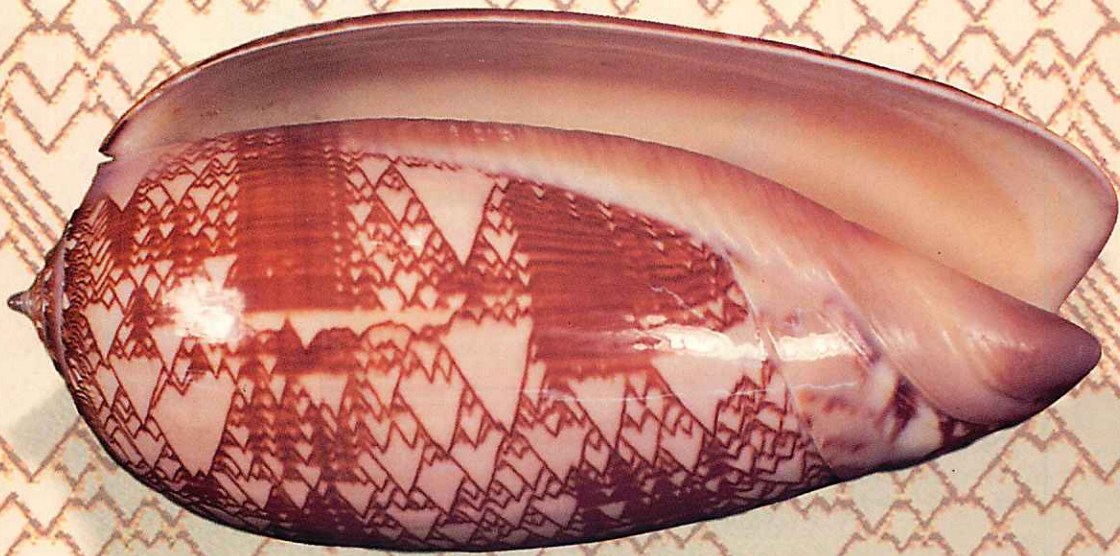


American Scientist

MAY-JUNE 1995

THE MAGAZINE OF SIGMA XI, THE SCIENTIFIC RESEARCH SOCIETY



SPACE-TIME ON A SEASHELL

Brian Hayes

We prize the pearl, but in many ways the more remarkable product of molluscan manufacturing is the shell. Seashells teach a geometry lesson on the variety of shapes that can be generated from a single basic form: the logarithmic spiral. Many shells also display intriguing decorative patterns on their surface. The stripes, wavy lines, chevrons, dots, triangles and other motifs are of particular interest to students of developmental biology and also to mathematicians and computer scientists. Although some of the patterns are quite elaborate, they are now understood in enough detail to reproduce their essential elements in computer simulations.

The modeling of shell forms and patterns is the subject of a new book, *The Algorithmic Beauty of Sea Shells* (1), by Hans Meinhardt of the Max-Planck-Institut für Entwicklungsbiologie in Tübingen. This is the second volume in a series begun five years ago with *The Algorithmic Beauty of Plants* (2), by Przemyslaw Prusinkiewicz of the University of Regina in Saskatchewan and the late Aristid Lindenmayer. Prusinkiewicz is the series editor, and he also contributes a chapter to the seashell book (in collaboration with Deborah R. Fowler, now of Hi Tech Toons).

In the earlier volume on plants, the algorithms chosen to describe the ramified structures of roots and stems and leaves were mostly based on recursive grammars, which model growth through the repeated application of transformational rules. Meinhardt's treatise on seashells draws on a quite different suite of mathematical tools, namely differential equations describing the creation, decay and diffusion of chemical factors that can either enhance or inhibit pigmentation. Meinhardt's mathematics is continuous where Prusinkiewicz's was discrete; Meinhardt's models are closely tied to details of biochemistry and physiology where Prusinkiewicz's were more abstract. And yet the two books share an important philosophical principle: They suggest that the way to understand a pattern in nature is to re-create it in a simulation. Meinhardt's book comes with software capable

of reproducing all the simulations he discusses (and many others as well).

