

effects of mutating *Rb* are partly overcome by mutating a second gene (*E2f1*, *E2f3* or *Id2*) that encodes an Rb-binding protein<sup>8–10</sup>. These genetic interactions were interpreted by assuming that Rb and the Rb-binding proteins interact functionally in the tissues that are affected in *Rb*-deficient animals. The results of Wu *et al.* raise a whole new set of questions. For example, mutation of *E2f1* or *E2f3* in *Rb*-deficient animals prevents the cell death that occurs in the central nervous system of *Rb*-deficient mice<sup>8,9</sup>. So, do the products of the *E2f* genes have a specific role in cell death in the nervous system? Or might a reduction in *E2f* activity alleviate the placental defect of *Rb*-deficient embryos and indirectly protect the central nervous system?

Inevitably, there are further questions. For instance, is an *Rb*-mutant placenta enough to cause embryonic death, as well as defects in the central nervous system and red-blood-cell development, in wild-type embryos? Perhaps the homozygous mutant phenotypes result from a combination of factors, requiring both the systemic changes caused by the placental defects and also intrinsic changes resulting from the loss of Rb protein in the affected tissues.

And what are the properties of trophoblast stem cells that make them particularly sensitive to the loss of *Rb*? Despite the tremendous progress in molecular studies of the Rb protein in the 16 years since its gene was identified, it remains uncertain which of the many cellular and biochemical functions attributed

to it are important for its role as a tumour suppressor. Retinoblastoma, a cancer of the retina, occurs only in very young children, and this temporal boundary is thought to reflect a window in eye development where a poorly defined group of cells is especially sensitive to the loss of *Rb*. One of the challenges is to work out which cell types need the Rb protein and why it becomes so important at certain times in development. Does its function vary, or does the 'wiring' of cells change so that Rb becomes critical? Further studies of *Rb*-deficient animals might provide clues.

Mutant phenotypes often result from complex interactions between multiple cell types, and one of the attractions of animal studies is the opportunity to study and dissect these effects. The work of Wu *et al.*<sup>1</sup> is a beautiful illustration of how even the best-studied animal phenotypes can have unexpected components. ■

Nick Dyson is at the Massachusetts General Hospital Cancer Center, Building 149, 13th Street, Charlestown, Massachusetts 02129, USA.  
e-mail: dyson@helix.mgh.harvard.edu

1. Wu, L. *et al.* *Nature* **421**, 942–947 (2003).
2. Lee, E. Y.-H. P. *et al.* *Nature* **359**, 288–294 (1992).
3. Jacks, T. *et al.* *Nature* **359**, 295–300 (1992).
4. Clarke, A. R. *et al.* *Nature* **359**, 328–330 (1992).
5. Rossant, J. & Cross, J. C. *Nature Rev. Genet.* **2**, 538–548 (2001).
6. Williams, B. O. *et al.* *EMBO J.* **13**, 4251–4259 (1994).
7. Maandag, E. C. *et al.* *EMBO J.* **13**, 4260–4268 (1994).
8. Tsai, K. Y. *et al.* *Mol. Cell* **2**, 293–304 (1998).
9. Ziebold, U., Reza, T., Caron, A. & Lees, J. A. *Genes Dev.* **15**, 386–391 (2001).
10. Lasorella, A., Nosedà, M., Beyna, M., Yokota, Y. & Iavarone, A. *Nature* **407**, 592–598 (2000).

## Oceanography

# The brawniest retroreflection

Arnold L. Gordon

The influence of the Agulhas system of currents and eddies around southern Africa extends far beyond that region. Hence the especial need for a better understanding of the complex phenomena involved.

An intriguing class of ocean-circulation pattern is that exhibiting a retroreflection — one in which a swift current, flowing along the western boundary of a continent, separates from the continental margin and curls back upon itself. Large buoyant pools of water detach from the resulting loop, injecting eddies into a neighbouring ocean province. The ocean's most pronounced retroreflections are associated with the Agulhas, Brazil, North Brazil and East Australian currents, and the Gulf of Mexico's Loop Current. The most energetic of these is the Agulhas retroreflection, for which the term was designated<sup>1</sup>. This brawniest of retroreflections is the subject of a special issue of a journal<sup>2</sup> — *Deep-Sea Research II* — in which 12 papers describe both observations and simulations of the retroreflection, and the consequential

exchange of water between the Indian and Atlantic oceans.

