An interplay between short- and long-range interactions is a crucial element in a mathematical model of biological pattern formation formulated by Alan Turing in 1952 [11,12]. Turing, whose 100th anniversary was commemorated earlier this year, formulated this mathematical model based on concentrations of two substances, an activator and an inhibitor. The activator activates its own synthesis and that of an inhibitor, which inhibits the activator, and both substances diffuse away from the source at different rates. Depending on which parameters are chosen, a regular periodic pattern of substance distribution can emerge. What is exciting about this model is that the pattern can basically arise from 'nothing', i.e. from very small fluctuations of initial concentrations. In that sense, it is appealing to think of the zebrafish stripes, which also have self-organising characteristics, as Turing patterns.

Turing conceived his model as a purely mathematical system in one dimension, but simulations based on Turing models can give rise to an amazing variety of biological patterns, from sea shells to cats [12]. Such a general model is naturally appealing for biologists who often lament the lack of unified theories in their field, but the challenge is to identify how it is implemented in the real world. Obviously, Turing could not know about the principles and intricacies of cellular signalling. So, in the study of real-life Turing patterns, the abstract roles of his 'activator' and inhibitor' need to be played by real molecules or cells. One of the most clear-cut incarnations of a Turing mechanism in the context of a periodic pattern was found in the spacing of hair follicles in mice, where the signalling molecule WNT is acting as an activator and its antagonist DKK as the inhibitor [13].

Sure enough, Turing patterns can also match with astonishing precision the colour patterns observed in zebrafish under various conditions [10]. However, it is not yet clear whether such an activator–inhibitor system is really at play here, and if so how it is implemented. It need not be as literal as in the case of mouse hair follicle spacing. Instead, the 'activator' could be a stimulation of proliferation, and the inhibitor could be the repulsion seen when melanophores and xanthophores bump into each other. Integrating the electrical properties of the pigment cells into a Turing model will be a challenge. But the idea that the stripes of zebrafish could be a Turing pattern come to life organised by membrane potentials — something rarely considered in the context of developmental pattern formation — is definitely an electrifying one.

References

1. Parichy, D.M. (2003). Pigment patterns: fish in stripes and spots. Curr. Biol. 12, R947–R950.
2. Inaba, M., Yamanaka, H., and Kondo, S. (2012). Pigment pattern formation by contact-dependent depolarization. Science 335, 677.
3. Yamaguchi, M., Yoshimoto, E., and Kondo, S. (2007). Pattern regulation in the stripe of zebrafish suggests an underlying dynamic and autonomous mechanism. Proc. Natl. Acad. Sci. USA 104, 4790–4793.
4. Parchem, R.J., Perry, M.W., and Patel, N.H. (2007). Patterns on the insect wing. Curr. Opin. Genet. Dev. 17, 300–308.
5. van Eeden, F.J., Granato, M., Schach, U., Brand, M., Furutani-Seiki, M., Haffter, P., Hammerschmidt, M., Heisenberg, C.P., Jiang, Y.J., Kane, D.A., et al. (1996). Genetic analysis of fin formation in the zebrafish, Danio rerio. Development 123, 255–262.
6. Haffter, P., Odenthal, J., Mullins, M.C., Lin, S., Farrell, M.J., Vogelsang, E., and Nüsslein-Volhard, C. (1996). Mutations affecting pigmentation and shape of the adult zebrafish. Dev. Genes Evol. 206, 260–276.
7. Maderspacher, F., and Nüsslein-Volhard, C. (2003). Formation of the adult pigment pattern in zebrafish requires leopard and obelix dependent cell interactions. Development 130, 3447–3457.
8. Watanabe, M., Iwashita, M., Ishii, M., Kurachi, Y., Kawakami, A., Kondo, S., and Okada, N. (2006). Spot pattern of leopard Danio is caused by mutation in the zebrafish connexin 41.8 gene. EMBO Rep. 7, 893–897.
9. Iwashita, M., Watanabe, M., Ishii, M., Chen, T., Johnson, S.L., Kurachi, Y., Okada, N., and Kondo, S. (2006). Pigment pattern in jaguar/obelix zebrafish is caused by a Kir7.1 mutation: implications for the regulation of melanosome movement. PLoS Genet. 2, e197.
10. Nakamasu, A., Takahashi, G., Kanbe, A., and Kondo, S. (2009). Interactions between zebrafish pigment cells responsible for the generation of Turing patterns. Proc. Natl. Acad. Sci. USA 106, 8429–8434.
11. Turing, A.M. (1952). The chemical basis of morphogenesis. Phil. Transact. Roy. Soc. London B 237, 37–72.
12. Kondo, S., and Miura, T. (2010). Reaction-diffusion model as a framework for understanding biological pattern formation. Science 329, 1616–1620.
13. Sick, S., Reinker, S., Timmer, J., and Schlake, T. (2006). WNT and DKK determine hair follicle spacing through a reaction-diffusion mechanism. Science 314, 1447–1450.

