

desertic conditions devoid of any suitable food sources. These observations imply that internal state factors, potentially neuromodulators, may regulate VES041 activity and influence the switch between search strategies (Figure 2D). The identification of the saccade-generating couplet circuit presents a unique opportunity to unravel the mechanistic basis and adaptive control of casting, a highly conserved behavior across diverse species. As Jacques Monod famously stated in 1972, “what is true for *E. coli* is true for the elephant”. Nearly 50 years later, sophisticated studies of the tiny fruit fly brain are opening doors to a more global understanding of sensorimotor control. After all, insights gained from *Drosophila* are likely to hold true for other insects and even offer valuable clues for our sometimes-zigzagging pursuit of the mechanistic bases of animal behavior.

DECLARATION OF INTERESTS

The author declares no competing interests.

REFERENCES

- Schone, H. (2014). *Spatial Orientation: The Spatial Control of Behavior in Animals and Man* (Princeton, NJ: Princeton University Press).
- Draft, R.W., McGill, M.R., Kapoor, V., and Murthy, V.N. (2018). Carpenter ants use diverse antennae sampling strategies to track odor trails. *J. Exp. Biol.* 227, jeb185124. <https://doi.org/10.1242/jeb.185124>.
- Ros, I.G., Omoto, J.J., and Dickinson, M.H. (2024). Descending control and regulation of spontaneous flight turns in *Drosophila*. *Curr. Biol.* 34, 531–540.
- Baker, T. (1990). Upwind flight and casting flight: complementary phasic and tonic systems used for location of sex pheromone sources by male moth. In *Proceedings of the Tenth International Symposium on Olfaction and Taste*, K.B. Doving, ed. (Oslo: Graphic Communication System), pp. 18–25.
- Kennedy, J.S., and Marsh, D. (1974). Pheromone-regulated anemotaxis in flying moths. *Science* 184, 999–1001. <https://doi.org/10.1126/science.184.4140.999>.
- Namiki, S., and Kanzaki, R. (2016). The neurobiological basis of orientation in insects: insights from the silkworm mating dance. *Curr. Opin. Insect Sci.* 15, 16–26. <https://doi.org/10.1016/j.cois.2016.02.009>.
- Khan, A.G., Sarangi, M., and Bhalla, U.S. (2012). Rats track odour trails accurately using a multi-layered strategy with near-optimal sampling. *Nat. Commun.* 3, 703. <https://doi.org/10.1038/ncomms1712>.
- Reddy, G., Murthy, V.N., and Vergassola, M. (2022). Olfactory sensing and navigation in turbulent environments. *Annu. Rev. Condens. Matter Phys.* 13, 191–213. <https://doi.org/10.1146/annurev-conmatphys-031720-032754>.
- Olberg, R.M. (1983). Pheromone-triggered flip-flopping interneurons in the ventral nerve cord of the silkworm moth, *Bombyx mori*. *J. Comp. Physiol.* 152, 297–307. <https://doi.org/10.1007/bf00606236>.
- Braitenberg, V. (1982). *Vehicles: Experiments in Synthetic Psychology* (Cambridge, MA: MIT Press).
- Steinbeck, F., Adden, A., and Graham, P. (2020). Connecting brain to behaviour: a role for general purpose steering circuits in insect orientation? *J. Exp. Biol.* 223, jeb212332. <https://doi.org/10.1242/jeb.212332>.
- Álvarez-Salvado, E., Licata, A.M., Connor, E.G., McHugh, M.K., King, B.M., Stavropoulos, N., Victor, J.D., Crimaldi, J.P., and Nagel, K.I. (2018). Elementary sensory-motor transformations underlying olfactory navigation in walking fruit-flies. *eLife* 7, e37815. <https://doi.org/10.7554/elife.37815>.
- van Breugel, F., and Dickinson, M.H. (2014). Plume-tracking behavior of flying *Drosophila* emerges from a set of distinct sensory-motor reflexes. *Curr. Biol.* 24, 274–286. <https://doi.org/10.1016/j.cub.2013.12.023>.
- Vogels, T.P., and Abbott, L.F. (2005). Signal propagation and logic gating in networks of integrate-and-fire neurons. *J. Neurosci.* 25, 10786–10795. <https://doi.org/10.1523/jneurosci.3508-05.2005>.
- Gardner, T.S., Cantor, C.R., and Collins, J.J. (2000). Construction of a genetic toggle switch in *Escherichia coli*. *Nature* 403, 339–342. <https://doi.org/10.1038/35002131>.
- Reddy, G., Shraiman, B.I., and Vergassola, M. (2022). Sector search strategies for odor trail tracking. *Proc. Natl. Acad. Sci. USA* 119, e2107431118. <https://doi.org/10.1073/pnas.2107431118>.
- Rayshubskiy, A., Holtz, S.L., D'Alessandro, I., Li, A.A., Vanderbeck, Q.X., Haber, I.S., Gibb, P.W., and Wilson, R.I. (2020). Neural control of steering in walking *Drosophila*. Preprint at bioRxiv, <https://doi.org/10.1101/2020.04.04.024703>.
- Flavell, S.W., Pokala, N., Macosko, E.Z., Albrecht, D.R., Larsch, J., and Bargmann, C.I. (2013). Serotonin and the neuropeptide PDF initiate and extend opposing behavioral states in *C. elegans*. *Cell* 154, 1023–1035. <https://doi.org/10.1016/j.cell.2013.08.001>.
- Götz, K.G. (1987). Course-control, metabolism and wing interference during ultralong tethered flight in *Drosophila melanogaster*. *J. Exp. Biol.* 128, 35–46. <https://doi.org/10.1242/jeb.128.1.35>.
- Leitch, K.J., Ponce, F.V., Dickson, W.B., van Breugel, F., and Dickinson, M.H. (2021). The long-distance flight behavior of *Drosophila* supports an agent-based model for wind-assisted dispersal in insects. *Proc. Natl. Acad. Sci. USA* 118, e2013342118. <https://doi.org/10.1073/pnas.2013342118>.

