biology could offer better and safer strategies. There are so many prejudices and fears just because of a lack of knowledge and understanding in this area.

Do you think that there is too much emphasis on 'big data'-gathering collaborations as opposed to hypothesis-driven research by small groups? In my career, I have witnessed several waves when certain approaches (indeed often omics strategies) were fashionable and often applied in projects, whether needed or not. I think that what is most important is the right scientific question, and approaches should be selected based on which of the available methods allows us to address the question in the best possible way.

What do you think is a big problem that science as a whole is facing today? What I see as a big challenge, not the biggest problem, is an avalanche of data that high-throughput approaches enable us to produce but that we do not manage to process properly. I get the impression that we spend less time on thinking, understanding, and interpreting the data than on their production.

If you could ask an omniscient higher being scientific questions, what would they be and why? The recent discussions surrounding artificial intelligence have prompted numerous questions about the nature of intelligence and consciousness. This has led me to contemplate the possibility of alternative life forms. So, my questions would be: is there any other way that life may evolve? What would the principles that govern such 'other' living systems be? We are so used to what we define as a principle of life that we cannot imagine what other forms of life could look like. Learning about alternative life forms could be inspiring and helpful to understand ourselves better.

DECLARATION OF INTERESTS

The author declares no competing interests.

Institute of Science and Technology Austria, Klosterneuburg 3400, Austria.
E-mail: eva.benkova@ist.ac.at

Quick guide

Coral guard crabs

Adrian C. Stier[1,2,*]
and Craig W. Osenberg[3]

What are 'coral guard crabs'? Crabs in the family Trapeziidae (Figure 1) are small crustaceans that have a specialized association with cauliflower corals in the genus *Pocillopora* and some other branching corals in the tropical Pacific Ocean. The over 20 species of Trapeziid crab live within the branches of coral colonies, have a symbiotic relationship with their host corals and are so dependent on their coral host for food and shelter that they cannot survive outside of their host. Many species of these crabs occur primarily as male–female pairs within their coral colony, with the number of pairs often increasing as the size of the coral colony increases. Trapeziid species, while superficially similar, vary in size, color pattern, and claw morphology, presumably reflecting differences in the size and shape of corals they occupy and the services they provide to corals.

What services are these? Trapeziid crabs act as guardians of, and housekeepers for, corals, thus increasing the growth and survival of their host. For example, the crown-of-thorns sea star (*Acanthaster planci*) and the pincushion star (*Culcita novaeguineae*) are voracious corallivores that can devastate coral reefs. Trapeziid crabs will attack these predators, which are much larger, and protect the coral from being eaten. The crabs also defend the coral against snails that graze on coral tissue, such as *Drupella cornus* and *Coralliophila violacea*. However, predators are not the only threat to corals — they can also be harmed by the deposition of sediments on the coral surface. Fortunately, the crabs also are good housekeepers, removing sediment from the coral, and further increasing coral growth and survival. By actively defending and cleaning their coral hosts, Trapeziid crabs play a crucial role in maintaining the health and survival of the coral colonies they inhabit and thus the persistence of coral reefs.

Why do Trapeziid crabs protect their coral? The fate of Trapeziid and their coral hosts is entwined, as is true in other symbiotic relationships that are mutually beneficial to both participants. The crabs cannot live outside of their host coral. In fact, most Trapeziids are restricted to living in a single species (or genus) of coral. The coral colonies provide the crabs with shelter and a constant food supply — coral tissue, mucus and lipid bodies, which the crabs obtain by agitating and scraping the coral with their claws. In exchange, the crabs provide the coral with crucial protection from predators and sedimentation that could kill the entire colony. If the coral dies, the crabs either die or must find a new host, which can involve risk of predation even if a new host is available and not occupied by other crabs. Thus, by protecting their coral host, Trapeziid crabs create a stable environment that helps ensure their own survival and successful reproduction. The evolution of this mutualism has not only facilitated the diversification of the crabs, but it also functions secondarily to facilitate the vast diversity of organisms that depend on the complex coral reef ecosystem.

But how effectively can a small crab protect a coral? Even though predatory sea stars are many times larger than the crabs, the crabs can effectively protect their host coral from these predators, much as tiny ants protect *Acacia* trees from elephants and other large herbivores. The crabs use their powerful claws to shove the sea star and pinch their tube feet. These behaviors deter or reduce the feeding activities of the sea stars, which could otherwise eat an entire colony in a single night. Similarly, the removal of sediment is not merely for appearances, but is critical to the survival of the coral; when researchers remove crabs from corals in coastal regions with high sedimentation rates, corals die, but when crabs are present the corals survive. While the effectiveness of Trapeziid defense can vary depending on factors, such as crab species and size, predator abundance and sedimentation rates, their role as defenders contributes significantly to the resilience and survival of their coral hosts and thus the diversity of coral reef ecosystems.

