Spiny Stellate	4	1,4	4	2,3,5,6
Pyramidal	5	1,4,5	5	2,3,5,6
Spindle	6	1,4	6	2,3,4,5,6

Table II Distribution of dendrites and axons of two excitatory intracortical neurons

Neuron Type	Layer Containing Cell Body	Layers for Dendrites	Layers for Axons
Horizontal Cell	1	1	1
Martinotti Cell	2	2	1
Martinotti Cell	3	3	1,2
Martinotti Cell	4	4	1,2,3
Martinotti Cell	5	5	2,3,5
Martinotti Cell	6	6	2,3,5,6

Table III Common inhibitory neurons in the cortex

Neuron Type	Layer Containing Cell Body	Layers for Dendrites	Layers for Axons
Golgi II	1	1	1
Golgi II	2	2	2
Chandelier	2	2	1,2
Golgi II	3	3	3
Basket	3	3	3
Chandelier	3	3	1,2,3
Golgi II	4	4	4
Basket	4	4	4
Double Piquet	4	4	1,2,3,4,5,6
Golgi II	5	5	5
Basket	5	5	5
Golgi II	6	6	6

CORTEX DYNAMICS AND ITERATED MAPS

An iterated function $f^n(x)$ is defined as

$$f^n(x_0) = x_n = f(x_{n-1}), \quad (1)$$

$$x_{n-1} = f(x_{n-2}), \dots, x_1 = f(x_0), \text{ i.e.,}$$

$$f^n(x) = f(\dots f(f(x)) \dots) \text{ where } f \text{ is applied } n \text{ times.}$$

Nonlinear functions allow a rich variety of behavior under iteration (Feigenbaum, 1980; Peitgen & Richter, 1985). Stable points may exist which act as attractors. The iterated function maps a set of points $X(i)$ the basin of attraction, into the attractor point y . For a system evolving in time, the membership of basins of attraction may change as well as the attractor set.

Our multi-layered model of the cortex is an iterated function. The looping from middle to upper to lower to middle layers provides the iteration and the all-or-none firing of model neurons provides the nonlinearity. Plasticity in the connection strengths allows for modifications of attractor points and basins of attraction.

In the auditory system, a word can be recognized despite differences in intensity, frequency shifts, and time duration. In the model this behavior is approximated when

$$f^n(ax_{1+m}^j(bt)) \rightarrow f^n(x_1^j(t)) \quad (2)$$

for an appropriate range of (a, b, m) where $\underline{x}_1^j(t)$ is the rate of firing of input neurons corresponding to frequency i (or location i because of the topographic mapping) for input pattern j , subscript m represents a shift in frequency, a corresponds to a change in intensity or rate of firing, b effects a time dilation. The underbar indicates a reference point, i.e., $\vec{x}^j(t) = (\underline{x}_1^j, \underline{x}_2^j, \dots, \underline{x}_n^j)$ is the input vector at a reference intensity, time duration and frequency. The arrow in Eq. (2) means that the iterated map of the transformed pattern reaches the same limit point as the iterated map of the reference pattern after a sufficient number of iterations.

Iterated maps are the subject of intense research activity in the field of dynamical systems theory. The maps represented by cortical activity involve many degrees of freedom and display a stochastic quality. The theory for such systems is still far from well-developed. However, there are strong suggestions that they are capable of having extremely large numbers of attractors and can converge very rapidly, two features that cortex seems to have. Studies of equation (2) in the context of the auditory system are in progress, but results will not be presented here.

3-D APPLICATION

A three-dimensional model has been constructed based on an hypothesis (Merzenich, et al., 1984) for spatial localization of sound. This would also provide a mechanism for separating simultaneous sound inputs. A strict tonotopic mapping is preserved throughout the auditory system. Several maps are recognized in auditory cortex; for each region, a well-defined tonotopic (frequency) mapping defines one of the two surface spatial dimensions. The

other spatial dimension represents a combination of input from both ears, arranged in alternating strips, labelled EE and EI (Fig. 19). In an EE strip, binaural stimulation produces more excitation than monaural stimulation. In EI strips, binaural stimulation results in less excitation than monaural. The contralateral ear in EI and EE is excitatory, the ipsilateral is inhibitory or excitatory.