Animal locomotion: Wing-like femoral lobes help orchid mantid nymphs glide

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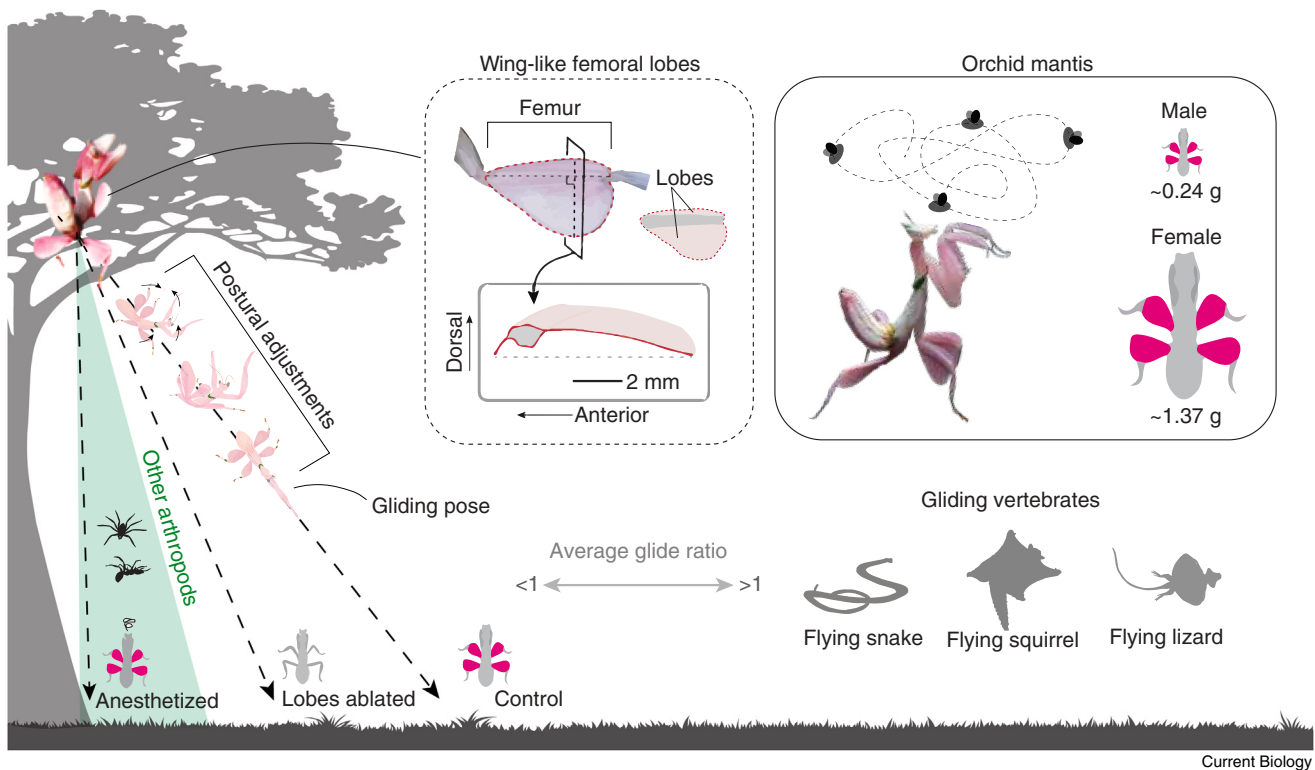
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The femoral lobes of the orchid mantis give this fierce predator a flower-like appearance, but they also assist in gliding, showing that form can match function in more ways than one.

