

neural activity of downstream cortical areas? Are expectations integrated during the delay period or only at a later stage, perhaps at the decision stage (as suggested in [14])? What about other biases that may affect perception as, for instance, response bias [17]? These questions remain open. However, the combination of this behavioral paradigm with the technological advances that allow us to image and manipulate the activities of large populations of neurons in the rodent brain guarantee more exciting findings to come in our journey to understanding how percepts are formed in the brain.

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Evolution: Contingent Predictability in Mammalian Evolution

Luke J. Harmon
 Department of Biological Sciences, University of Idaho, Moscow, ID 83843, USA
 Correspondence: lukeh@uidaho.edu
<http://dx.doi.org/10.1016/j.cub.2017.04.013>

Convergence of distantly related species to similar forms speaks to the predictability of evolution, but we still lack general insights into whether convergence is more common or rare than we would expect. Using a global dataset of mammalian species, Mazel and colleagues find that both convergence and divergence occur more often than expected. Convergence was especially common at broad scales that involved Australia, speaking to the extraordinary replicate mammalian communities found there.

Biologists tend to think of life on Earth as being exceptionally diverse. No matter the group, we marvel at its extraordinary diversity and at evolution's propensity for endless inventions [1]. For example, mammals include several bizarre creatures that, were they not real, would be ideal sci-fi aliens (Figure 1A).

At the same time, we are also amazed when evolution, rather than creating something new, instead reinvents [2]. As a

prime example, Australia is home to many species that are strikingly similar to their counterparts in other parts of the world (for example, Figure 1B–D). It seems that, at least in some cases, entire communities of interacting species have evolved repeatedly and independently on isolated landmasses around the world [3].

But which pattern dominates? Is macroevolution dominated by

divergence, with a world inhabited by species that are exceptionally divergent from one another? Or does convergence rule, so that continents fill with repeated examples of very similar species evolving over and over again? Current research is often focused on particular clades, such as Caribbean anoles, famous for convergence [4]. However, although these studies provide interesting proofs-of-concept for convergence, they do not



Figure 1. Examples of divergent and convergent mammals.

(A) The aye-aye, a spectacularly strange species from Madagascar, alongside three convergently evolved desert rodents: (B) Heermann's kangaroo rat (*Dipodomys heermanni*) from California, USA; (C) hopping mouse (*Notomys* sp.) from Australia; and (D) lesser Egyptian jerboa (*Jaculus jaculus*) from Egypt. Photos by (A) Frank Vassen and (C) Stephen Michael Barnett distributed under a CC-BY 2.0 license, (B) Olivia Kosterlitz distributed under a CC-BY-SA 4.0 license, and (D) Elias Neideck under a CC-BY-SA 3.0 license.

really speak to the overall prevalence of this pattern. Likewise, intensive studies of unusual species are incredibly interesting and valuable [5], but do not inform us about the overall prevalence of dramatic evolutionary divergence. Furthermore, the few attempts to synthesize across broad sections of the tree of life have come to wildly different conclusions [6,7].

There is a lot at stake here beyond just an accurate description of evolutionary patterns. The overall frequency of extreme convergence and divergence speaks to evolutionary predictability [8]. If convergence is common, then the implication is that evolutionary dynamics over long time scales have predictable outcomes. This line of argument has been extended by Conway-Morris [6] to conclude that the evolution of humans was inevitable. On the other hand, if convergence is rare, then evolution might be dominated by chance contingencies, with ultimate outcomes strongly dependent on starting conditions — and

our own existence a fluke amid a myriad of other possible outcomes [7].

In a recent paper in *Current Biology*, Mazel *et al.* [9] used a novel statistical approach on a global mammalian dataset to show that both exceptional convergence and exceptional divergence are more common than we might expect. Although many species of mammals are no more different than one might expect under a simple 'null' model, we can identify many pairs of species that are more similar than we would expect — and, at the same time, many pairs that are more different. Most intriguingly, the authors suggest that at the level of whole assemblages of species, convergence dominates, especially when considering Australia.

To carry out this study, Mazel *et al.* [9] gathered data on nearly 5,000 mammalian species (about 90% of all extant mammalian species). The study focused on the evolution of species' traits, including their body mass, diet, activity

cycle (such as diurnal versus nocturnal), and where they forage in their habitat. The authors also included data on each species' range, which was used in conjunction with climatic data to characterize the conditions where species live.

