plane[6,7]. But if the S paths were significantly inclined with respect to the shear plane, the observations could possibly be matched[1]. Roughly horizontal shearing of perovskite associated with a deforming Tonga slab[8] may therefore explain the S-wave observations of Wookey *et al.*[1] as well as the apparent absence of large splitting from the lower mantle in SKS and ScS phases that travel almost vertically beneath the Tonga subduction zone[9,10].

The work of Wookey *et al.*[1] and McNamara *et al.*[5] suggests that strong anisotropy may be a common feature of regions where subducting slabs enter the lower mantle. Accurately modelling the full waveform interaction of seismic phases with anisotropic structure, rather than just their arrival times, is a formidable task. But applying such approaches to waves that sample the mid-mantle could help to explain the dynamics of mantle convection. ■

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Developmental biology

Precision patterning

Nipam H. Patel and Sabbi Lall

Many developmental events depend on gradients of key molecules to tell cells where they are. These gradients vary between embryos, but a noise-filtering mechanism ensures that development proceeds normally.

Embryos develop in a precise pattern that varies little from individual to individual within a given species. Such precision and reproducibility make this an excellent example of biological robustness. For instance, embryos tend to be patterned normally, regardless (within reason) of how large or small they are, and even in the face of environmental perturbations such as fluctuations in temperature. This seems remarkable given that certain patterning steps rely on molecular gradients to tell cells where they are in the embryo, and hence how they should develop. Variations in temperature and size would be expected to disrupt such gradients and to lead to errors later on in development.

On page 798 of this issue, Houchmandzadeh and colleagues[1] investigate this robustness by taking a close look at one of the classic gradient systems — that of the Bicoid protein — in embryos of the fruitfly *Drosophila melanogaster*. They find that the gradient can vary greatly from embryo to embryo, but that the positional readout is still quite precise. In other words, the noise in the system is filtered out.

Proteins such as Bicoid are known as morphogens, and work in the following way. First, a localized source of morphogen is established in the embryo. Subsequent diffusion (or active movement) and degradation of the morphogen produces a concentration gradient that imparts information to cells about their position within a developmental field. So, for example, the gradient of Bicoid protein in fruitflies tells cells where they are along the head-to-tail (anterior–posterior) axis of the embryo. Bicoid is provided in the form of messenger RNA (mRNA) from the mother during egg development and becomes localized to the anterior pole. As the mRNA is translated after fertilization, the resulting protein begins to diffuse from its source. It is not hindered by cell boundaries because the embryo initially develops as a syncytium, in which thousands of cell nuclei share the same cytoplasm.

The formation of the Bicoid protein gradient is presumably influenced by such factors as the quantity of maternal mRNA, the precision of mRNA localization, the rate of translation into protein, and the activity of enzymes that subsequently degrade the protein. All of these processes may be susceptible to perturbations. So how much does the Bicoid gradient differ from embryo to embryo? Houchmandzadeh *et al.*[1] carefully measured the profile of Bicoid protein in a large number of wild-type embryos, and found that it is indeed quite variable (Fig. 1). After normalizing the profile for embryo length, the position at which the Bicoid concentration crosses a chosen level can be anywhere within a region encompassing about 30% of the length of the embryo.

One of the functions of Bicoid protein is to control the production of mRNA (transcription) from a series of 'gap genes' in different spatial domains along the embryo's anterior–posterior axis. One of these, the Hunchback gene, is transcribed in an anterior domain, with a sharp boundary of expression about halfway down the embryo. Previous studies[2,3] suggested that the Hunchback gene is switched on in response to a specific threshold concentration of Bicoid protein. Indeed, embryos produced by mothers containing two or four extra copies of the Bicoid gene (introduced as 'transgenes') show a prominent posterior shift in the position of the Hunchback boundary[3]. So, the posterior edge of Hunchback expression apparently acts as a direct readout of the concentration of Bicoid protein.