One of the central objectives of organismal biology revolves around the form–function question: how does a morphological structure relate to its function? Part of the appeal of this question is that often the obvious may not

be what it seems. For centuries, the orchid mantis *Hymenopus coronatus* has been a safe example of the obvious: looking like a flower, this mantis preys upon pollinating insects. Alfred Russell Wallace used the term “protective



Current Biology

Figure 1. Gliding in orchid mantids is augmented by femoral lobes.

Chen, Zhao and colleagues report that wing-like femoral lobes (left inset) in orchid mantids assist in gliding⁵. The right inset shows an orchid mantis and the sexual dimorphism between males and females, with females attaining much larger adult sizes. Chen, Zhao and colleagues tested gliding capabilities in orchid mantids with femoral lobes present, with lobes ablated, and with anesthetized mantids. Orchid mantids with lobes ablated attained glide ratios higher than other gliding arthropods, but these values are lower than those observed in vertebrate gliders. Anesthetized specimens dropped nearly vertically, showing the importance of active postural adjustments for gliding. (Gliding vertebrates, spider and ant illustrations: Dr. Mary K. Salcedo; tree and grass photo: Larisa/Adobe Stock.)

resemblance” to describe its alleged predatory pollinator mimicry¹, which became a case example in textbooks and in popular works such as Richard Dawkins’ book about evolution, “*The Greatest Show on Earth*” (plate 7)². But case examples can be just-so stories.

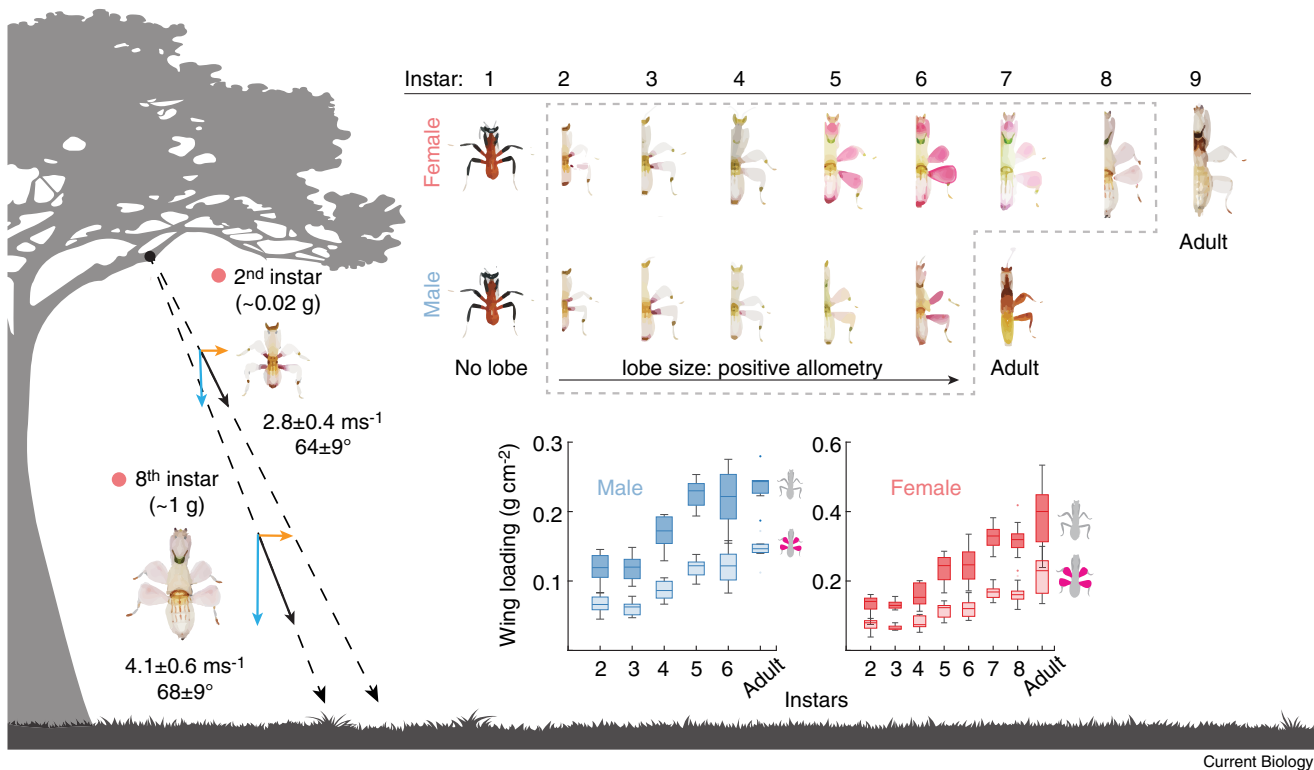
The flower-like resemblance of this beautiful yet rarely seen predator from southern China and Southeast Asia arises from a combination of attributes. Its color ranges from white to yellow and pink and purple³; its patterning includes stripes on the abdomen, a feature thought to appeal to pollinators⁴; its posture can include the abdomen angled upward; and, it possesses four somewhat round lobes, one each on the femora of the middle and hind legs. These femoral lobes are not present in the smallest, 1st-instar mantids, but emerge in the 2nd instar and persist through adulthood⁵. As an alleged flower mimic, these lobes suggest the