Growth at the Margin

Here is the most important thing to know about the pattern on a mollusk shell: It is a two-dimensional record of a one-dimensional process. The shell grows along one edge only, where material is laid down by a row of cells at the margin of the animal's mantle. Pigment deposited at the growing edge forms patterns that (with few exceptions) are never altered thereafter. If you could unroll a shell and flatten it out into a rectangle, the pattern would form a space-time diagram, with position in space measured along one axis (say from left to right) and sequence in time recorded along the other axis (from top to bottom). A physicist would look at the flattened shell and call it a Feynman diagram; lines within the pattern are "world lines," tracing the entire history of motions through space.

Given this generating mechanism, some shell patterns are easy to understand. A series of vertical stripes—that is, stripes running perpendicular to the growing edge—implies a static distribution of pigment-secreting cells in the mantle margin. Where a cell or a group of cells is permanently turned on, there is a dark stripe of pigment, and where the cells are dormant, there is an unpigmented space. The complementary pattern—horizontal stripes, parallel to the growing edge—results from a temporal rather than a spatial oscillation. All the secretory cells switch off and on in synchrony, so that light and dark bands are left behind on the surface of the shell as the growing edge moves on.

An oblique stripe records the passage of a traveling wave of excitation in the row of pigment cells. Each cell is stimulated to a brief pulse of pigment secretion; then, as the cell's own activity fades, it passes the excitation along to a neighboring cell. The slope of the resulting line indicates the velocity of the traveling wave: The steeper the slope (that is, the more nearly vertical), the slower the wave. Shells with a complex pattern of oblique lines can look very much like the physicist's idea of a space-time diagram. In some cases the diagonal lines are created in pairs, like electrons and positrons, with one line propagating to the left and the other to the right; furthermore, lines moving

Brian Hayes is a former editor of *American Scientist*. Address: 211 Dacian Avenue, Durham, NC 27701. Internet: bhayes@mercury.interpath.net.

in opposite directions annihilate each other when they meet, just as matter and antimatter do.

The study of pattern formation in living organisms has long been one of the more mathematically sophisticated areas of biology. D'Arcy Wentworth Thompson set the standard in his thousand-page survey *On Growth and Form* (3), which included an extensive discussion of seashells. Alan M. Turing is known as a pioneer of computer science, but in 1952 he published a paper on biological morphogenesis (4) that is still taken seriously today. In 1969 C. H. Waddington (a biologist) and Russell J. Cowe (a computer scientist) collaborated on a computer simulation of certain mollusk-shell patterns (5). A few years later, computer studies of one-dimensional cellular automata (6, 7) yielded patterns that were strikingly reminiscent of shell pigmentation.

Hans Meinhardt reports that his interest in shell patterns was aroused during dinner at an Italian restaurant, when he noticed a shell bearing W-shaped red lines. "To my surprise," he writes, "it seemed that the mathematical models we had developed to describe elementary steps in the development of higher organisms were also able to account for the red lines on my shell." Meinhardt's earlier work (done in collaboration with Alfred Gierer) had focused on fundamental events in biological development and differentiation, such as the emergence of "polarity," or spatial orientation, in the embryo. The primary tools for understand-

ing these events were differential equations describing gradients and fluctuations in chemical concentration. Now he found that the same equations could generate shell patterns as well.

Activators and Inhibitors

The root idea from which Meinhardt's models spring is the interplay of activators and inhibitors: substances produced in the pigment cells and also acting on those same cells. Specifically, he considers a hypothetical activator molecule that promotes not only pigment production but also its own synthesis—that is, the more activator is present in a cell, the more the cell makes. This positive feedback loop is kept in check by an inhibitor, whose synthesis also depends on the activator concentration. The rates of synthesis, decay and diffusion of the activator and the inhibitor determine the pattern generated as the shell grows. Small changes in these rates can cause major reorganizations of the pattern.