Florian Maderspacher is Current Biology's Senior Reviews Editor.
E-mail: florian.maderspacher@current-biology.com

Sensory Ecology: Giant Eyes for Giant Predators?

Mathematical models suggest the enormous eyes of giant and colossal squid evolved to see the bioluminescence induced by the approach of predatory whales.

Julian C. Partridge

In the American Museum of Natural History, a striking diorama (Figure 1) depicts a battle between one of the world's largest mammals and its second largest invertebrate: in the darkness of a deep ocean, a sperm whale wrestles a giant squid. Although this interaction has never been witnessed, these species have captured the human imagination for millennia, and their putative combat for centuries. In stories and myth sperm whales (*Physeter macrocephalus*) and giant squid (*Architeuthis* spp.) are conjured as terrible and terrifying animals, easily provoked to attack both seafarers and their ships. Such attacks on ships may have occurred, but attacks by whales on squid are certainly much more common: giant squid are undoubtedly important components of the diet of sperm whales, squid beaks often being found in sperm whale guts, and the skin of sperm whales often baring scars from giant squids' formidable suckers. Indeed, predation of giant squid by sperm whales can be considered the culmination of an approximately 30 million year evolutionary arms race between cephalopods and whales. This race is marked by an interesting sensory imbalance, in which whales depend on reflected sound to find

their prey, but the squid, in arguments developed by Nilsson and colleagues [1] in this issue of *Current Biology*, rely mainly on vision to detect their predators. Moreover, this new work suggests that the extraordinarily large eyes of the giant squid, and the related colossal squid *Mesonychoteuthis* sp., have evolved *specifically* to see large predators.

Like vertebrates, squid eyes are 'simple' or 'camera-type', in which a single lens forms an image on the photoreceptor layer of the retina, but giant and colossal squid do indeed have giant eyes. Human eyes, for comparison, are roughly 24 mm in diameter and those of horses or cows are about 34 mm, whilst ostriches (the terrestrial animal with the largest eyes) have eyes some 50 mm in diameter. Sperm whales have similar sized eyes to those of ostriches (55 mm) and blue whales, the world's biggest vertebrate, have eyes some 150 mm in diameter, though up to a third of that is taken up with a very thick sclera, and internal dimensions are less and thus they, and other giants of the sea such as swordfish, effectively have comparibly sized eyes, some 90 mm in diameter. In contrast, the eyes of *Architeuthis* and *Mesonychoteuthis* are huge, up to 270 mm in diameter and bigger than a soccer ball, begging the question: 'why?'

The answer is likely to lie in the optical biophysics of their eyes and, just as importantly, what they have evolved to see. In general, big eyes provide both higher sensitivity and higher spatial resolution. Temporal resolution (the 'shutter speed' of an eye) aside, sensitivity and resolution are the main variables underpinning ocular anatomy: big eyes perform better; the counteracting costs being metabolic expense and physical bulk. In the deep sea, which is essentially dark and where animals occur in very low densities, sensitive eyes confer an important advantage as they allow their owners to see smaller objects further away, and therefore visually to survey a greater volume of their surrounds. Sensitivity is, however, highly dependent on visual task [2–4]. For broad sources of light, with which we are most familiar in our environment, retinal irradiance, and hence sensitivity is determined by the f-number: the ratio of the focal length (f) to the lens diameter. For this reason the small eyes of mice (f-number = f/0.9)

Figure 1. Battle of the giants.
Life sized models of *Physeter* and *Architeuthis* battle it out in the famous 'Squid and Whale' diorama of the American Museum of Natural History's Milstein Hall of Ocean Life (credit: AMNH/D. Finnin).

are much more sensitive than ours (f-number = f/2 in darkness with open pupil), and provide them with a retinal image some five times brighter [5]. For the visualisation of point sources, such as stars, however, it is pupil diameter that counts — which is why the best telescopes tend to have the largest mirrors or lenses. Viewing stars is obviously not a visual task of relevance in the deep sea, but point sources of light are common, in the form of bioluminescence, and the ability to see bioluminescence may be exactly what giant squid depend on to see approaching whales. What is unusual, argue Nilsson and colleagues [1], is it is not individual point sources that the giant squid need to visualize, but rather the combined light from many such sources flashing in unison.