appearance of an orchid’s petals, but a new study in a recent issue of *Current Biology*⁵ by Zhanqi Chen, Xin Zhao and colleagues provides new insight into their function.

Up until recent years, the idea of the orchid mantis as a flower mimic aided by femoral lobes was widely accepted but untested. In a series of experimental studies, James O’Hanlon and colleagues examined the behavioral ecology of the mantid’s color and morphology^{4,6–9}. Their findings were mixed. Orchid mantids lure pollinators and exhibit colors similar to 13 sympatric flowers that are visited by hymenopteran pollinators⁶, and also absorb UV light^{4,7} compared to leaves or bark in their habitat, suggesting that the orchid mantis could be conspicuous and appear as an average flower type to pollinators. A manipulation using physical models of orchid mantids revealed a more surprising

result — models with no femoral lobes or lobes that had been arranged asymmetrically proved no less attractive to pollinators than the full, intact model. However, pollinators were put off by color: brown models were visited less often than white or UV-reflecting models⁷. A different study by Takafumi Mizuno and colleagues showed that juvenile mantids emitted pheromone-like acids in the air that attracted honeybees, demonstrating that they could be employing chemical mimicry as well¹⁰. Taken together, the mantis appears to use a form of generalized food deception rather than the stricter form of model mimicry that their orchid moniker implies⁷. Coloration and chemical cues, but not the lobes, seem to matter.

What then could be the function of the prominent femoral lobes? The curiosity of Zhanqi Chen inadvertently led to new work to address this question. In 2020, Chen was playing with a juvenile orchid



Current Biology

Figure 2. Positive allometric change in femoral lobe size leads to similar gliding capabilities across instar stages.

The top panel shows positive allometry in lobe size from instar 2 until the adult stage in both males and females. The bottom panel shows that positive allometry in lobe size reduces wing loading compared with instars without lobes, leading to similar gliding capabilities of the second and eighth female instars⁵ (left illustration). (Orchid mantis photo: kuritafsheen/Adobe Stock; tree and grass photo: Larisa/Adobe Stock.)

mantis in his office in the Xishuangbanna Tropical Botanical Garden, home to native orchid mantids, and his lab houses a unique colony of these colorful insects. Chen placed the nymph up on a bookshelf and it jumped onto him, appearing to glide. Chen found the behavior unexpected: although multiple non-winged insects have been identified as gliders^{11–13}, they represent only a small fraction of the immense diversity of Insecta. He suspected that the rigid femoral lobes might assist in locomotion. So he took two specimens to a higher 8.2 m location and released them, and watched them glide to the ground, astonished. Inspired by this intriguing trial, Chen, Zhao and colleagues designed an experimental study that would later reveal a new locomotor role of the femoral lobes — gliding⁵.

