

Simulated Annealing in Networks for Computing Possible Arrangements for Red and Green Cones

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Introduction. One aspect of the retina which influences the information available to the visual system is the geometrical arrangement of the cones. The packing arrangement of the cones in the central fovea has been carefully measured in retinal preparations from monkeys.^[1] Psychophysical measurements have been made using laser interferometry in humans.^[2] Although these measurements are indirect, they are free from possible histological artifacts. The psychophysical techniques for observing the arrangement are based on the moire patterns which are perceived when very fine gratings are imaged on the retina by laser interferometry. The results of the technique depend on the regularity of the cone array. In the center of the fovea, where the cones can be very regularly packed, the moire pattern is fairly regular and the technique gives both the orientation and the spacing of the cone array. In the center of the fovea, there are very few blue cones, so they will be ignored here and only the red and green ones will be considered. The arrangement of the red or green cones alone is not known. There is no definitive information about the relative number of red and greens in the central fovea, although there is indirect evidence indicating that there are twice as many red cones as green cones.^[3] In support of psychophysical investigations of the arrangement of the red and green cones, we have been studying models which generate possible red-green arrangements and then looking at the aliasing patterns that would be generated by fine gratings which stimulated only the red or the green cones.

Our search for appropriate models has led us to network models in which each cone is given a provisional color at random and then cones are allowed to determine the colors of their neighbors through an iterative process. Initially, we used a version of the pigmentation model of Boon and Neullez, which has exactly the structure of a classic network of artificial neurons.^[4] We then became aware of spin-glass models and modified this model to give it the symmetric structure of a spin-glass model, gaining at least the knowledge that the iterative process would certainly converge. This model allowed us to generate arrays ranging from completely random arrangements of red and green to arrays with the about the same amount of disorder as the parafoveal cones.^[5] Recently, we have added simulated annealing to the process in an attempt to find processes which can generate color arrangements with more regularity and hence more revealing moire patterns than the arrangements resulting from quenched spin-glass processes.^[6]

We have found a simulated annealing process which reliably computes a regular rosette pattern on a 300 cone hexagonal array. When we apply this process to a cone array section from the central fovea of a monkey retina we find that it can generate arrays of red and green cones which are essentially as regular as the original array.

Figure 1. The rosette pattern on a 300 cone hexagonal array. The pattern was computed using the network model with annealing as described in the text. The dark disks represent green cones and the open disks red cones.

The Model Network. In their discussions of possible models for the development of the fruitfly retina, Hafen et al. distinguish two possible kinds of models.^[7] In one the cells are influenced only by their contiguous neighbors through direct membrane contacts. In the other the cells influence their neighbors through agents which diffuse through space and whose effects diminish with distance. We agree with their point that these models are difficult to distinguish and have arbitrarily chosen to study models of the first kind and we were pleased that they favored this type of mechanism. We chose a contact connection model to study rather than a distance-based connection model because we wanted to be able to get the coloring to follow the rosette pattern as closely as possible. The distances between the cone centers vary greatly in situations where there are exactly six neighbors. On the other hand, rods begin to intrude between the cones in the outer fovea, so a contact model lacks plausibility except in the very central fovea. For a perfect hexagonal

array of cones, each cone has exactly six neighbors in contact with it. For our monkey retina data, we have x-y coordinates specifying the apparent center of a cone. To select the neighbors of a cone we have used the expedient of considering that cones are neighbors if their Dirichlet regions touch, that is, if there are points which are equidistant from the two centers which are not closer to any other center. The network can be represented by the simple symmetric connection matrix,

$$J(j,k) = 1, \text{ if cones } j \text{ and } k \text{ are neighbors,} \\ = 0, \text{ otherwise.}$$

The Model Dynamics. Our model dynamics are similar those described elsewhere.^[8-10] We let $S(k)$ be +1 if cone k is red and -1 if cone k is green and define the usual function representing the agreement of the color with the wishes of the neighbors and a bias or threshold,

$$h(k) = -S(k) \text{ Sum over } j \{S(j)J(j,k) - t(k)\}.$$

The minus sign indicates that a cone wants to be opposite in color to its neighbors. We cycle through the array and flip the color according to the temperature and the agreement with the wishes of neighbors:

$$\text{Prob}\{S(k) = -S(k)\} = 1/\{1+\exp[h(k)/T]\},$$

where T is the annealing temperature. If the temperature is zero, then the color is flipped only if $h(k)$ is strictly negative. A new random permutation of the array elements is used on each cycle through the array.

Threshold Function. The role of the threshold, $t(k)$, is to bias the ratio of reds to greens away from 0.5. At first we tried letting the threshold be constant, but we discovered that since cones near the edge had fewer neighbors, the effect of the threshold was much stronger for them than for those in the middle, preventing a perfect rosette pattern. To compensate for this we set the threshold according to the number of neighbors. We found the thresholds that minimize the maximum (over all desired configurations for that number of neighbors) of the probability of a flip out of a desired configuration. For the rosette pattern these thresholds are 3, 3, 2, 2, and 1, for numbers of neighbors of 6, 5, 4, 3, and 2, respectively.