To understand the evolutionary trajectories of mammalian species, the researchers carried out their statistical analyses using a time-scaled phylogenetic tree, again taken from previous work. This phylogenetic tree provides a framework for understanding the relationships among species, and in particular the time that has passed since any particular pair of species shared a common ancestor. The researchers then used a random-walk model, in which species' traits change randomly from one time interval to the next, to quantify a simple expectation for how much mammalian species should differ from one another. This null expectation predicts how different each pair of

mammalian species ought to be. Following on much previous work, the authors used a Brownian-motion model as their null expectation — although they also explored a few other models without qualitatively changing their results. With this null model, the authors could then identify unexpectedly close or distant pairs of species.

The paper's first main finding was that there are many of pairs of mammalian species that deviate strongly from the null model. This includes both pairs that are exceptionally distinct and pairs that are exceptionally similar. Exceptionally divergent pairs often included closely related pairs of species where one species inhabited an extreme environment. For example, polar bears are quite different from their relatives, even though they diverged from a common ancestor quite recently. Most instances of exceptional divergence, then, reflected a combination of long dispersal and unique adaptations to extreme environments.

At the same time, many pairs of species stood out as exceptionally similar. A large number of mammalian species pairs share more trait similarity than expected given how long they have been evolving since they shared a common ancestor. As the authors point out in their paper, similar pairs can potentially come from two sources: convergence and conservatism. Similarities between a pair of species could represent sets of traits that have evolved repeatedly and independently in each lineage, and thus represent an example of convergent evolution. Alternatively, conservatism results from an overall slowdown in the rate of evolution within a clade. Species in such a slow-evolving clade would then share many similarities with one another, all of which are inherited from their common ancestor. The hallmark of conservatism is that it should result in a large set of similar and closely related species, while convergence should lead to similar species spread widely across the tree.

Mazel *et al.* [9] uncovered both novel and well-known examples of both conservatism and convergence. Bats, for example, have been speculated to be subject to strong constraints due to their specialized flying lifestyle. Indeed, the

authors showed that many pairs of bat species are more similar than one would expect given their null model, sharing similar body mass and foraging traits. By contrast, many similar pairs were spread across the tree, and cannot be explained by conservatism. These pairs include many classic examples of convergent evolution, including among small insectivores and between marsupial and placental mammals.

Mazel *et al.* [9] then scaled up their analysis to whole assemblages. To do this, they calculated an index of trait similarity among assemblage pairs. This index summarizes the ‘trait turnover’ between two sets of species, comparing the proportion of total trait evolution among a set of species that is shared versus unique among the two assemblages. Assemblage pairs that have a low trait turnover index likely include species that are very similar in their trait composition — which, again, could be due to either convergence or conservatism paired with dispersal. They again compared this index to what one would expect under their null model.

Many differences among assemblages are not different from that null model, suggesting that either communities are effectively random at this scale, or the data used here cannot be distinguished from a simple random model. However, Mazel *et al.* [9] find striking patterns in the assemblages that deviate from the null model. First, similar pairs almost always involve one assemblage from Australia, which includes assemblages that are strikingly similar to assemblages from across the globe. This pattern of repeated community convergence is likely related to both Australia's isolation and the tendency for groups there to undergo adaptive radiations, rapidly filling niches that on other continents are occupied by distantly related competitors. Exceptional convergence has also been seen in other non-mammalian clades in Australia (see, for example, [10]). Critically, Mazel *et al.* [9] use their climatic data to show that convergent pairs of species tend to live in areas with a similar climate, supporting the idea that convergence is driven by natural selection and repeated adaptation to particular environments.

By contrast, unusually divergent assemblages are quite rare, and again

typically include close relatives of species that have adapted to extreme environments. For example, arctic assemblages tend to be more divergent than one would expect from assemblages that are made up of close relatives that live in temperate or tropical regions.

Mazel *et al.* [9] focus on relatively simple models for trait evolution, and deal only indirectly with heterogeneity in both rates and patterns of evolution across clades. Because of this, their paper focuses on patterns of convergence and divergence while remaining a bit vague about the particular processes of selection and drift that produce them. Future work might be able to merge their innovative look at convergence with methods that better capture the rich variety of tempos and modes for trait macroevolution across the tree of life [11].

