

NATURE

50 YEARS AGO

With the appearance of a new journal, Virology (pp. 140. New York: Academic Press, Inc.; 9 dollars per vol.), this useful, but ugly, word of doubtful parentage presumably takes its place as the official designation of the study of viruses.

From Nature 9 July 1955

100 YEARS AGO

Even with things as they are, Oxford and Cambridge, though much injured by competitive examinations, have been far less injured than England in general; and this they owe to the residential system. Little thought of, perhaps neglected, by the builders, the head-stone of the educational edifice is here to be found. Where mind meets mind in the free intercourse of youth there springs from the contact some of the fire which, under our present system, is rarely to be obtained in any other way; and not only this, but many other priceless advantages in the battle for life are also conferred. To these influences we owe in large part all that is best in the English character, and so valuable are the qualities thus developed, or at least greatly strengthened, that we regard residential colleges as essential to the success and usefulness of the newer universities.

ALSO:

An Angler's Hours. By H. T. Sherringham. Mr. Sherringham deserves the thanks of all anglers who have an idle hour and no fishing for having re-published his essays in book form, and he who is forced by sad circumstance to enjoy his fishing vicariously will find his time well spent in our scribe's company... he despairs of nothing, but finds good in all; if there are no fish he can study nature, and if there is no water he can shrewdly meditate on the ways of fish and men; an hour with him and his rod by a troutless tarn is as good as an hour by the Kennet in the mayfly time... A word of praise is also due to the publishers, who have produced a book the size and print of which add to its convenience as an adjunct to a pipe, an easy chair, and idleness. From Nature 6 July 1905

Figure 1 Arion lusitanicus — conservation agent.

grassland sown with rye grass (Lolium perenne) and white clover (Trifolium repens) on a former arable field that contained its own residual seed bank of weed and other plant species.

The surface soil was thoroughly mixed to avoid local patchiness in the seed bank, and a series of experimental 2×2 -m plots was established, each surrounded by a slug-proof fence. Local slugs were placed in selected plots at a density of 22 individuals per plot during the first year, with an additional 10 slugs in subsequent years; this represents a high but realistic concentration of the molluscs. Wooden slug shacks provided shelter for these easily desiccated creatures in times of drought. The control plots were treated with molluscicide to prevent any inadvertent slug invasion. Analysis of the vegetation composition over the following three years provided the data needed to determine the effect of slug grazing.

In the first two years, the species richness and the diversity were lower in the slug-grazed plots than in controls. (Species richness is the number of species per plot; diversity also takes into account the proportions of different species, and is measured by the Shannon diversity index.) This result confirms the expectation that slug selection of seedlings

would reduce the number of \mathbb{Z} species from the local seed bank that become established. In the third year of the experiment, however, species richness in the grazed plots was 23% higher than in the controls.

The reason for this enhancement of richness and diversity in the more mature stages can be attributed to the consistent removal of biomass by the slugs. The yield from primary productivity was reduced by around 25% as a result of slug grazing (comparable to the removal of biomass by sheep

in a grazed pasture⁴). Holding back the development of dominance by fast-growing species provided an opportunity for the germination and establishment of less-competitive species, including annual plants. In other words, slug grazing permits the establishment of plant species that might otherwise find it difficult to maintain populations in developing grassland. So, on this account at least, slugs are good for diversity.

Slugs will never act as sheep substitutes by creating a pastorally idyllic landscape and inspiring poets. But they could well be an answer to the conservationist's prayer silently grazing beneath our feet, they provide an alternative way to mow a meadow. Peter D. Moore is in the Division of Life Sciences, King's College London, Franklin-Wilkins Building, 150 Stamford Street, London SE1 9NH, UK. e-mail: peter.moore@kcl.ac.uk

- Buschmann, H., Keller, M., Porret, N., Dietz, H. 1. & Edwards, P. J. Funct. Ecol. 19, 291-298 (2005).
- 2. Tansley, A. G. (ed.) Types of British Vegetation (Cambridge Univ. Press, 1911).
- Grime, J. P. Plant Strategies, Vegetation Processes, and 3. Ecosystem Properties (Wiley, Chichester, 2001).
- 4. Perkins, D. F. in Production Ecology of British Moors and Montane Grasslands (eds Heal, O. W. & Perkins, D. F.) 375-395 (Springer, Heidelberg, 1978).

NONLINEAR DYNAMICS When instability makes sense

Peter Ashwin and Marc Timme

Mathematical models that use instabilities to describe changes of weather patterns or spacecraft trajectories are well established. Could such principles apply to the sense of smell, and to other aspects of neural computation?

Dynamical stability is ubiquitous in many systems — and more often than not is desirable. Travelling down a straight road, a cyclist with stable dynamics will continue in more or less a straight line despite a gust of wind or a bumpy surface. In recent years, however, unstable dynamics has been identified not only as being present in diverse processes, but even as being beneficial. A further exciting candidate for this phenomenon is to be found in the realm of neuroscience — mathematical models¹⁻³ now hint that instabilities might also be advantageous in representing and processing information in the brain.

A state of a system is dynamically stable when it responds to perturbations in a proportionate way. As long as the gust of wind is not too strong, our cyclist might wobble, but the



Figure 1 | **Stable and unstable dynamics in 'state space'. a**, A stable state with stationary dynamics. The system returns to the stable fixed point in response to small perturbations. **b**, An unstable saddle state is abandoned upon only small perturbations. The paths indicating possible evolutions of this system (solid lines) may pass close by such a state but will typically then move away. Only some of the exceptional

direction and speed of the cycle will soon return to their initial, stable-state values. This stable state can be depicted in 'state space' (the collection of all possible states of the system) as a sink — a state at which all possible nearby courses for dynamic evolution converge (Fig. 1a).