Suppose the inhibitor diffuses much more rapidly along the mantle margin than the activator does. Under these conditions, if a small group of cells has a slightly higher activator concentration than its neighbors, the disparity will increase still further as the activator enhances its own production. The inhibitor will also be made copiously in these cells, but it will diffuse away and spread its effect over a wider area; as a result the neighboring cells, where activator levels were already low, will be further suppressed. In this way random spatial variations

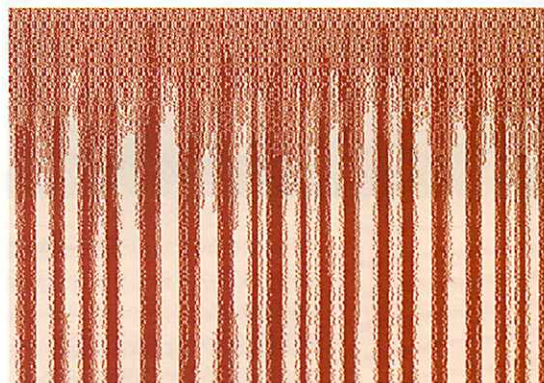
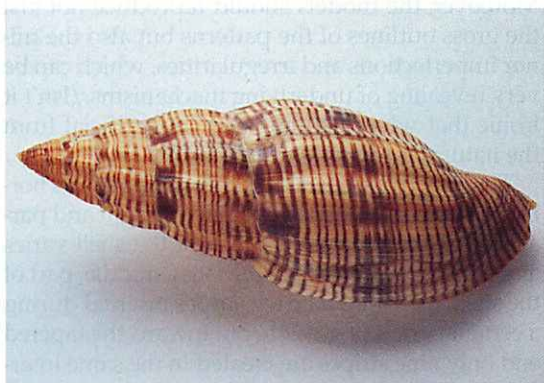


Figure 1. "Vertical" stripes, perpendicular to the growing edge of a mollusk shell, result from a stable spatial pattern of alternating active and dormant pigment-secreting cells. In the simulation (right) the pattern emerges spontaneously. The shell (left) is a specimen of *Lyra taiwanica*. (All photographs courtesy of Hans Meinhardt.)

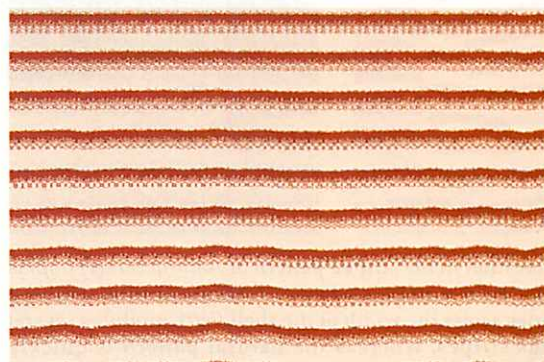
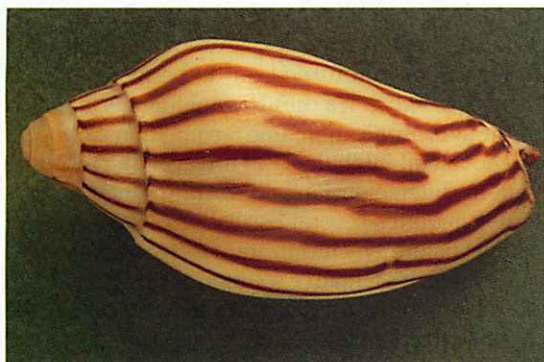


Figure 2. "Horizontal" stripes, parallel to the growing edge, reflect a temporal oscillation in pigment-cell activity in which all the cells turn on and off almost simultaneously. The shell is *Amoria dampieria*.

in activator concentration and pigment production are amplified and then become "frozen in," remaining stable over long intervals. In other words, the mollusk creates a shell with vertical stripes.