The geography of the Agulhas system is shown in Fig. 1. On rounding the southern rim of Africa, the Agulhas Current abruptly turns anticlockwise, to flow back to the Indian Ocean as the Agulhas return current. The special nature of the Agulhas retroreflection stems from the unique regional geography and wind patterns. The southern coast of Africa is about 5° of latitude closer to the Equator than the westerly wind maximum, the latitude where western boundary currents in the subtropics are expected to separate from the continental margin to turn into their ocean's interior. The Agulhas 'runs out' of western continental margin before the wind allows for such separation. The resulting retroreflection is shaped by the sea-floor morphology and by regional to large-scale winds<sup>3</sup>; its form is expected to

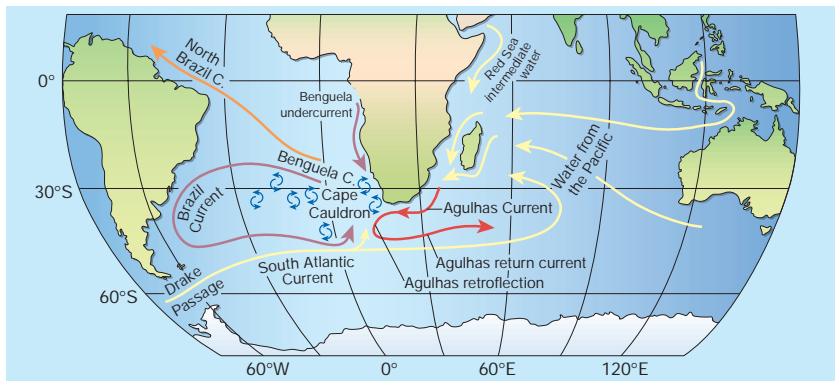
alter with changes of the maximum westerlies, or with the strength of the Agulhas Current. The warm surface water trapped within the Agulhas retroreflection transfers heat to the atmosphere, the largest such exchange in the Southern Hemisphere. The effects are considerable, for instance in influencing rainfall patterns as far away as Australia<sup>4</sup> or deep-ocean 'overturning' in the northernmost Atlantic<sup>5</sup>.

The significance of the Agulhas retroreflection does not end with its momentary loop into the southeast corner of the South Atlantic, for there are its outputs and inputs to consider. A major output, for instance, is the considerable 'leakage' of water from the Indian Ocean into the upper kilometre of the Atlantic Ocean. The magnitude of this phenomenon has been the subject of conflicting results and much debate over the past 15 years, as have the wider implications<sup>6,7</sup>. These include the effects of Agulhas leakage on the heat flow towards the Equator within the South Atlantic, and on the formation of North Atlantic Deep Water (NADW). Deep-water formation in the North Atlantic is one of the central features of ocean circulation. This overturning circulation involves water movement on a massive scale — the surface flow of warm water northwards, its sinking at high latitudes, and the return flow of cooler water at depth.

The various and widespread inputs to the Agulhas system are shown in Fig. 1. Streams of water are derived from far-distant parts of the Pacific Ocean, and may be part of a NADW-induced global balance<sup>8–11</sup>. Red Sea intermediate water is part of the picture<sup>12,13</sup>, as is eastward-flowing water in the South Atlantic, both of which contribute to the mix in the Indian Ocean. All of the return pathways must pass through or become entangled with the Agulhas retroreflection, which may act as a 'valve' regulating the buoyancy of water in the upper kilometre of the South Atlantic Ocean and may in turn regulate NADW overturning.

Clearly, then, the Agulhas retroreflection presents a challenge to oceanographers. Equally clearly, the convenient but unrealistic notion of a 'steady-state ocean' is particularly deficient in portraying this system. This is where the *Deep-Sea Research II* special issue<sup>2</sup> comes in. Comprehensive time-series observations (*in situ* and from satellites) and accurate computer simulations are required to capture the detailed behaviour of the retroreflection and its effects. The various contributors describe the advances that have been made on both fronts.

Much information has been provided by acoustically tracked instruments, known as RAFOS — Ranging and Fixing of Sound — floats, that were allowed to drift at depths ranging from 200 to 1,350 m. The data show that the mean circulation in the Cape Basin (the first Atlantic basin to receive leakage of Agulhas water) is obscured by a cauldron of



**Figure 1** The Agulhas system and associated flow patterns. The Agulhas Current draws water from the Pacific Ocean through the Indonesian throughflow and Drake Passage, and from the Tasman Sea. It abruptly turns back towards the Indian Ocean near 20° E. Here, at the Agulhas retroflection, 'leakage' of water occurs within an array of cyclonic (clockwise) and anticyclonic (anticlockwise) eddies that are injected into the vigorous stirring and mixing environment of the Cape Basin (the 'Cape Cauldron'). The South Atlantic Current adds water to the cauldron, as does the subsurface flow of the Benguela undercurrent along the west coast of Africa, and salty Red Sea water along the east coast. A blend of these waters spreads into the Brazil and North Brazil currents. The latter is part of the large-scale 'overturning circulation' induced by the formation of North Atlantic Deep Water.

powerful eddies, 100–400 km in diameter. All of these eddies are generated within or along the periphery of the retroflection, some of them originating from the Indian Ocean, others from the South Atlantic Current (Fig. 1). These eddies are not just large anticyclonic rings, cast off from the retroflection at an average rate of six per year. Rather, they are a hodgepodge of types, which interact with each other and with the main retroflection, in a general milieu of vigorous stirring and mixing. Indian Ocean water is trapped within the eddy cores, and is often lost in the process, blending into the regional background (this is usually 'thermocline water' — that is, water from above about 800-m depth — but can take in the upper kilometre or two).