Gliding is an aerial behavior in which potential energy of position is traded for kinetic energy of movement, whereby aerodynamic forces are created that

move the glider farther horizontally than would be achieved by ballistic movement alone^{14,15}. Chen, Zhao and colleagues conducted multiple experiments that demonstrated key features of gliding in orchid mantids (Figure 1). In one experiment, they dropped intact 6th-instar nymphs from a 10-meter height in an open field with no perceivable wind. The nymphs glided, reaching an average horizontal distance of ~6 m from the original drop point⁵. The authors then ablated the femoral lobes and repeated the drop trials. Without the lobes, the nymphs only reached ~4 m, a ~33% reduction in glide performance, demonstrating that the lobes must have been producing a positive aerodynamic contribution to the glide. Interestingly, the lobe-ablated orchid mantids still glided well compared to other arthropods: their mean glide angle (the path angle relative to horizontal) was ~67°, shallower than that of gliding ants at ~75° (Figure 1). This result shows that the mantid's body

and legs contribute towards gliding performance, perhaps through their morphology and body posture adjustments. With lobes intact, the 6th-instar mantids glided with an arthropod-record mean angle of ~52°.

In a second experiment, the authors recorded drops from 8th-instar females (Figure 2), which possess the largest femoral lobes of any developmental stage. In this experiment, they compared 10-meter drops of intact nymphs with drops of anaesthetized ones. The anaesthetized nymphs did not glide at all, falling almost straight down (Figure 1). This manipulation showed that the nymphs use active control of their posture to effectuate aerial locomotion. From video recordings, the intact nymphs could be seen changing their posture in stereotyped fashion, first elevating the legs and abdomen, and then depressing the abdomen and reconfiguring their legs so that the front pair were pointing forward and the mid and rear pairs were pointing laterally. The importance of

posture for control is not surprising given that other arthropods also exhibit characteristic body or leg postures when they glide¹⁶. The orchid mantids might also be using postural control to steer, which the authors observed in a third experiment to test the insect's preference of moving toward a large black sheet as a visual target⁵. However, questions about the mechanisms of maneuverability and control remain open. Precise three-dimensional tracking of trajectories, close-in high-speed imaging, and aerodynamic modeling would help address the issue. Orchid mantids might also be amenable for study in vertical wind tunnels, as has been done for gliding ants¹⁶ and salamanders¹⁷.

The authors also examined morphological changes that occur through development and how they influence glide performance, which had not been previously examined for any gliding species. They found that both the mass and projected area of the mantids increased with geometric isometry⁵ (maintaining the same shape as size changes) (Figure 2). But the isometry of projected area was driven strongly by a positive allometric change in area of the femoral lobes, meaning that larger nymphs had relatively greater lobes. The lobes also changed from more elongated to more rounded throughout ontogeny (Figure 2). A third set of drop trials examined the sum effect of these morphological changes. Glide distance and glide angle stayed relatively constant, meaning that small and large nymphs performed similarly despite massive changes in body size. By contrast, glide speed increased with size, a known consequence of increasing wing loading (the ratio of body weight to 'wing' area). Interestingly, the femoral lobe exhibits a common wing-like feature: it is curved in cross-sectional shape (camber), with its camber aided by the thick femur at the leading edge (Figure 1). Camber is well-known to help augment aerodynamic force production, including in some gliding animals¹⁸, adding to the evidence that the lobes serve a locomotor function.

That the orchid mantis glides and its femoral lobes augment gliding performance do not preclude other roles for the flower-like morphological features. It is possible that selective

pressures on increasing lobe size have resulted in the dual benefit of a greater flower-like signal and improved glide performance. But with increasing size, at some point large lobes must become a detriment. Future modeling would be useful to reveal if the mantid's lobe size and shape are an optimal compromise. It is also possible that the lobes help the orchid mantis to employ an anti-predator strategy⁸. Mantids are not toxic, but predators like birds don't eat flowers, a plausible rationale for the orchid mantis's flowery features. However, little is known about the ecology of this species³. To test these competing or complementary hypotheses, data are needed to determine its behavior in the wild, which would also reveal if and how gliding is used in the animal's life history.