The temporal oscillations that give rise to horizontal stripes can also be explained by a model of this kind. If inhibitor production lags behind activator production, the delay allows the activator to overshoot its equilibrium level. When the inhibitor eventually catches up, it also overshoots and thus deeply suppresses activator output. Now the inhibitor level also falls, and so the activator begins to recover. The cycle repeats indefinitely with a period determined by the rates of synthesis and decay.

One way of forming oblique lines is with an activator that diffuses faster than the inhibitor. When a single cell becomes spontaneously active, the diffusion of the activator molecule soon turns on the two adjacent cells (to the left and the right). Meanwhile, the buildup of inhibitor in the central cell shuts down pigment production there and leaves the cell in a refractory state where it cannot be stimulated again for a time. The neighboring cells eventually meet the same fate: They pass on the wave of activation to the next cells in line as their own ac-

tivity is extinguished. The record of these events on the surface of the shell is a \wedge -shaped pair of lines radiating from the site of the first excitation.

When two of these traveling waves collide, there is a further interesting consequence. A wave can survive only by continually invading fresh territory, or in other words by moving into cells that have not been poisoned by an accumulation of inhibitor. But an eastbound wave has nowhere to go when it meets a westbound wave. The cells in the wake of each wave have been left in the refractory state, so that the wave cannot reverse direction; nor can it continue ahead because the cells there have been poisoned by the oncoming wave. Hence both waves are annihilated in a \vee -shaped vertex.

Imperfections and Irregularities

Concocting models to account for the most conspicuous features of these patterns is not really difficult. The simplest cellular automata will do nicely for creating stripes at any rational slope between vertical and horizontal. Such models dispense with all the messy chemistry of activators and inhibitors. They require only abstract computational "cells" that make transitions from one discrete state to another according to straightforward rules.

Meinhardt's aim, however, goes beyond modeling the rudiments of a few selected shell patterns. The goal is to devise a coherent set of biologically plausible models that can account for *all* shell patterns—or at least as many as possible. Moreover, the models should reproduce not just the gross outlines of the patterns but also the minor imperfections and irregularities, which can be very revealing of underlying mechanisms. (Isn't it ironic that what distinguishes the artificial from the natural is too much perfection?)

The shell of the gastropod *Amoria turneri* has horizontal stripes that tend to remain straight and parallel even though the diameter of the shell varies along the shell's length. In the fatter, middle, part of the shell, there might be ten stripes inserted during a certain period of growth, but toward the tapered end only nine stripes are created in the same interval. Somewhere between these two regimes there must be a discontinuity, like a dislocation in a crystal lattice. Inspection of the shell reveals that the disturbance caused by the mismatched stripes is confined to a small region both spatially and temporally. Meinhardt writes: "Attempts to simulate this phenomenon turned out to be more difficult than expected.... If a diffusing inhibitor is involved in the synchronization, line termination can occur due to lateral inhibition.... However, the resulting pattern differs substantially from the natural pattern. It requires several oscillations in the zone of conflict before synchronization is re-established."

Meinhardt's tentative solution to this puzzle is to postulate another oscillating chemical system, in addition to the pigment-secreting one. The substances forming the second oscillator are distributed globally throughout the mollusk's tissues in a "hormone-like" way, meaning that they can transmit signals