Studies of specific, newly formed Agulhas rings have exposed their turbulent birth and early evolution as they drift into the cauldron, with numerical simulations adding further detail to our picture of the complex Cape Basin circulation. These simulations can resolve quite fine-grained behaviour, and they reveal the coexistence, in dipoles, of anticyclonic eddies intensified at the surface with cyclonic partners intensified at the sea floor. The cyclonic eddies are caged in by the topography of the Cape Basin. But the anticyclonic eddies can break out of the basin and enter the South Atlantic, although with substantial energy loss.

Other authors in the special issue<sup>2</sup> describe how the witch's brew of the Cape Cauldron feeds blended water, via the Benguela Current, into the subtropical gyre of the South Atlantic. Some of this water remains within the gyre, eventually finding its way back to the Indian Ocean in what can be thought of as a super-subtropical gyre spanning the South Atlantic and Indian Oceans. But some enters the Northern Hemisphere within the North

Brazil Current, as part of the NADW overturning circulation. About three Agulhas rings shed from the retroflection survive the blender, and make stately progress over the mid-ocean ridge and into the western South Atlantic Ocean. There, three to four years later, they will impinge upon the Brazil Current. It is encouraging to note the close agree-

#### Cell polarity

## From embryo to axon

Melissa M. Rolls and Chris Q. Doe

Many cell types in our body, ranging from neurons to the epithelial cells that line the lungs and skin, must be polarized to function properly. The same mechanism may establish the polarity of many of these cells.

How are we to make sense of the complexity of our brains? Filled with billions of nerve cells, each making hundreds or thousands of precise connections to other neurons, this organ develops anew in each of us. Not only that, but if you were to take a closer look at the individual cells, you would see that they come in thousands of stunning shapes. But there is a theme that emerges from studying these shapes. In vertebrates, most neurons have a single long protrusion, the axon, that is specialized to transmit signals to other cells, as well as many shorter, branched protrusions called dendrites that are specialized to receive signals (Fig. 1). Perhaps understanding this fundamental polarity would be a good starting point for understanding the brain's complexity. Over the past few years, progress has been made in defining how axons and dendrites differ. But less is known about how they are initially established.

ment of the RAFOS float speeds to results of the MODAS — Modular Ocean Data Assimilation System — model, which assimilates satellite altimetric measurement of sea-level variability.

There is still a great deal to learn about the Agulhas valve, and its variation under different climatic conditions. Ensuring that it is properly represented in global ocean and climate models remains a daunting challenge. But this collection of papers<sup>2</sup> shows how the brotherhood of observers armed with new tools, aided by satellite-based remote sensing, and modellers with their increasingly realistic simulations, can take us forward. ■

Arnold L. Gordon is at the Lamont-Doherty Earth Observatory, Columbia University, Palisades, New York 10964, USA.

e-mail: agordon@ldeo.columbia.edu

1. Bang, N. D. S. *African Geog. J.* **52**, 67–76 (1970).
2. Richardson, P. L. (ed.) *Deep-Sea Res. II* **50**, 1–319 (2003).
3. Matano, R. P. *J. Phys. Oceanogr.* **26**, 2267–2279 (1996).
4. Reason, C. J. *J. Clim.* **14**, 2769–2778 (2001).
5. Gordon, A. L. *J. Geophys. Res.* **91**, 5037–5046 (1986).
6. Gordon, A. L. in *Ocean Circulation and Climate* (eds Stedler, G., Church, J. & Gould, J.) 303–314 (Academic, 2001).
7. de Ruijter, W. A. et al. *J. Geophys. Res.* **104**, 20885–20910 (1999).
8. Gordon, A. L., Weiss, R. F., Smethie, W. M. Jr & Warner, M. J. *J. Geophys. Res.* **97**, 7223–7240 (1992).
9. Sloyan, B. M. & Rintoul, S. R. *J. Phys. Oceanogr.* **31**, 1005–1030 (2001).
10. Gordon, A. L. & Fine, R. A. *Nature* **379**, 146–149 (1996).
11. Speich, S. et al. *Geophys. Res. Lett.* **29**, 10–13 (2002).
12. Beal, L. M., Ffield, A. & Gordon, A. L. *J. Geophys. Res. Oceans* **105**, 8549–8564 (2000).
13. Weijer, W., de Ruijter, W. P. M. & Dijkstra, H. A. *J. Phys. Oceanogr.* **31**, 2385–2402 (2001).