Annealing Rules. The annealing rules we use to find crystalline arrangements were found by cut and try to produce a high proportion of perfect rosette patterns in a 300 cone perfect hexagonal lattice. This size is as large as the largest perfectly hexagonal region in any of the retinal sections we currently have. We start at a temperature about twice the @newpage@comment(4) critical temperature and decrease it slowly and linearly. The initial temperature is set to 0.6 and decreased it by 0.0005 each cycle. When there is no change in the non-edge elements of the array for 4 consecutive cycles, a state of accelerated cooling is entered in which the temperature increment is multiplied by 4. After 4 consecutive cycles with no changes in any elements, the process is stopped.

Figure 2 shows why it is reasonable to call 0.3 a critical temperature. We define an overall goodness-of-fit measure, the hamiltonian, to be the sum of the $h(k)$ over the internal elements. It is convenient to disregard the edges so that all 3 of the possible rosette patterns have the same fit. Figure 2 shows how the average hamiltonian varies with cycle number when the temperature is kept constant. If the temperature is too low (0.1), the process behaves almost as though the temperature is zero and then very slowly drifts toward an equilibrium near perfection.

Figure 2. Average hamiltonian goodness of fit over cycles for 50 simulations at initial temperatures of 0.0, 0.1, 0.3 and 0.6. At the left the temperature remained constant. At the right the temperature was decremented by 0.0005 after each cycle.

If the temperature is too high (0.6), the equilibrium is quickly reached, but is at a low value of the hamiltonian. For the value of 0.3, the process reaches a relatively high level with relatively high speed. The right side of Figure 2 shows the performance when the temperature is slowly lowered. Now the initial temperature of 0.6

gives nearly perfect performance (hamiltonian of 720) after 600 trials.

Figure 3 shows the performance of the rule in terms of percent perfect rosette patterns and trials to criterion as the initial temperature and the temperature decrement are varied. Although increasing the initial temperature and decreasing the decrement further would both improve performance, we were satisfied with this level of performance. In this region both parameters affect the number of cycles principally through the number of cycles required to reach the critical temperature.

Figure 3 Percent perfect patterns and average trials to criterion for 50 simulations with two initial temperatures and temperature decrements.

The stage of accelerated cooling was introduced because in the later stages of cooling the central region becomes fixed and only the edge cones are flipping in color. Because the maximum value of $h(k)$ is lower for the edge cones, they are effectively at a higher temperature than those in the center. At first we tried adjusting the temperature of the edges, so they would cool at the same rate as the internals, but different edge regions have different preferences among the three possible rosette patterns and cause regional "wars" if they are not cooled more slowly. However, once the center is set the edges can be cooled rapidly, because the center then controls them, rather than *visa versa*.

Applying the Model to Data. After adjusting the parameters of the annealing process so that it would almost always make a perfect rosette pattern on a 300 cone hexagonal array, we applied the model to actual measurements of cone positions. Figure 4 shows the cone positions of a square section of monkey fovea measured by Hirsch and Miller.[1] The apparent center of the fovea (by density and regularity) is at the center of the left hand edge of the section, and the center of the right hand edge has an eccentricity in visual angle of 0.23 deg. The connection network was computed as described above and the colors are assigned by the spin-glass procedure with the temperature at zero (the quenched procedure).

Figure 4. A section of retina colored by the quenched spin-glass rule.

Figure 5. A section of retina colored by the annealed spin-glass rule.

This model gives arrangements where greens tend to be surrounded by reds, but not completely. Figure 5 shows an application of the spin-glass procedure with the annealing process as described above. The process ran 800 cycles before reaching the final criterion. The section has two large regions of perfect hexagonal connections: one is the lower right hand corner and the other is the rest of the section. Both of these regions have been colored in a perfect rosette pattern by the process. The spin-glass model with annealing provides a biologically plausible mechanism by which cone color arrangements can be done with perfect regularity in regions as large as the perfectly hexagonal regions of the fovea.

Perceptual Implications. The annealed coloring rule leads to isolated red and green cone arrays which have the same aliasing qualities as the original array, but at grating spacings multiplied by the square root of 3 and orientations rotated by 90 deg. Although the average spacing is different for the red and green arrays, they have the same periodicity and hence the same moire aliases. If the central fovea has this type of arrangement, under appropriate isolation conditions these predictions should be verifiable by direct observation. It should be pointed out that the roles of red and green can just as well be reversed, although the 2:1 ratio is of course required for the pattern. Figure 6 shows the monkey data annealed with the same parameters as Figure 5, but with no threshold bias. In this case the coloring pattern has about the same regularity as that of Figure 6, the 2:1 quenched pattern.

Figure 6. A section of retina colored by the annealed spin-glass rule with no threshold bias.

Summary. We have used a locally connected planar network with simulated annealing to compute highly regular possible arrangements for the red and green cones in the retina. This procedure allows us to find for arrays with arbitrary disorder a coloring arrangement as similar as possible to the regular rosette

arrangement for a perfect hexagonal array.

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