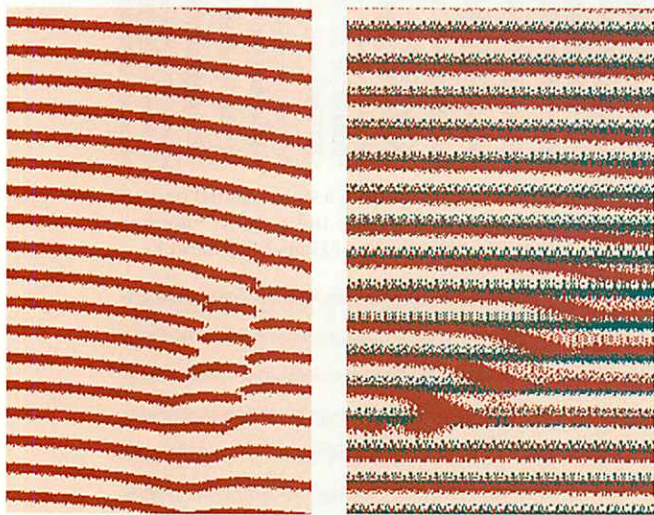
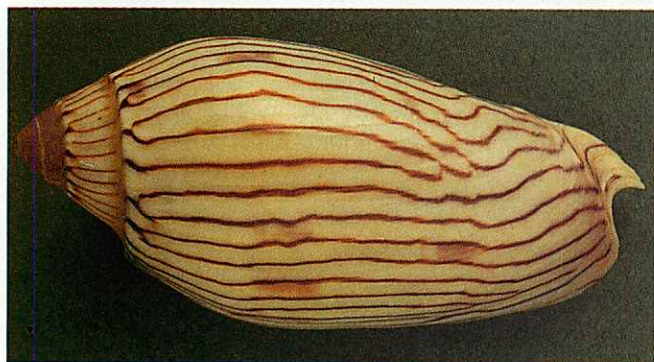


Figure 3. Dislocation in the striped pattern of *Amoria turneri* (top) is a challenge to the simulation scheme. A single oscillator whose frequency varies across the width of the shell (left), produces several discontinuous stripes, whereas the natural pattern is quickly resynchronized. Adding a central hormone-like oscillator (shown here in green, although its actual products are presumed to be invisible) yields a more realistic output (right).

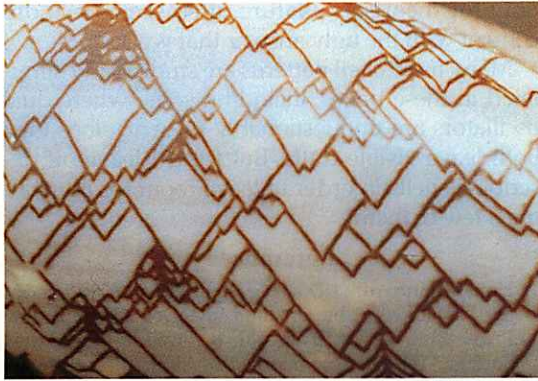


Figure 4. Oblique stripes on *Oliva porphyria* (left) record the passage of traveling waves in the line of pigment cells. The stripes are created and annihilated in pairs, like particles of matter and antimatter. To account for the frequent synchronization of creation events, the model (right) includes a global hormone-like signal (green). A larger sample of the output of this simulation, without the green hormone, is shown on the cover of this issue.

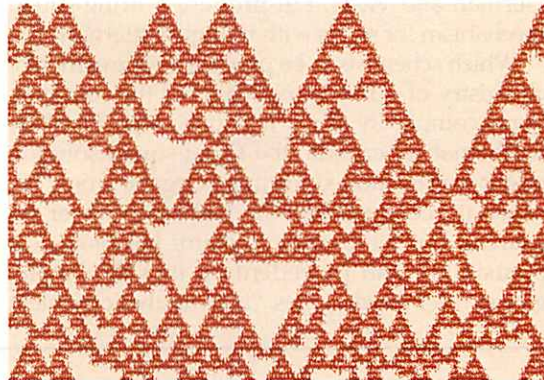
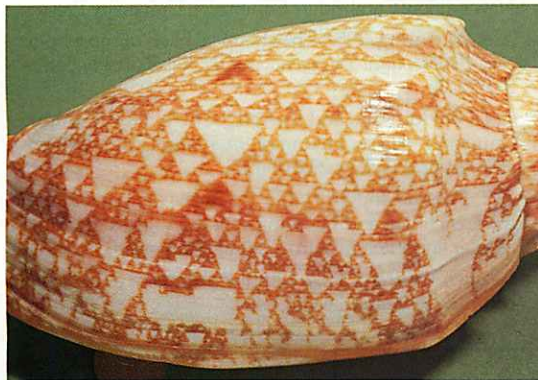