Does hosting Trapeziids cost the coral? In some mutualisms (e.g., ants

Figure 1. Trapeziid coral crabs within cauliflower corals.
In each picture crabs (*Trapezia* sp.) are perched embedded between the coral branches, grasping onto the coral with their claws (photos: Thomas Vignaud).

and acacias; or pollinators and plants), one partner pays a small price in return for the greater rewards it receives. Trapeziid crabs, as mutualists of coral, generally impose a relatively low cost on their host colonies. Although they consume small amounts of coral tissue (which can reduce coral growth in the absence of predators and sediments), their feeding behavior primarily targets damaged or dying tissue rather than healthy portions. Some studies suggest that their feeding activities may even benefit the coral by removing potential sites for infection or disease. While Trapeziid crabs occupy space within the coral branches, their presence does not appear to greatly impede the growth or reproduction of the coral. The benefits provided by the crabs typically greatly outweigh any potential harm caused by their feeding or space occupation.

Are all Trapeziids good defenders? No. While Trapeziid crabs, as a group, are known for their defensive behaviors and their role in protecting their coral hosts, the effectiveness of individual crabs can vary. Variation in size, claw morphology and genotype can affect their defensive capabilities. Larger and stronger crabs may have more formidable claws and may be better equipped to deter predators. Additionally, there can be geographic and individual variation within a species — crabs in different regions or individuals within a population may exhibit different levels of defense. The relative magnitude of costs and benefits can also vary depending on factors such as predator prevalence, coral species, and overall ecological context.

Do Trapeziids have effects beyond their coral? Yes. By defending their coral hosts against corallivores, Trapeziid crabs indirectly support the survival and growth of coral colonies. Healthy coral populations provide essential habitat and food sources for numerous other reef organisms, including fish, invertebrates and other invertebrate symbionts. Furthermore, the presence of Trapeziid crabs can influence the distribution and behavior of other organisms within the reef ecosystem. By protecting their host coral, the Trapeziids can create “halos” of protection around the coral colonies, creating zones of reduced predation pressure. As a result, other nearby corals that don’t harbor crab symbionts may also be protected from predators, facilitating the survival of small fishes and other invertebrates that rely on the coral and thus benefit from the services provided by the crabs.

Is climate change affecting Trapeziid crabs? As you can see, Trapeziid crabs are intimately linked to the success of corals. But corals are vulnerable to may stressors in addition to predators and sediments. Indeed, global climate change imposes profound risks to corals, which are highly vulnerable to ocean warming and acidification. Rising sea temperatures can lead to coral bleaching events and coral death; acidification can reduce coral growth and also lead to their death. These stressors might also affect Trapeziid crabs, even if their host coral isn't killed. In experiments simulating future climate change, increased water temperature caused reductions in crab abundance and egg production, and caused crabs to expel their mates and other crustaceans that also help defend corals. The resulting decline in Trapeziid densities and defense of corals might further accelerate the demise of coral reefs, underscoring the urgent need for conservation efforts to protect corals and their inhabitants by dramatically reducing global carbon emissions.

Where can I find out more?

Doo, S.S., Carpenter, R.C., and Edmunds, P.J. (2018). Obligate ectosymbionts increase the physiological resilience of a scleractinian coral to high temperature and elevated pCO2. Coral Reefs *37*, 997–1001. https://doi.org/10.1007/s00338-018-1731-1739.

Glynn, P.W. (1980). Defense by symbiotic crustacea of host corals elicited by chemical cues from predator. Oecologia *47*, 287–290. https://doi.org/10.1007/BF00398518.

Lai, J.C.Y., Ahyong, S.T., Jeng, M.-S., and Ng, P.K.L. (2009). Are coral-dwelling crabs monophyletic? A phylogeny of the Trapezioidea (Crustacea: Decapoda: Brachyura). Invert. Systematics *23*, 402. https://doi.org/10.1071/IS09012.

McKeon, C.S., and Moore, J.M. (2014). Species and size diversity in protective services offered by coral guard-crabs. PeerJ *2*, e574. https://doi.org/10.7717/peerj.574.

Pratchett, M.S. (2001). Influence of coral symbionts on feeding preferences of crown-of-thorns starfish *Acanthaster planci* in the western Pacific. Mar. Ecol. Prog. Ser. *214*, 111–119.