Intensity and timing differences between the input from the two ears are somehow used by the cortex together with some subcortical auditory nuclei to determine spatial location of sounds simultaneously with the cortex analyzing the informational content of sounds. The spatial location function probably involves the "binaural" dimension of auditory cortex. An interesting feature of this dimension is its alterability throughout life. A possible mechanism of spatial location would simply involve mapping of a sound onto different coordinates of the binaural dimension of auditory cortex, as shown in Fig. 20. The calculation described below shows this is a possibility.

The model has the same layered structure previously described but the input to layer 4 is modified. In the x-direction, a strict tonotopic map is maintained. In the y-direction, (the other horizontal direction) radii of influence are considerably larger for input neurons, and input from each ear is alternated so as to form the EE and EI strips. Also, the number of neurons has been increased to 20,160 and the total number of interconnections has increased strongly, to about 0.77 million. On average, each neuron receives input from about 40 other neurons. Two input trains are directed into the cortex model, one train is slightly shifted in intensity from the other. The resulting activity pattern in the cortex at 100 msec is shown in Figs. 21-24. The calculation was repeated with the input patterns from the ears switched,

representing a shift in spatial location of the sound source. The activity pattern generated by this switched input signal was subtracted at each time step from the field generated in the previous simulation. Figures 25 and 26 show contours of this difference field for layers 3 and 5 at 100 msec. The differences are organized roughly into bands. The same sound maps into different cortical patterns when the binaural input balance changes.

This analysis has many limitations; for example, it does not yet fully represent the processing that occurs in subcortical nuclei, nor does it couple several cortical topographic maps, nor does it include connections to other cortical regions. Also, although it contains a lot of neurons, it is still several orders of magnitude from the actual structure. Nevertheless, it is sufficiently realistic to use in exploring the dynamics of neurophysiological systems.

SUMMARY

A computational model of the auditory system has been developed. Applications include a three-dimensional simulation of auditory cortex with binaural input showing that different spatial locations of sounds, encoded as differences in intensity and timing between the two ears, map into different regions in the auditory cortex.

REFERENCES

- Ackerly, D. H., G. E. Hinton and T. J. Sejnowski (1985). "A Learning Algorithm for Boltzmann Machines," *Cognitive Science*, **9**, 147-169.
- Allen, J. B., (1977). "Two-dimensional Cochlear Fluid Model: New Results," *Journal of the Acoustical Society of America*, **61**, 110-119.
- Brodman, K. (1909). "Vergleichende Lokalisationlehre der Grosshirnrinde in ihren Prinzipien dargestellt auf Grund des Zellenbaues, Leipzig: J. A. Barth.
- Buhmann, J. and K. Schulten (1986). "Associative Recognition and Storage in a Model Network of Physiological Neurons," *Biological Cybernetics*, **54**, 319-335.
- Chen, H. H., Y. C. Lee, G. Z. Sun, H. Y. Lee, T. Maxwell, and C. L. Giles (1986). "High Order Correlation Model for Associative Memory," New York: American Institute of Physics, Conference Proceedings No. 151, Neural Networks for Computing, Snowbird, Utah, 1986, 86-99.
- Clark, J. W., J. Rafelski, and J. V. Winston (1985). "Brain Without Mind: Computer Simulation of Neural Networks with Modifiable Neuronal Interactions," *Physics Reports (Review Section of Physics Letters)*, **123**, 215-273.
- Edelman, G. H. and L. H. Finkel (1984). "Neuronal Group Selection in The Cerebral Cortex," Chapter 22 in G. H. Edelman, W. E. Gall and W. M. Cowan, eds., (1984). *Dynamic Aspects of Neocortical Function*, New York: John Wiley & Sons.
- Feigenbaum, J. (1980). "Universal Behavior in Nonlinear Systems," *Los Alamos Science*, **1**, 4-27.
- Gilbert, C. (1983). "Microcircuitry of the Visual Cortex," *Annual Review of Neuroscience*, **6**, 217-247.

