

sider theoretical problems and solutions to the evolutionary challenge of making brains bigger or smaller<sup>7</sup>. For other body organs, as well as for bridges and buildings, the problems of changes in scale have been investigated thoroughly<sup>8</sup>. It is now time to do the same for brains and to find out whether theory and evolution would cope with these problems in similar ways. ■

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## Climate change

# The Indonesian valve

James D. Wright

The behaviour of the North Atlantic is often invoked to explain the effects of climate change. But for certain episodes, including perhaps a period in human evolution, events elsewhere may have had a greater influence.

The climate of East Africa became drier between about 5 million and 2.5 million years ago, and that may have been the catalyst that forced our ancestors to adapt to a savannah environment as the forests dwindled<sup>1,2</sup>. At about the same time, the Earth entered a climate mode dominated by the waxing and waning of large continental ice sheets. The coincidental timing of global cooling, African aridity and human evolution invites speculation about a common link<sup>3</sup>. For that, we must look to the oceans — in redistributing heat and influencing greenhouse-gas concentrations globally, they are the main component in determining climate change. Marine records tell us that the transition to large-scale glacial cycles took at least a million years; and plate-tectonic motions that opened or closed ocean gateways are thought to have triggered these events<sup>4</sup>.

On page 157 of this issue, Cane and Molnar<sup>5</sup> present an analysis of changes in surface-ocean circulation that they believe occurred as an oceanic gateway — the Indonesian seaway — narrowed over the past 5 million years. This gateway acts as a valve for water flowing from the Pacific into the Indian Ocean. Plate tectonics in the Indonesian region is complicated, but Cane and Molnar show that the passages regulating water flow from the Pacific to the Indian Ocean 5 million years ago were wider and deeper, and were located further to the south, than they are today. Surface water in the South Pacific is warmer and saltier than that in the North Pacific. Cane and Molnar argue that the more southerly position for the Indo-Pacific connection meant that the warmer South Pacific flowed into the Indian Ocean. The result was warmer sea surface temperatures in the Indian Ocean and high levels of evaporation and precipitation — and wet East African climates.

Over the past 5 million years, the constriction and northern movement of the Indonesian seaway have progressively shut off the South Pacific source of water, while increasing the influence of the colder North Pacific. These changes should have cooled the tropical Indian Ocean and reduced the precipitation, leading to a gradual drying of East Africa. Again, then, the idea is that the Indonesian seaway, controlled by the northern movement of New Guinea and smaller islands, has acted like a valve, regulating the relative amount of warm and cool water entering the Indian Ocean.

A more speculative aspect of Cane and Molnar's paper deals with the possible effects on global climate of this narrowing of the Indonesian seaway. The authors argue that, when the seaway was farther south, conditions in the tropical Pacific would have been more like those observed during modern El Niños (that is, both east–west and vertical thermal gradients in the ocean would have been weaker). This configuration would have promoted greater heat transport to the high northern latitudes than at present; and that higher heat flux would have inhibited the growth of large ice sheets in the Northern Hemisphere. In support of Cane and Molnar's speculation, palaeoceanographic reconstruction of the tropical Pacific between 5 million and 3 million years ago matches the prediction of smaller east–west and vertical temperature differences<sup>6</sup>.

This speculation is especially provocative because it requires a new principle for understanding the glacial cycles that developed 3.5–2.5 million years ago. Existing models for large-scale Northern Hemisphere glaciation focus on increased circulation of the North Atlantic 'conveyor', which includes the Gulf Stream, as the cause of ice-sheet development<sup>4,7–9</sup>. The finer points in these

models vary, but most of them begin with increased precipitation at high northern latitudes as a result of a more vigorous Gulf Stream. And going back one step, the closure of the Panamanian isthmus is seen as the trigger for initiating the more powerful Gulf Stream.