Shmuel, Y., Ziv, Y., and Rinkevich, B. (2022). Coral-inhabiting Trapezia crabs forage on demersal plankton. Front. Mar. Sci. *9*, 964725.

Stella, J.S., Munday, P.L., and Jones, G.P. (2011). Effects of coral bleaching on the obligate coral-dwelling crab *Trapeziid cymodoce*. Coral Reefs *30*, 719–727. https://doi.org/10.1007/s00338-011-0748-0.

Stier, A.C., McKeon, C.S., Osenberg, C.W., and Shima, J.S. (2010). Guard crabs alleviate deleterious effects of vermetid snails on a branching coral. Coral Reefs *29*, 1019–1022. https://doi.org/10.1007/s00338-010-0663-9.

Vannini, M. (1985). A shimp that speaks crab-ese. J. Crust. Biol. *5*, 160–167. https://doi.org/10.1163/1937240X85X00137.

DECLARATION OF INTERESTS

The authors declare no competing interests.

[1]Department of Ecology, Evolution, and Marine Biology, University of California Santa Barbara, Santa Barbara, CA 93106, USA. [2]Marine Science Institute, University of California Santa Barbara, Santa Barbara, CA 93106, USA. [3]Odum School of Ecology, University of Georgia, 140 E. Green Street, Athens, GA 30602, USA.
*E-mail: astier@ucsb.edu

Primer

The cerebellum

Megan R. Carey

The cerebellum, that stripey 'little brain', sits at the back of your head, under your visual cortex, and contains more than half of the neurons in your entire nervous system. The cerebellum is highly conserved across vertebrates, and its evolutionary expansion has tended to proceed in concert with expansion of cerebral cortex. The crystalline neuronal architecture of the cerebellar cortex was first described by Cajal a century ago, and its functional connectivity was elucidated in exquisite anatomical and physiological detail by the mid-20th century. The ability to clearly identify molecularly distinct cerebellar cell types that constitute discrete circuit elements is perhaps unparalleled among brain areas, even within the context of modern circuit neuroscience. Although traditionally thought of as primarily a motor structure, the cerebellum is highly interconnected with diverse brain areas and, as I will explain in this Primer, is well-poised to influence a wide range of motor and cognitive functions.

What does the cerebellum do? Part I: Movement

Some of the earliest descriptions of the effects of cerebellar damage were of World War 1 veterans who displayed visible deficits in coordinating movements across the body. Cerebellar dysfunction leads to a characteristic ataxia, or uncoordinated movement, across vertebrate species. Additionally, oculomotor disturbances, slurred speech, intention tremor, and balance difficulties can all reflect cerebellar dysfunction. Cerebellar neurons are particularly susceptible to the effects of ethanol, leading to the familiar phenomenon of alcohol-induced cerebellar dysfunction that presents as drunken incoordination.

In addition to its clear role in the coordination of movement, a crucial role for the cerebellum in learning has been revealed by many experiments in humans and animal models. This includes basic forms of associative learning like classical conditioning, as well as a form of motor learning known as motor adaptation. Motor adaptation is typically studied as a gradual shift in motor output in response to a consistently applied external perturbation (Figure 1). Motor adaptation occurs rapidly and can be thought of as a re-calibration of well-established movement commands. Movements that are consistently associated with an error are tuned or calibrated to alter the motor output, thereby avoiding future errors. This cerebellar calibration signal is largely unconscious, or 'implicit', and remarkably, it persists even when explicit strategies, like aiming or other forms of cognitive control, attempt to override it.

Motor learning experiments reveal the robust plasticity of motor systems, in that behaviors we perform hundreds or thousands of times a day can be substantially altered within just minutes of exposure to a consistent perturbation. However — of course! — the cerebellum did not evolve just so that we would be prepared when an experimenter handed us a pair of prism goggles. Rather, motor adaptation reveals one of the brain's most powerful solutions to the problem of rapid, effective control in the face of delayed feedback. To avoid having to wait for sensory feedback that an error has occurred, the cerebellum learns to predict likely errors, and uses those predictions to pre-emptively generate compensatory adjustments. The end result is that our movements are effortlessly accurate, in a wide variety of contexts, most of the time.

The cerebellum works together with many other brain areas to control movement; not all forms of motor control or learning are cerebellum-dependent. Instead, the cerebellum seems to be particularly important for forms of motor learning — and aspects of motor control — that require temporally-precise predictions. How could such predictive mechanisms be embedded within cerebellar circuits?

The cerebellar circuit

The cerebellum consists of an intricately foliated cortical sheet surrounding output nuclei, often aptly termed the 'deep' cerebellar nuclei.