Yet when they looked again at wild-type

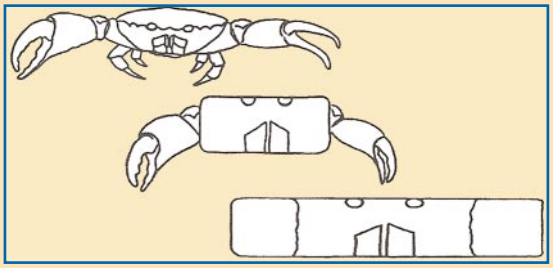
Animal behaviour

Snap judgements

Twice a day, coinciding with tidal motion, climbing crabs *Sesarma leptosoma* leave the canopy of the mangroves they inhabit and migrate down the trunks to the swamp below. But nature being what it is, they run the risk of being eaten on their journey by another crab, *Epixanthus dentatus*.

Stefano Cannicci *et al.* decided to investigate what visual cues alert the climbing crabs to the predator (*Animal Behaviour* **63,** 77–83; 2002). They wrapped two 70-cm lengths of mangrove trunk with PVC sheeting, and placed raffia on the top to create a test pathway. The authors then recorded their subjects' response to the dummies shown here.

The first is a preserved specimen of *E. dentatus* in ambush posture. The second is a wooden rectangle, painted naturalistically, but with real claws attached. The third is a wooden trapezium, the same size and coloration as *E. dentatus*, but otherwise not like the real thing. Cannicci *et al.* kept all the dummies in mud for a week to give them an authentic swampy tang. In tests, *S. leptosoma* recognized the first two dummies as dangerous from about 30 cm away, and took avoiding behaviour, but they were unperturbed by the third. So it seems that claws in particular provide the warning. With up to six predators per tree, the climbing crabs probably don't get a second chance to mistake identity. **Tim Lincoln**



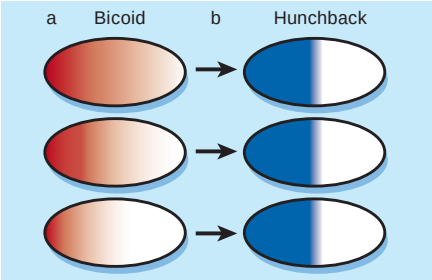


Figure 1 **Filtering out noise in development.** a, **Houchmandzadeh *et al.*[1] find that, within a group of wild-type fruitfly embryos, the profile of the Bicoid gradient (red) can vary significantly (exaggerated somewhat here).** b, **However, the profile of Hunchback expression (blue) is relatively precise and constant, even though Bicoid regulates Hunchback expression. In fact, the addition of extra copies of the Bicoid gene does lead to shifts in the Hunchback pattern[3] (not shown). But Houchmandzadeh *et al.* find that these shifts are not as great as might be expected if the Hunchback pattern depended solely on Bicoid concentration.**

embryos, Houchmandzadeh *et al.*[1] found that the Hunchback boundary — at the level of both mRNA and protein — is very precise, showing far less variation than the Bicoid gradient (Fig. 1). Normalizing for egg length, about two-thirds of the embryos showed a precise Hunchback boundary in a range that spanned only about 1% of the total egg length, a precision equivalent to the width of a single nucleus. Furthermore, unlike the Bicoid gradient, the Hunchback boundary position directly correlates with egg length, suggesting that information about proportion is included in the Hunchback expression pattern.

This observation, that the precision of the wild-type Hunchback boundary is unaffected by variations in the Bicoid gradient, seems to be at odds with the finding[3] that increasing the number of maternal Bicoid transgenes leads to posterior shifts in the Hunchback boundary. However, when Houchmandzadeh *et al.* repeated the transgene experiments they found that the shift in Hunchback expression was clear, but smaller than expected. When they raised embryos at different temperatures they found that, although the Bicoid protein profile at equivalent developmental stages is significantly altered by temperature changes, the position of the Hunchback boundary is almost unaffected. The implication is that this boundary is subject to correction mechanisms that filter out variability in the Bicoid gradient, as well as a mechanism that imparts scaling information.