The discovery of gliding in the orchid mantis is another elegant example of the inverse Krogh principle¹⁹: not all biological questions demand a model organism. Asking specific questions about specific species can lend new insight into how biology works. This study is also a historical stepchild of the pioneering approach of Steve Yanoviak, Robert Dudley and colleagues in their studies of wingless arboreal arthropods^{11,12,16}: take the critter to a height, drop it, and see what it does. Falling from a height can lead to negative consequences even if body weight is light enough to not cause harm, and many species exhibit surprisingly non-intuitive ways of directing their aerial descent²⁰. Such gliding should be viewed as less and less surprising.

DECLARATION OF INTERESTS

The authors declare no competing interests.

REFERENCES

- Wallace, A.R. (1877). The colors of animals and plants. *Am. Nat.* 11, 641–662. <https://doi.org/10.1086/271979>.
- Dawkins, R. (2009). *The Greatest Show on Earth: The Evidence for Evolution* (New York, NY: Simon and Schuster).
- Zhao, X., Liu, J.-X., and Chen, Z. (2023). The orchid mantis exhibits high ontogenetic colouration variety and intersexual life history differences. *Evol. Ecol.* 37, 569–582. <https://doi.org/10.1007/s10682-023-10230-y>.

- O'Hanlon, J.C., Li, D., and Norma-Rashid, Y. (2013). Coloration and morphology of the orchid mantis *Hymenopus coronatus* (Mantodea: Hymenopodidae). *J. Orthoptera Res.* 22, 35–44.
- Zhao, X., Liu, J.-X., Charles-Dominique, T., Campos-Arceiz, A., Dong, B., Yan, L., O'Hanlon, J.C., Zeng, Y., and Chen, Z. (2024). Petal-shaped femoral lobes facilitate gliding in orchid mantises. *Curr. Biol.* 34, 183–189.e4. <https://doi.org/10.1016/j.cub.2023.11.003>.
- O'Hanlon, J.C., Holwell, G.I., and Herberstein, M.E. (2014). Pollinator deception in the orchid mantis. *Am. Nat.* 183, 126–132. <https://doi.org/10.1086/673858>.
- O'Hanlon, J.C. (2014). The roles of colour and shape in pollinator deception in the orchid mantis. *Ethology* 120, 652–661. <https://doi.org/10.1111/eth.12238>.
- O'Hanlon, J.C., Holwell, G.I., and Herberstein, M.E. (2014). Predatory pollinator deception: Does the orchid mantis resemble a model species? *Curr. Zool.* 60, 90–103. <https://doi.org/10.1093/czoolo/60.1.90>.
- O'Hanlon, J.C., Rathnayake, D.N., Barry, K.L., and Umbers, K.D.L. (2018). Post-attack defensive displays in three praying mantis species. *Behav. Ecol. Sociobiol.* 72, 176. <https://doi.org/10.1007/s00265-018-2591-610>.
- Mizuno, T., Yamaguchi, S., Yamamoto, I., Yamaoka, R., and Akino, T. (2014). "Double-Trick" visual and chemical mimicry by the juvenile orchid mantis *Hymenopus coronatus* used in predation of the oriental honeybee *Apis cerana*. *Zool. Sci.* 31, 795–801.
- Yanoviak, S.P., Dudley, R., and Kaspari, M. (2005). Directed aerial descent in canopy ants. *Nature* 433, 624–626.
- Yanoviak, S.P., Munk, Y., and Dudley, R. (2015). Arachnid aloft: directed aerial descent in neotropical canopy spiders. *J. R. Soc. Interface* 12, 20150534.
- Zeng, Y., Lin, Y., Abundo, A., and Dudley, R. (2015). Visual ecology of directed aerial descent in first-instar nymphs of the stick insect *Extatosoma tiaratum*. *J. Exp. Biol.* 218, 2305–2314.
- Socha, J.J., Jafari, F., Munk, Y., and Byrnes, G. (2015). How animals glide: from trajectory to morphology. *Can. J. Zool.* 93, 901–924. <https://doi.org/10.1139/cjz-2014-0013>.
- Dudley, R., Byrnes, G., Yanoviak, S.P., Borrell, B., Brown, R.M., and McGuire, J.A. (2007). Gliding and the functional origins of flight: biomechanical novelty or necessity? *Annu. Rev. Ecol. Syst.* 38, 179–201. <https://doi.org/10.1146/annurev.ecolsys.37.091305.110014>.
- Yanoviak, S.P., Munk, Y., and Dudley, R. (2011). Evolution and ecology of directed aerial descent in arboreal ants. *Integr. Comp. Biol.* 51, 944–956. <https://doi.org/10.1093/icb/icr006>.