Spontaneous bioluminescence in the deep sea is remarkably uncommon, but bioluminescent animals (and some 90% of deep sea animals have the ability) are easily induced to flash when disturbed [6], a fact no doubt well appreciated by naval submariners. For this reason, it might be considered advantageous for deep-sea predators to adopt a sit-and-wait strategy and many, including giant squid, may well do so. For the highly energetic mammalian whales, however, this is not an option, as food is too widely dispersed and too rarely encountered in the mesopelagic to do without active

searching. What little we know of sperm whale foraging suggests that they descend at about 1.5 ms^{-1} [7] before actively searching, and some studies [8] suggest they intersperse steady 2 ms^{-1} swimming with bursts of speed, including sprints up to 9 ms^{-1} (32 kph). Such swimming speeds are similar to those of other cetacean-hunting toothed whales [9] and will undoubtedly trigger bioluminescence: dolphins swimming at much lower speeds through seas rich in bioluminescent organisms glow brightly (Figure 2), revealing striking detail about their body form [10]. Even in relatively impoverished mesopelagic water, foraging sperm whales may thus be similarly illuminated, particularly if giant squid favour zones with higher biomass and hence more potential bioluminescence.

What Nilsson and colleagues [1] have done is to calculate how the size of an eye is optimised for different visual tasks and, having taken into consideration a raft of variables about the emission and transmission of light underwater, eye geometry, visual optics, photoreceptor properties, and so on, they conclude that giant and colossal squids' eyes have evolved for a purpose not shared by other animals: the detection of form illumination due to bioluminescence induced by foraging whales. Their models show that, in shallow water, objects are most easily detected as dark silhouettes
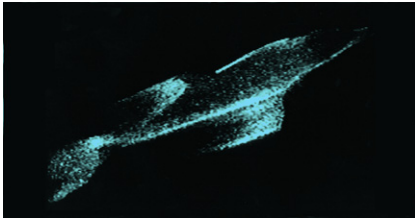
Figure 2. Revealed by bioluminescence. Bioluminescence induced by a 2.7 m long Atlantic bottle-nosed dolphin (*Tursiops truncatus*) gliding at ~0.1 ms^{-1} in San Diego Bay and filmed with an intensified video camera. (Photograph from Michael Latz, Scripps Institution of Oceanography, University of California San Diego.)

seen against the brighter down-welling space light but, under most conditions, the detection of bright point sources provides the longest visual range. For these tasks, eyes no bigger than 90 mm in diameter are needed, and returns diminish rapidly for larger eyes. The only notable feature that sets very large eyes apart is that they are superior for detecting big, low contrast, luminous objects at long visualisation ranges and depths where daylight is insignificant. Thus, counter-intuitively, the authors suggest that the huge eyes of giant and colossal squid have evolved for a particular low-resolution visual task: to spot large, dimly glowing, approaching whales.

The evolution of the toothed whales has long been intimately associated with hunting cephalopods [11] and today squid and octopus feature in the diets of 90% of toothed whales: perhaps unsurprising as oceanic cephalopods are a massive food resource. Rising in the early Oligocene some 34 million years ago, the earliest echolocating toothed wales were relatively late arrivals in the evolutionary history of squid. The ancient cephalopods arose in the Cambrian, but squid are evolutionary upstarts, evolving 'only' some 150 millions years ago. Vision may have been important for the first whales, but sonar soon evolved, perhaps to help hunting in shallow seas at night, and perhaps because cephalopods are essentially deaf to whales' sonar. Squids do not hear the clicks and creaks of whale echolocation, the sonar frequencies being beyond their sensitivity spectrum despite the intense sounds whales produce [12,13]. Squids are poor acoustic targets, lacking gas filled swim

bladders or dense skeletal elements to reflect sound, although their muscular arms and mantle, and chitinous beak will produce some echo. The first echolocating toothed whales may have eaten solid-shelled nautiloids that would have been easy to detect with sound, but detecting softer-bodied squids is harder. In consequence, sperm whales make one of the loudest noises in the animal kingdom and are calculated to be able to detect 250 mm *Loligo* squid up to 325 m away, and muscular 1.5 m long Humboldt squid (*Dosidicus gigas*) at as far as 1000 m [12–14]. No doubt relatively flaccid mesopelagic squid, giant squid included, are more acoustically cryptic and so difficult to detect, but it is likely that these are detectable beyond 100 m. Neatly, this is about the distance at which giant squid might see approaching whales calculated by Nilsson and colleagues [1].