- Hogg, T. and B. A. Huberman, (1984). "Understanding Biological Computation: Reliable Learning and Recognition," Proceedings of the National Academy of Sciences, USA, 81, 6871-6875.
- Hogg, T. and B. A. Huberman (1985). "Attractors on Finite Sets: The Dissipative Dynamics of Computing Structures," Physical Review A, 32, 2338-2346.
- Holmes, M. H., (1982). "A Mathematical Model of the Dynamics of the Inner Ear," Journal of Fluid Mechanics, 116, 59-75.
- Hopfield, J. J., (1982). "Neural Networks and Physical Systems with Emergent Collective Computational Abilities," Proceedings of the National Academy of Sciences, USA, 79, 2554-2558.
- Hudspeth, A. J., (1985). "The Cellular Basis of Hearing: The Biophysics of Hair Cells," Science, 230, 745-752.
- Imig, T. J. and A. Morel (1983). "Organization of the Thalamocortical Auditory System in the Cat," Annual Review of Neuroscience, 6, 95-120.
- Kolb, B. and I. Q. Whishaw (1985). "Principles of Neocortical Organization," Chapter 8 in Fundamentals of Human Neuropsychology, New York: W. H. Freeman and Co.
- Kosco, B. (1986). "Differential Hebbian Learning," New York: American Institute of Physics, Conference Proceedings No. 151, Neural Networks for Computing, Snowbird, Utah, 1986, 277-282.
- Krone, G., H. Mallot, G. Palm and A. Schüz (1986). "Spatiotemporal Receptive Fields: A Dynamical Model Derived from Cortical Architectonics," Proceedings of the Royal Society of London B, 226, 421-444.
- Lapedes, A. S. and R. M. Farber (1986). "Programming a Massively Parallel, Computation Universal System: Static Behavior," New York: American Institute of Physics, Conference Proceedings No. 151, Neural Networks for Computing, Snowbird, Utah, 1986, 283-298.

- Marr, D. (1982). "The Philosophy and the Approach," Chapter 1 in *Vision*, San Francisco: W. H. Freeman & Co.
- Merzenich, M. M., W. M. Jenkins, and J. C. Middlebrooks (1984). "Observations and Hypotheses on Special Organizational Features of the Central Auditory Nervous System," Chapter 12 in G. H. Edelman, W. E. Gall, and W. M. Cowan, eds., *Dynamic Aspects of Neocortical Function*, New York: John Wiley & Sons.
- Oster, G. F. and E. O. Wilson (1978). "A Critique of Optimization Theory in Evolutionary Biology," Chapter 8 in *Caste and Ecology in the Social Insects*, Princeton, N.J.: Princeton University Press.
- Peitgen, H.-O. and P. H. Richter (1985). "Frontiers of Chaos," Universität Bremen: Forschungsgruppe Komplexe Dynamik.
- Pellionisz, A. J. (1984). "Coordination: A Vector-Matrix Description of Transformations of Overcomplete CNS Coordinates and a Tensorial Solution Using the Moore-Penrose Generalized Inverse," *Journal of Theoretical Biology*, 110, 353-375.
- Pickles, J. O. (1982). "Introduction to the Physiology of Hearing," Orlando: Academic Press.
- Shamma, S. A. (1985a). "Speech Processing in the Auditory System I: The Representation of Speech Sounds in the Responses of the Auditory Nerve," *Journal of the Acoustical Society of America*, 78, 1612-1621.
- Shamma, S. A. (1985b). "Speech Processing in the Auditory System II: Lateral Inhibition and the Central Processing of Speech-Evoked Activity in the Auditory Nerve," *Journal of the Acoustical Society of America*, 78, 1622-1632.
- Shepherd, G. M. (1979). "The Synaptic Organization of the Brain," New York: Oxford University Press.

- Sinex, D. G. and C. D. Geisler (1984). "Comparison of the Responses of Auditory Nerve Fibers to Consonant-Vowel Syllables with Predictions from Linear Models," *Journal of the Acoustical Society of America*, 76, 116-121.
- Truex, R. C. and M. B. Carpenter (1969). "The Cerebral Cortex," Chapter 22 in *Human Neuroanatomy*, Baltimore: Williams & Wilkins.
- Von Economo, C. (1929). *The Cytoarchitectonics of the Human Cerebral Cortex*, London: Oxford University Press.