By contrast, at unstable states of a system, the effect of a small perturbation is out of all proportion to its size. A pendulum that is held upside-down, for example, although it can in theory stay in that position for ever, will in practice fall away from upright with even the smallest of disturbances. On a state-space diagram, this is depicted by paths representing possible evolutions of the system running away from the state, rather than towards it. If the unstable state is a 'saddle' (Fig. 1b), typical evolutions may linger nearby for some time and will then move away from that state. Only certain perturbations, in very specific directions, may behave as if the state was stable and return to it.

There is, however, nothing to stop the pendulum from coming back very close to upright if frictional losses are not too great. This is indicated on a state-space diagram by a path travelling close to what is known as a heteroclinic connection between two saddles. Heteroclinic connections between saddle states (Fig. 1c) occur in many different systems in nature. They have, for example, been implicated in rapid weather changes that occur after long periods of constant conditions⁴. Engineers planning interplanetary space missions⁵ routinely save enormous amounts of fuel by guiding spacecraft through the Solar System using orbits that connect saddle states where the gravitational pulls of celestial bodies balance out.

Several studies^{1–3,6,7} have raised the idea that this kind of dynamics along a sequence of saddles (Fig. 1c) could also be useful for processing information in neural systems. Many traditional models of neural computation share the spirit of a model⁸ devised by John Hopfield, where completion of a task is equivalent to the system becoming stationary at a stable state. Rabinovich *et al.*¹ and, more recently, Huerta *et al.*² have shown that, in mathematical models of the sense of smell, switching among unstable saddle states — and not stable-state dynamics — may be responsible for the generation of characteristic patterns of neural activity, and thus information representation. In creating their models, they have been inspired by experimental findings in the olfactory systems of zebrafish and locusts⁹ that exhibit reproducible odour-dependent patterns.

of neural computation.

Huerta et al.² model the dynamics in two neural structures known as the antennal lobe and the mushroom body. These form staging posts for processing the information provided by signals coming from sensory cells that are in turn activated by odour ingredients. Whereas activity in the mushroom body is modelled by standard means using stable dynamics, the dynamics of the antennal lobe is modelled in a non-standard way using networks that exhibit switching induced by instabilities. In these models, the dynamics of the neural system explores a sequence of states, generating a specific pattern of activity that represents one specific odour. The vast number of distinct switching sequences possible in such a system with instabilities could provide an efficient way of encoding a huge range of subtly different odours.

Both Rabinovich *et al.*¹ and Huerta *et al.*² interpret neural switching in terms of game theory: the neurons, they suggest, are playing a game that has no winner. Individual states are characterized by certain groups of neurons being more active than others; however, because each state is a saddle, and thus intrinsically unstable, no particular group of neurons can eventually gain all the activity and 'win the game'. The theoretical study¹ was restricted to very specific networks of coupled neurons, but Huerta and Rabinovich have now shown³ that switching along a sequence of saddles occurs naturally, even if neurons are less closely coupled, as is the case in a biological system.

Similar principles of encoding by switching along a sequence of saddles have also been investigated in more abstract mathematical models (see refs 6, 7 for examples) that pinpoint possible mechanisms for directing the switching processes. One problem with these proposals from mathematical modelling^{1-3,6,7} is that there is no clear-cut experimental evidence of their validity in any real olfactory system. Nevertheless, all of the mathematical models rely on the same key features saddles that are never reached but only visited in passing, inducing non-stationary switching — that have been shown to be relevant in other natural systems^{4,5}. In biology, the detection of odours by populations of neurons could be only one example.

c, A collection of saddles linked by 'heteroclinic' connections (dashed lines).

The system evolves close to the heteroclinic connections between different

saddles, lingering near one saddle state before moving on to the next. It is this last type of dynamics that several studies^{1-3,6,7} find in models

Much remains to be done in fleshing out this view of natural processes in terms of dynamics exploiting saddle instabilities. Then we will see just how much sense instability really makes.

Peter Ashwin is at the School of Engineering, Computer Science and Mathematics, University of Exeter, Exeter, Devon EX4 4QE, UK. Marc Timme is at the Max Planck Institute for Dynamics and Self-Organization, and the Bernstein Center for Computational Neuroscience, Bunsenstraße 10, 37073 Göttingen, Germany.

e-mails: P.Ashwin@ex.ac.uk;

timme@chaos.gwdg.de

- 1. Rabinovich, M. et al. Phys. Rev. Lett. 87, 068102 (2001).
- 2. Huerta, R. et al. Neural Comput. 16, 1601-1640 (2004).
- 3. Huerta, R. & Rabinovich, M. Phys. Rev. Lett. 93, 238104 (2004)
- Stewart, I. Nature 422, 571-573 (2003).
- Taubes, G. Science 283, 620-622 (1999)
- Hansel, D., Mato, G. & Meunier, C. Phys. Rev. E 48, 3470-3477 (1993).
- Kori, H. & Kuramoto, Y. Phys. Rev. E 62, 046214 (2001).
 Hopfield, J. J. Proc. Natl Acad. Sci. USA 79, 2554–2558 (1982)
- 9. Laurent, G. Nature Rev. Neurosci. 3, 884-895 (2002).

CORRECTION

In the News and Views article "Granular matter: A tale of tails" by Martin van Hecke (*Nature* **435**, 1041-1042; 2005), an author's name was misspelt in reference 9. The correct reference is Torquato, S., Truskett, T. M. & Debenedetti, P. G. *Phys. Rev. Lett.* **84**, 2064–2067 (2000).