Overall, this analysis takes a nuanced view of long-standing debates about predictability in evolution. One might think of this result as ‘contingent contingency’ — evolution can be highly contingent or highly predictable, with the distinction depending strongly on the interaction between organisms and their environment. So, returning to the old question — is evolution predictable? Perhaps there isn't a simple answer — but we may be moving towards a time when we can predict predictability itself, knowing when (and why) we can predict evolution, and when we cannot.

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Hippocampus: Activity-Driven Maturation of Neural Circuits for Navigation

Francesca Cacucci^{1,*}, Patricia Salinas², and Thomas J. Wills²

¹Department of Neuroscience, Physiology and Pharmacology, University College London, London WC1E 6BT, UK

²Department of Cell and Developmental Biology, University College London, London WC1E 6BT, UK

*Correspondence: f.cacucci@ucl.ac.uk

<http://dx.doi.org/10.1016/j.cub.2017.04.006>

New research reveals that neural activity is required for post-natal maturation of hippocampal neural circuits underlying memory and navigation; this activity-dependent maturation occurs sequentially along the classic ‘tri-synaptic’ pathway, following the direction of information flow found in the adult hippocampus.

During development, billions of neurons are generated making thousands of synaptic connections, which are assembled in complex circuits. Understanding how these circuits form remains a key research frontier in neuroscience. Two main types of mechanism are thought to guide circuit development: some require neural activity, for example the firing of action potentials, while others proceed independently of it. A new study by Donato *et al.* [1] delineates the role of neural activity in the maturation of hippocampal circuits during post-natal development.

The hippocampal formation is known to support spatial memory and navigation in vertebrates. It contains neurons whose activity is modulated by an animal’s position and orientation in space, such as place cells (coding for position), head direction cells (coding for orientation) and grid cells (whose regularly repeating firing may code for distance travelled) [2]. Anatomically, the hippocampus can be subdivided into hippocampus proper — dentate gyrus (DG), the cornu ammonis (CA) fields 1–3, and the subiculum — and the parahippocampal complex, which includes the medial and lateral entorhinal

cortices (mEC and IEC, respectively). Information flow through the adult hippocampal formation is classically portrayed as uni-directional, moving from the periphery through the superficial layers of the EC, to the DG, CA3, CA1 and subiculum, before finally reaching the deep layers of the EC from where information is broadcast to the rest of the cortical mantle (Figure 1A) [3].

Donato *et al.* [1] report that neuronal maturation in the mouse hippocampus occurs in a sequential manner, which (almost) faithfully follows the direction of information flow through this circuit in the adult (Figure 1B). The authors use the levels of the microtubule-associated protein Doublecortin as a marker of immature neurons. Stellate neurons in mEC-L2 are the first to silence Doublecortin expression around postnatal day 14 (P14), followed by L2 pyramidal cells and the CA3 (P20), then CA1 (P23), subiculum, DG, mEC and IEC L5 (all P26). Finally, the IEC L2 matures from P30. Consistent with this sequence of neuronal maturation, the authors also report that the levels of Bassoon, a pre-synaptic marker protein, and Parvalbumin (PV), which labels a subset of GABAergic neurons, increase sequentially along the

transverse hippocampal axis, suggesting that synaptogenesis and the maturation of interneurons also proceed in the same unidirectional pattern. The authors also confirm previous reports of the existence of a dorso-ventral gradient of maturation within the mEC [4], with glutamatergic (stellate and pyramidal cells) and PV+ neurons in the most dorsal part of mEC being the first to mature.

An interesting question that remains to be addressed is whether the morphological maturation of neurons — measured by dendritic branching and spine formation [5] — also follows the same step-wise pattern observed by Donato *et al.* [1]. Surprisingly, the timing of emergence of the spatial tuning of hippocampal neurons, which occurs concurrently with the wave of maturation described by Donato *et al.* [1], in the second-to-third post-natal week, does not follow this entorhinal-to-subiculum maturation pattern. Indeed, parahippocampal and sub-cortical head direction cells emerge first, followed by place cells in CA1, with grid cells in superficial mEC emerging latest of all [6,7]. It would therefore be of great interest to understand how the changes in the levels of Doublecortin, Bassoon and