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 x 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 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 pasture). 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 pastoral 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


Figure 1 | Arion lusitanicus — conservation agent.

**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 models 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
and, more recently, Huerta find in models have raised the idea that
2,1041–1042; 2064–2067 (2000).

NEWS & VIEWS

Stable and unstable dynamics in ‘state space’. a
that exhibit

■
was

a state but will typically then move away. Only some of the exceptional
evolutions may linger nearby for some time and will then move away from that state. Only certain perturbations, in very specific direc-
tions, 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 conditions1. Engineers planning interplanetary space missions2 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 studies3–5,6 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 model7 devised by John Hopfield, where completion of a task is equivalent to the
system becoming stationary at a stable state. Rabinovich et al.3 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 gener-
ation 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 locusts8 that exhibit
reproducible odour-dependent patterns.

Huerta et al.1 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 insta-
bilities. 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 intrin-
sically unstable, no particular group of neurons can eventually gain all the activity and ‘win the game’. The theoretical study4 was
restricted to very specific networks of coupled
neurons, but Huerta and Rabinovich have now shown5 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 pin-
point possible mechanisms for directing the
switching processes. One problem with these
proposals from mathematical modelling1–3,6,7 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
— have been shown to be relevant in other
natural systems3,5. In biology, the detection of
odours by populations of neurons could be
only one example.

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

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
paths come back to the saddle state (dashed lines pointing inwards).
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 studies1–3,6,7 find in models
of neural computation.


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.,
84, 2064–2067 (2000).