Recently, however, a fly in the ointment for these hypotheses has appeared<sup>10</sup>. An evaluation of North Atlantic circulation for between 5 million and 2 million years ago contradicts the enhanced Gulf Stream mechanism for Northern Hemisphere glaciation. The new data<sup>10</sup> indicate that the North Atlantic conveyor became considerably weaker, not stronger, 3.5–2.5 million years ago.

Cane and Molnar<sup>5</sup> propose a shift in thinking away from the North Atlantic to the Indonesian gateway as a factor governing global climate change. There are good reasons to take this idea seriously, speculative though it may be, because the Indonesian region is undoubtedly important in the redistribution of heat received at the Earth's surface and in moisture fluxes to the atmosphere. Moreover, Cane and Molnar make several predictions that can be tested.

The most obvious prediction is that sea surface temperatures in the Indian Ocean cooled between 5 million and 2 million years ago. This may be difficult to test, however. The change in temperature was probably 2–3 °C. Oxygen-isotope analysis of planktonic foraminifera, a useful tool for estimating past sea surface temperatures, can resolve this change. But because of evaporation, the South Pacific is saltier, as well as warmer, than the North Pacific. The evaporation that increases the salinity also increases the oxygen-isotope value of the surface water, offsetting the temperature effect. Advances in measuring the Mg/Ca ratios in foraminifera, and then using those ratios to estimate temperature, may solve the problem.

My own view is that Cane and Molnar are correct in their view that African aridity is linked to sea surface temperatures in the Indian Ocean, and that the most likely cause of cooling there was a narrowing of the Indonesian seaway. I am less confident that these changes had much to do with glaciation of the Northern Hemisphere, for one simple reason: from 10 million to 5.6 million years ago, cyclic glaciation was highly active in the Northern hemisphere and glaciation was suppressed between 5.5 million and 3.5 million years ago. Moreover, changes in the North Atlantic conveyor circulation cannot be ruled out in driving these glaciations. The conveyor delivers a substantial amount of heat to the high northern latitudes; the link with glaciation might have been through reduced heat fluxes as conveyor circulation decreased<sup>11</sup>, rather than through precipitation. Nonetheless, Cane and Mol-

nar have armed the palaeoclimate community with the theory and predictions that will allow us to examine events in the Pacific, Indian and Atlantic oceans — especially the valves controlling water flow into and out of them — as drivers of Earth's climate. ■

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## Evolution

# Developmental circuits rewired

Eörs Szathmáry

Body segmentation occurs during the development of many invertebrate animals. Advances are being made by those striving to produce computer models of the genetic networks underlying the process.

You might think that key features of embryo development would not be easily altered during evolution. Such changes should be lethal, but they are surprisingly common. So how can the underlying genetic regulatory circuits be rewired without making the whole population of organisms inviable? Writing in the new journal *Evolution and Development*<sup>1,2</sup>, Salazar-Ciudad *et al.* show that evolution favours alternative genetic circuits, depending on the size and the complexity of the patterning task to be accomplished.

It has long been known that the beginning and the end of embryological development are fairly variable traits in evolution. Diversity at an early developmental stage (in the mechanism of gastrulation, for example) can be attributed to evolutionary adaptations to the ecological setting in which the embryo begins to unfold. The later phases must also differ, otherwise species would all look the same<sup>3</sup>.

Development in parasitic wasps has diverged widely, for example. Early cell divisions of the fertilized egg, establishment of head-to-tail polarity, and the genetic circuit for body segmentation (the mechanism by which stripes are created through intergene regulation) have all been modified, apparently as adaptations to the parasitic lifestyle<sup>4</sup>. A wasp known as *Copidosoma*, for instance, has many features resembling those of mammalian development, apparently to enable the embryo to tap into the host for nutrition. But developmental malleability can go beyond this. Although the external appearance of an organism may be fixed, the genetic network — in which genes switch one another on and off so that programmed development runs successfully — seems to be changeable. This is analogous

to rewiring your laptop without changing the housing. It seems to have occurred in the fruitfly *Drosophila*, in which two genes, *fushi tarazu* and *bicoid*, appear to have been recruited for segmentation as an afterthought<sup>5</sup>. At first sight, the observation seems to run counter to the finding<sup>6</sup> from computer modelling that the genetic network responsible for setting up polarity within segments is highly robust to change. So, how does one reconcile conservation and change?