FIGURE CAPTIONS

1. Map of functional areas of brain cortex, (Brodman, 1909).
2. Layered structure of neocortex, (Brodman, 1909).
3. Variations in cortex structure, showing five cortical types: 1) agranular; 2) frontal; 3) parietal; 4) polar; 5) granular, (Economo, 1929).
4. A pyramidal cell in layer 2. Note branching of axonal process, (Gilbert and Wiesel, 1979).
5. A pyramidal cell in layer 5. Apical and basal dendritic regions are visible. Note the very large horizontal extension of axonal collaterals, (Gilbert and Wiesel, 1979).
6. Gross structure of the cochlea.
7. Cross-section of cochlea, showing the three chambers and detailed picture of basilar membrane and organ of Corti, (Allen, 1977).
8. (a) Properties of basilar membrane vary rapidly. Innervation of inner hair cells fairly specific; that of outer hair cells is diffuse.
(b) Traveling wave moves along basilar membrane, causing peak amplitude at a location corresponding to input frequency.
(c) Map of frequency components for two simple sounds.
9. Series of midbrain nuclei in the auditory pathway. Each consists of 2 or 3 layers with very regular structure, (Truex and Carpenter, 1969).
10. Multiple tonotopic maps in cat auditory cortex.
11. (a) Each point on the cochlear partition is represented on a strip of cortical tissue in cortex areas A, AI, P, VP. Association fibers connecting, for example, map A with map P, connect neuron groups of essentially the same frequency, but with considerable divergence in the isofrequency direction.

12. Connectivity to a spindle cell in layer 6.
13. Connectivity to a pyramidal cell in layer 2.
14. Contours of activity at 100 msec. Y-axis represents depth, X-axis is in direction of increasing frequency.
15. Activity of a pyramidal cell from the model simulation.
16. Activity of another pyramidal cell from the model simulation.
17. Connection strength history for a model pyramidal neuron.
18. Connection strength history for another model pyramidal neuron.
19. Two-dimensional map into auditory cortex. In one direction, a well-defined frequency-to-location map is maintained. In the orthogonal direction, alternating bands of excitatory-excitatory and excitatory-inhibitory bands are found, integrating input from the two ears.
20. Intensity and timing differences between signals from the right and the left ear may lead to unique representation in auditory cortex as a function of spatial location, allowing separation of inputs from multiple sound sources.
21. Contours of neural activity in layer 1 at 100 msec.
22. Contours of neural activity in layer 3 at 100 msec.
23. Contours of neural activity in layer 5 at 100 msec.
24. Contours of neural activity in layer 6 at 100 msec.
25. Contours of differences in activity resulting from intensity shift in binaural input, for layer 3 at 100 msec.
26. Contours of differences in activity resulting from intensity shift in binaural input, for layer 5 at 100 msec.

Fig. 6

Neural Response in Cochlea

Traveling wave along basilar membrane

(b)

(c)

Tonotopic Organization in CAT Auditory Cortex

(a)

(b)

layer

MAP OF NEURONS CONNECTING TO NEURON 40 OF TYPE 1 IN LAYER 2

legend

1. pyramidal cell	6. horizontal cell
2. spindle cell	7. basket cell
3. spiny stellate cell	8. chandelier cell
4. Golgi II	9. double bouquet
5. Martinotti	X. cell receiving input from others shown.

layer

MAP OF NEURONS CONNECTING TO NEURON 20 OF TYPE 2 IN LAYER 6

1

6 6 6 6 4 6 6 6

2

1 1 1 1 1

3

1 1 1 1

4

4 4 4

5

1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1

6

2 2 1 2 2
5 5 5

AT
TIME - 100.00

X-Z1

AVERAGE ACTIVITY

ACTIVITY FOR NEURON

AT
I,J - 00

CONNECTION STRENGTH FOR NEURON

AT
I,J - 30-1

Fig. 1

CONNECTION STRENGTH FOR NEURON

^{RT}
I,J - 15-1

Fig. 15-1

EE—contra.+, ipsi.+

E I —contra.+, ipsi.-

Two Dimensional Map onto Auditory Cortex

Auditory 'Cortex'

TIME (MSECS) = RT 100.00

X-Y, 1 TYPE--1

ACTIVITY CONTOURS

TIME (MSECS) = RT 100.00

X-Y, 3 TYPE=-1

ACTIVITY CONTOURS

TIME (MSECS) = AT 100.00

X-Y,5 TYPE--1

ACTIVITY CONTOURS

TIME (MSECS) - AT 100.00

X-Y, 6 TYPE--1

ACTIVITY CONTOURS

TIME (MSECS) - AT 100.00

X-Y,3 TYPE--1

ACTIVITY CONTOURS

TIME (MSECS) = RT 100.00

X-Y,5 TYPE=-1

ACTIVITY CONTOURS