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How to Make a Neurocrystal: Modeling the developmental patterning of the fly's retina

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Animals' ability to create the complex patterns found in many organisms is an enduring source of wonder and a topic that has long drawn the interest of scientists of all stripes. Famously, it was an attempt to model developmental patterning that led to the discovery of the Turing instability. Here, we study one of the most remarkable and best-characterized examples of such pattern formation, the development of the fruit fly's compound eye. In the fly larva, a front of differentiation moves across the sheet of tissue that will become the adult retina. It leaves behind it a striking hexagonal array of cells marked by high levels of the protein Atonal. It has previously been noted that a standard activator-inhibitor model might explain this process [Meinhardt, 1992], but only recently has the basic genetic logic governing photoreceptor specification been deciphered [e.g. Frankfort and Mardon, 2002]. We build on these advances with the first model of retinal patterning based on experimentally verified interactions. Surprisingly, we conclude that a Turing-instability-based mechanism alone cannot reproduce the observed behavior. Instead, we propose that the pattern is generated primarily by a novel "epitaxial" process in which, as the front progresses, each newly-created row of unit cells acts as a template for the next one. A clear prediction of this model is that if the communication between successive rows is broken, even transiently, a striped pattern will appear. Preliminary experimental tests suggest that just such a phenomenon occurs in some mutants. Related patterning processes have been observed in systems as diverse as chick feather buds and vertebrate retinal ganglion cells [Pichaud, Treisman, and Desplan, 2001]; our model may thus describe an evolutionarily conserved module.