As they describe in their first paper<sup>1</sup>, Salazar-Ciudad *et al.* have simplified the question by concentrating on a row of cells (or cell nuclei where there is initially no membrane between them, as in *Drosophila*). It is in this row of cells that genes interact by regulating the activities of some other genes in the system (Fig. 1). A series of artificial selection experiments is carried out in the computer until a pre-specified goal pattern is reached. Perhaps the most enchanting feature of this model is that it puts embryonic pattern formation, and the evolution of pattern formation, into a unified theoretical framework.

One of the pre-specified tasks is segmentation. Similar phenomena, including stripes on animal coats, fascinated Alan Turing, who in 1952 proposed a mechanism for pattern formation<sup>7</sup>. He showed that, in a chemical system that starts off as spatially homogeneous, a diffusing activator and an inhibitor could give rise to stationary-wave-like concentration profiles of chemicals (Fig. 2a). Similar reaction–diffusion mechanisms may be at work in some biological systems, such as in the skin of the angelfish<sup>8</sup>. But other systems, previously thought to be produced by a Turing-like system, such as stripe formation in *Drosophila*, seem to use a mechanism<sup>9</sup>

in which each stripe's identity is determined by a different combination of regulatory elements, following an initial spatial heterogeneity (Fig. 2b). The underlying genetic circuit has a hierarchical structure<sup>3</sup>.

Several conclusions emerge from Salazar-Ciudad and colleagues' model<sup>1</sup>. First, evolving networks always fall into one of the two categories: 'emergent' (reaction–diffusion) or hierarchical<sup>10</sup>. Second, the network producing the target pattern tends to be hierarchical when the number of stripes to be generated is fewer than four, and to be emergent above four; also, emergent networks generally produce the more complex patterns. Third, emergent networks are more changeable than hierarchical ones when subject to mutations — this means that the patterns become more dissimilar from the original one than in the case of hierarchies (deviation from the morphological norm can often be selectively disadvantageous). Fourth, hierarchical networks can produce more finely tuned patterns than emergent ones.

Together, these results indicate that a whole set of possible hierarchical networks covers a larger territory in 'morphological space' (understood as the set of possible gene-expression patterns in the modelled row of cells) than a whole set of emergent

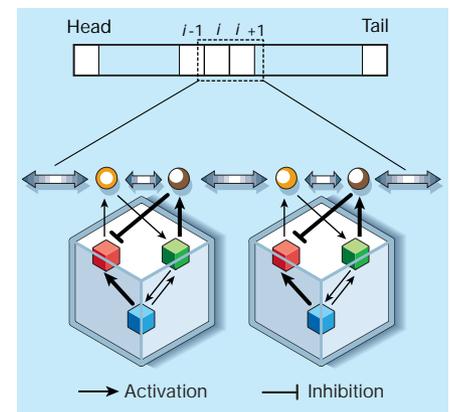


Figure 1 A model for the evolution of pattern generation. Salazar-Ciudad *et al.*<sup>1</sup> model the early developing embryo from head to tail as a row of 25 cells (or cell nuclei) in which genes (boxes) and diffusible factors (circles) interact. Two cells, occupying the  $i$ th and  $(i+1)$ th position in the row, are enlarged here. Each cell has the same set of genes and the same intergene interactions. The network functions as a nonlinear dynamical system. The concentrations of non-diffusible and diffusible gene products are calculated numerically, and a pattern is generated when at least one gene product attains different levels in different cells. (Modified from ref. 2.) Overall network evolution is simulated with a population of 100 such networks, the 'fitness' (viability) of each being inversely proportional to the distance of its generated pattern from the target pattern. Changing the interaction weights randomly generates the variation on which selection acts.