17. Brown, C.E., Sathe, E.A., Dudley, R., and Deban, S.M. (2022). Gliding and parachuting by arboreal salamanders. *Curr. Biol.* 32, R453–R454.
18. Khandelwal, P.C., and Hedrick, T.L. (2022). Combined effects of body posture and three-dimensional wing shape enable efficient gliding in flying lizards. *Sci. Rep.* 12, 1793.
19. Clark, C.J., Hutchinson, J.R., and Garland, T., Jr. (2023). The inverse Krogh principle: all organisms are worthy of study. *Physiol. Biochem. Zool.* 96, 1–16.
20. Khandelwal, P.C., Ross, S.D., Dong, H., and Socha, J.J. (2023). Convergence in gliding animals: Morphology, behavior, and mechanics. In *Convergent Evolution: Animal Form and Function*, V.L. Bels, and A.P. Russell, eds. (New York, NY: Springer), pp. 391–429.

Motor control: Snake neurons speed up

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How are motor neurons tuned for very different jobs? Classic work has focused on variations in motor neuron size and their premotor networks. New results in rattlesnakes show that shifting a motor neuron's temporal precision can be as simple as changing its potassium channel conductance.

Animals move around the environment by rhythmic contraction of their muscles at a variety of speeds. For example, hummingbirds can flap their wings at fast frequencies (40–60 Hz)¹, whereas seagull wings flap more slowly (~3 Hz)². Despite this variation, the basic building blocks that control spinal cord movement are highly conserved, consisting of muscle-innervating motor neurons along with spinal interneurons³. Although these classes of neurons are conserved across vertebrates, it remains unclear how neurons and networks are adapted to operate at such different speeds. Prior work has focused either on the overall size and conductance of neurons, or on differential network connectivity^{4,5}. In a recent issue of *Current Biology*, Bothe and colleagues provide compelling evidence that a specific potassium channel conductance distinguishes motor neurons for slower and faster movements⁶.

This work used a novel model system, the western diamondback rattlesnake, to examine motor neurons with distinctly different jobs — and rhythmic activity — within a single animal. The snake's undulatory locomotor movements are relatively slow (1–2 Hz)⁷, whereas the tail rattles at much higher frequencies (90–100 Hz)⁸. Therefore, the motor neurons for locomotion and for tail rattling must be rhythmically active at different

frequencies, despite the fact that they are both controlling tail movements. The authors leveraged this intra-animal range of activity to investigate key differences between the motor neurons responsible for these movements.

The authors began by assessing the muscle contraction patterns of both the locomotor and rattle muscles in the snake. *In vivo* electromyography recordings showed that rattle muscles have faster contractions than locomotor muscles, requiring rapid motor neuron activation and membrane potential oscillations. The next step involved analyzing the differences between the electrical properties of locomotor and rattle neurons. Using whole-cell patch clamp electrophysiology, the authors found that rattle motor neurons exhibited properties common to neurons that innervate fast muscle, such as low input resistance and high rheobase values, compared to the values in locomotor neurons. These properties indicate that rattle motor neurons require more input to reach threshold to fire than locomotor neurons. These results might predict that rattle motor neurons are much larger than locomotor neurons, based on the longstanding size principle that fast muscle is driven by larger motor neurons that require more input to fire^{9,10}. However, anatomical experiments did not show any differences in soma size⁶,

suggesting that differences in firing properties must be accounted for by other changes.

To identify these changes, Bothe and colleagues examined the response of both types of motor neurons to depolarizing input and found that rattle motor neurons fired just a few action potentials, with short latency and low variability. In contrast, locomotor neurons could fire many action potentials but took longer to start firing and had more variable timing. These observations led the authors to hypothesize that potassium channels, which govern the timing and precision of neural spiking¹¹, could explain the differences between the two types of motor neurons. After ruling out the Kv1 class of channels, they focused on testing Kv7_{2/3} channels given their role in modulating motor neuron activity in animals^{12–14}. Through pharmacological blockade of Kv7_{2/3} channels, Bothe and colleagues could convert the short-latency, precisely-timed spiking of rattle motor neurons into long-latency, variably-timed spiking, similar to the activity of locomotor neurons (Figure 1). Going in the opposite direction, application of retigabine, an agonist of Kv7_{2/3} channel activity, converted locomotor neuron properties to resemble those of rattle motor neurons (Figure 1). Together, these experiments demonstrate that Kv7_{2/3} channels are necessary and sufficient to