Figure 5. Triangular pattern on *Cymbiola imexa* Reeve (left) also suggests the presence of some synchronizing mechanism, since many secreting cells must shut off at once to form the upper edge of a white triangle. In the simulation (right) another global signal is introduced for this purpose.

faster than any substance moving by simple diffusion. The second oscillator can therefore serve as a master clock, keeping distant cells synchronized. The frequencies of the two oscillators are close enough that the pigmentation system becomes entrained by the hormonal oscillator as long as the phase difference is not too great; then, when an adjustment is needed, the pigment-secreting oscillator "skips a beat" and quickly resynchronizes. Simulations based on this model more closely match the pattern observed on real *Amoria turneri* shells.

Parsimony and Elegance

Introducing an entire system of chemical oscillators just to explain one anomalous detail on the shells of one mollusk species offends against the principle of parsimony. The hypothesis of a hormonelike pacemaker begins to seem more plausible, however, when Meinhardt finds evidence of similar mechanisms at work elsewhere. A case in point is the shell of *Oliva porphyria*, one of the most treasured finds of tropical shell collectors and also one of the favorite subjects of mathematical shell modelers. The shell of *O. porphyria* is distinguished by oblique lines that have frequent branch points, which implies that in the row of pigment-secreting cells a wave of excitation moving to the right can

suddenly spawn a backward wave moving to the left (or vice versa). What is more, the branch points are often correlated over long distances: When one line branches, there is a good chance that others will also branch at about the same time. Meinhardt's global control element could explain this long-range synchronization.

The central clock is seen yet again in shells decorated with triangle patterns, where a pigmented region begins at a single point and grows steadily wider until all of the pigment-producing cells suddenly shut off at the same time. "The sharply straight lower edge of triangles indicates that termination occurs strictly simultaneously. This excludes the possibility of a signal being initiated at a particular position and spreading by diffusion."

The appeal to a master timekeeper, and the assertion that such a central authority is needed for long-range synchronization, brings up a curious cultural issue—a question of differing intellectual habits and biases among the tribes of science. For the developmental biologist, it seems, proposing a new chemical oscillator is a natural and perhaps obvious way of solving a problem. A mathematician or computer scientist working on the same puzzle—how to coordinate the activity of many distant cells—might well be tempted by a different

kind of explanation. In particular, someone immersed in the tropes and idioms of computer science would not be so quick to dismiss the possibility of synchronizing a row of cells with a signal that spreads by diffusion.

One of the standard exercises of computer science is called the firing-squad problem, which asks how a group of soldiers without a leader can arrange to fire their weapons simultaneously. A number of ingenious solutions have been worked out, involving multiple signals passed up and down the line and forming intricate fanlike patterns as they reflect and propagate. The problem was originally intended to illuminate some of the difficulties of synchronizing the multiple processors of a distributed computing system, but the solutions can clearly be applied to the synchronization of seashell patterns as well. Indeed, G. T. Herman and W. H. Liu propose a firing-squad mechanism for shells with triangle patterns (6).

Which scheme is to be preferred—the extra biochemistry of a master oscillator or the computational complexity of a firing-squad algorithm? By mathematical criteria, the firing-squad solution might well be judged the more elegant, if only because it accomplishes the task with fewer resources. But the central oscillator has biological plausibility and precedent on its side. "Inelegance," Meinhardt writes, "is an aesthetic problem

only for theorists." Nature often seems blandly content with the ugly answer that works.

Many more shell patterns are studied and simulated in these pages, including some where dual oscillators are unquestionably present, since they both leave visible trails. But I must leave off describing shells in order to leave room for illustrating a few of them.