Houchmandzadeh *et al.* conclude that the precision of the Hunchback boundary is independent of Bicoid. So what does regulate the Hunchback boundary? The most obvious candidates are other embryonic gap genes. The authors show, however, that eliminating any one of these genes has little or no effect on the absolute position of the Hunchback boundary and, more importantly, has no effect on the boundary's precision. The authors screened 80% of the fruitfly genome by eliminating entire chromosomes, and still found no embryonically expressed gene that disrupts the precision of the Hunchback boundary.

The most obvious maternally derived candidates — the posteriorly focused gradient of Nanos protein, and maternal Hunchback — affect the position of the embryonic Hunchback boundary but not its precision[1]. But Houchmandzadeh *et al.* identified specific mutant forms of the maternal Staufen gene that did affect this precision. Staufen is known to affect the localization of maternally derived mRNAs at both embryonic poles[4], but Houchmandzadeh *et al.* show that the effect of Staufen on the Hunchback boundary appears to be independent of an effect on Bicoid localization.

These results have several implications. First, the obvious embryonic candidates for regulating the Hunchback boundary are not solely responsible for its precision. So theories proposing that interactions between gap genes are responsible for generating precise expression boundaries may be missing a crucial component. The identification of mutant forms of the Staufen gene that affect precision might provide the key to unravelling the mechanism.

Second, it is thought that the Bicoid gene evolved relatively recently, within the Dipterans (the large group of insects that includes *Drosophila*). But evolutionarily distant insects such as grasshoppers also show anterior domains of Hunchback expression[5] that are presumably wholly independent of Bicoid. So maybe the genetic system that produces precise Hunchback boundaries in *Drosophila* will give us clues to the regulation of Hunchback in these other insects.

Finally, the phenomenon of noise filtration may be a general property of morphogenetic systems, made necessary by their inherent susceptibility to perturbations. Indeed, studies[6] of the morphogen Dpp in the *Drosophila* wing disc indicate that the concentration gradient of Dpp can differ from its 'activity' gradient (its output). So mechanisms that correct and modulate morphogen gradients may be common to, and required for, the precise, robust and elaborate patterning of different developmental fields. ■

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Daedalus

Fresh flavours

Our past as hunters and gatherers has left us with distinctive taste in food. We like it fresh. An animal or vegetable that was living and growing only a few minutes ago has quite a different taste to one that has been stored. Many foods, from sprouts to fish, lose their pleasant flavour very quickly. Even the British diet would be delightful if it were fresh. But in bulk farming, a large amount of food is harvested at the same time and is then stored. This is clearly at variance with our animal nature. But this type of farming is highly efficient, and so has sadly become a fact of life.

While an animal or vegetable is alive, its immune system protects its evanescent compounds or regenerates them. When it dies, all this stops. Bacterial attack, crosslinking and decomposition all start at once. Freezing, that brutal attempt to stop the clock, seems to work best with the bulk components. One food-processing company claims to freeze its vegetable product within 2 hours of picking it, hoping to trap the brief trace compounds of freshness while they last. Daedalus also recalls how the makers of instant coffee put a key flavour volatile in the space at the top of each jar, so the illusion of the real thing survives at least for a moment. DREADCO biochemists are now studying the trace compounds present in fresh foodstuffs.

This delicate and tricky work must be done quickly, using food picked or killed and transported to the lab with equal rapidity. For each foodstuff, Daedalus hopes to identify or synthesize just those elusive volatiles that restore the illusion of freshness to the long-stored product. Farming, that dreary but efficient business, will at last be matched to our instinctive nature.

Standard condiments, such as salt, pepper or monosodium glutamate, are 'amplifiers': they exaggerate whatever taste the food has at the time. By contrast, each DREADCO 'elixir of freshness' will restore the food's own character, so it tastes fresh again. Like pepper, it will be added at the table rather than in the pot. It may take the form of an inert tasteless powder with an added volatile, or a spray-can of liquid or vapour. Daedalus cannot guess how many will be needed. In the worst case, every foodstuff will need its own elixir. But with luck, only a few elixirs will be needed to revive that elusive sense of freshness — one for meat, say, and one for vegetables. Even calorie-counting, vegetarianism and other dietary extremes will gain new pleasure and respectability. David Jones