Where behaviour is difficult or impossible to observe, modelling visual performance is one way to gain insights about how animals may interact, and to identify selective pressures that might be operating on their evolution. In the context of giant squid the mathematical models of Nilsson and colleagues [1] suggest why they may have such giant eyes, although, much as it is fascinating to speculate, significant caveats inevitably remain. For instance, although giant squid have eyes much larger than those of similar sized, or larger, fish and whales, they may not actually be out of proportion compared with those of other cephalopods. At this point, the allometric scaling of eye size with body size, such as has been undertaken for many taxa of vertebrates [15], remains unresolved for squid but, as always in comparative biology, phylogeny needs to be considered; even when physics appears to dominate an argument. The extinct ichthyosaurs, giant marine reptiles that lived 250–90 million years ago, had eyes at least as big as those of giant squid, for similar body sizes [16], and a cursory examination suggests squid eye sizes may fit within the confidence limits of ichthyosaur eye size allometry. Did ichthyosaurs too need to detect large glowing predators? Despite the efforts of both scientists and filmmakers, we know too little about the way in which sperm whales catch giant squid and,

until we have direct observations, intriguing mathematical models and imaginative dioramas may be the best we have.

References

1. Nilsson, D.-E., Warrant, E.J., Johnsen, S., Hanlon, R., and Shashar, N. (2012). A unique advantage for giant eyes in giant squid. Curr. Biol. *22*, 683–688.
2. Land, M.F. (1981). Optics and vision in invertebrates. In Handbook of Sensory Physiology, *Vol. VII/6B*, H. Autrum, ed. (Berlin, Heidelberg, New York: Springer), pp. 471–592.
3. Warrant, E.J., and Locket, N.A. (2004). Vision in the deep sea. Biol. Rev. *79*, 671–712.
4. Warrant, E.J. (2004). Vision in the dimmest habitats on earth. J. Comp. Physiol. A *190*, 765–789.
5. Land, M.F., and Nilsson, D.-E. (2002). Animal Eyes (Oxford, New York: Oxford University Press).
6. Widder, E.A. (2001). Bioluminescence and the pelagic visual environment. Mar. Fresh Behav. Physiol. *35*, 1–26.
7. Miller, P.J.O., Johnson, M.P., Tyack, P.L., and Terray, E.A. (2004). Swimming gaits, passive drag and buoyancy of diving sperm whales *Physeter macrocephalus*. J. Exp. Biol. *207*, 1953–1967.
8. Aoki, K., Amano, M., Sugiyama, N., Muramoto, H., Suzuki, M., Yoshioka, M., Mori, K., Tokuda, D., and Miyazaki, N. (2007). Measurement of swimming speed in sperm whales. Symposium on Underwater Technology and Workshop on Scientific Submarine Cables and Related Technologies 2007. pp. 467–471.
9. Soto, N.A., Johnson, M.P., Madsen, P.T., Díaz, F., Domínguez, I., Brito, A., and Tyack, P. (2008). Cheetahs of the deep sea: deep foraging sprints in short-finned pilot whales off Tenerife (Canary Islands). J. Anim. Ecol. *77*, 936–947.
10. Rohr, J., Latz, M.I., Fallon, S., Nauen, J.C., and Hendricks, E. (1998). Experimental approaches towards intercepting dolphin stimulated bioluminescence. J. Exp. Biol. *201*, 1447–1460.
11. Lindberg, D.R., and Pyenson, N.D. (2007). Things that go bump in the night: evolutionary interactions between cephalopods and cetaceans in the tertiary. Lethaia *40*, 335–343.
12. Madsen, P.T., Wilson, M., Johnson, M., Hanlon, R.T., Bocconcelli, A., Aguilar Soto, N., and Tyack, P.T. (2007). Clicking for calamari: toothed whales can echolocate squid *Loligo pealeii*. Aquatic Biol. *1*, 141–150.
13. Wilson, M., Hanlon, R.T., Tyack, P.L., and Madsen, P.T. (2007). Intense ultrasonic clicks from echo locating toothed whales do not elicit anti-predator responses or debilitate the squid *Loligo pealeii*. Biol. Lett. *3*, 225–227.
14. André, M., Johansson, T., Delory, E., and van der Schaar, M. (2007). Foraging on squid: the sperm whale mid-range sonar. J. Mar. Biol. Ass. UK *87*, 59–67.
15. Howland, H.C., Merola, S., and Basarab, J.R. (2004). The allometry and scaling of the size of vertebrate eyes. Vis. Res. *44*, 2043–2065.
16. Montani, R., Rothschild, B.M., and Wahl, W. (1999). Large eyeballs in diving ichthyosaurs. Nature *402*, 747.

School of Biological Sciences, University of Bristol, Woodland Road, Bristol BS8 1UG, UK.
E-mail: j.c.partridge@bristol.ac.uk