References

1. Hans Meinhardt. 1995. *The Algorithmic Beauty of Sea Shells*. With contributions and images by Przemyslaw Prusinkiewicz and Deborah R. Fowler. New York: Springer-Verlag. Accompanied by simulation software for computers running the MS-DOS operating system.
2. Przemyslaw Prusinkiewicz and Aristid Lindenmayer with James S. Hanan, F. David Fracchia, Deborah R. Fowler, Martin J. M. de Boer and Lynn Mercer. 1990. *The Algorithmic Beauty of Plants*. New York: Springer-Verlag.
3. D'Arcy Wentworth Thompson. 1942. *On Growth and Form*. New edition. Cambridge: Cambridge University Press.
4. Alan M. Turing. 1952. The chemical basis of morphogenesis. *Philosophical Transactions of the Royal Society Series B* 237:37-72.
5. C. H. Waddington and Russell J. Cowe. 1969. Computer simulation of a molluscan pigmentation pattern. *Journal of Theoretical Biology* 25:219-225.
6. G. T. Herman and W. H. Liu. 1973. The daughter of Celia, the French flag and the firing squad: Progress report on a cellular linear iterative-array simulator. *Simulation* 21:33-41.
7. Stephen Wolfram. 1984. Cellular automata as models of complexity. *Nature* 341:419-424.

Scientific Graphs and Statistics GRAPHING POWER

New 32-bit Version: Access the power of WINDOWS 4.0, WINDOWS NT, WIN32s and OLE 2.0 with Plot-IT.

New Features include true 32-bit operation, Graph Group Selection; ability to plot automatic multiple curves directly from a worksheet, support for Macintosh generated ASCII files, new worksheet with 32,700 rows, "Help Wizard" to speed learning.

Advanced capabilities and error-free performance. Used and tested by over 45,000 scientists and engineers worldwide.

Total control to customize graphs. Linear, log, semi-log, probit and percentage scales with user labels on any x or y axis. Define hundreds of curves and axes, place multiple graphs per page and add notes, graphics, and legends anywhere.



Total flexibility, 90+ graph types including 2D, 3D and SP/QC, hundreds of predefined graphs and samples, a full menu of data analysis applications, support for all types of data files including Lotus, Quattro, Excel, dBase, ASCII and user-defined functions.

Ease of use - Choose from menu, mouse or script operation with support for DDE and OLE.

Free tech support and extensive Online Help for every feature. Also includes Demonstration Mode.

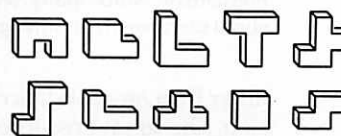
We are so confident you will find Plot-IT 3.2 for WINDOWS to be an indispensable research tool, we offer a **90-day money back guarantee**.

Call Now: 517-339-9859

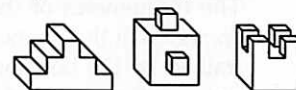
SP SCIENTIFIC PROGRAMMING ENTERPRISES
Plot-IT®

P.O. Box 669 • Haslett, MI 48840

Assemble A 3x3x3 Cube,



and problem shapes like these.



CUBE5™ is a Three Dimensional Reasoning Puzzle from Organized Thinking. Using different selections of the ten wooden CUBE5 pieces you can construct the 3x3x3 Cube, and other interesting problem shapes. Fifty puzzles in all!

The 3x3x3 cube assembled out of six CUBE5 pieces is 2 1/4 inches on a side.

To order CUBE5, please call 800-298-4947, or mail payment to our address below. CUBE5 costs \$25 plus \$5 for Shipping and Handling. (MA Residents add 5% Sales Tax.) We will include a Catalogue of our other puzzles with your order.

Organized Thinking
220 Boylston Street
Newton, MA 02167

CUBE5
PATENT
PENDING ams