

frequency-dependent phenomenon. To explain within-sex colour polymorphism in hummingbirds, Falk and colleagues borrow an intriguing idea – long suspected, but currently languishing in the mimicry literature – that species mimic each other to gain access to resources. The authors reframe this hypothesis as an example of within-species variation. This long-standing idea is that a convergence in form between different species is used to gain access to resources through competitive mimicry, such that smaller and less-competitive species mimic the appearance of larger, more-dominant species⁹. For example, a smaller species of woodpecker or toucan resembles the appearance of another larger woodpecker or toucan living in the same area to get priority access to food sources. This constitutes a different sort of dishonest mimicry signalling from the textbook examples of a palatable prey resembling an unpalatable organism (Batesian mimicry) or two unpalatable prey types resembling each other (Müllerian mimicry).

Falk and colleagues' research focused on *Florisuga mellivora* (Fig. 1), a hummingbird in which all males and around 20% of females sport an iridescent blue head and a white neck and tail (called androchromic), whereas 80% of females are non-ornamented (termed heterochromic) with green plumage, a speckled throat and dark tail. Androchromes (of unknown sex) initiate more chases than their peers such that members of the same species and other hummingbird species avoid them¹⁰. This might give androchrome females better access to food compared with heterochromic females.

Although this suggests that some females are mimicking males, another explanation is possible. It could be that androchrome males and females are simply more aggressive and territorial and that they signal this through gaudy plumage, whereas heterochrome females are not territorial. Such examples of aggression are seen in lizards and fish. However, after taking a variety of measurements (morphometric and standardized colour data) for adult hummingbirds at a field site in Panama, Falk *et al.* found that birds' power bursts (weights lifted in flights under controlled conditions), wing load (mass in flight by wing area), wing shape and body size did not differ between androchrome and heterochrome females. By contrast, males had greater physical strength and agility (greater burst power, lower wing loads and larger wing lengths, widths, area and tapering) than was the case for both types of female.

Falk *et al.* also assessed feeding strategies by putting out a grid of sugar feeders, and followed the movements of individual birds using a tracking method (PIT tags and a radio-frequency identification system). Both types of female bird increased their use of space (number of feeders visited) as their feeding frequency rose, whereas males reduced their feeder-space use

as their feeding frequency increased, implicating territoriality. In conjunction with a previous study¹⁰ indicating that androchrome females were subject to less aggression than heterochrome females were, the findings by Falk and colleagues suggest that androchrome females can fool members of their own species about their ability to defend food resources.

Mimicry in just one sex is not unusual in nature, but it usually manifests as males mimicking females to get between courting partners, as is the case, for example, in Atlantic salmon (*Salmo salar*)¹¹. But for hummingbirds, and perhaps several other species, female mimicry of males is maintained because of extra access to resources. In classic Batesian mimicry, deception is frequency dependent because mimics gain more when they are rare. Similarly, if androchrome females became common, they might be challenged by heterochrome females so often that the flamboyant plumage, which probably incurs some developmental costs, would be unprofitable.

This study adds to a growing list of unexpected explanations for the evolution of coloration that have come to light because of current intense research in this area. These examples include using iridescence as camouflage¹², ultra-black scales that make deep-sea fish seem invisible¹³ and contrasting wing surfaces that reduce in-flight collisions of large birds¹⁴. Falk and colleagues' work also provides an alternative explanation for

the sex-linked deceptive mimicry in swallow-tail butterflies¹⁵ highlighted by the naturalist Alfred Russel Wallace (who, alongside Charles Darwin, proposed natural selection). Females of some of these species, but not males, are polymorphic to mimic different species that have an unpleasant taste to predators. Wallace would have surely loved this parallel explanation from birds.

Tim Caro is in the School of Biological Sciences, University of Bristol, Bristol BS8 1TQ, UK, and at the Center for Population Biology, University of California, Davis, USA. e-mail: tmcaro@ucdavis.edu

1. Cuthill, I. C. *et al.* *Science* **357**, eaan0221 (2017).
2. Caro, T. *BioScience* **55**, 125–136 (2005).
3. Falk, J. J., Rubenstein, D. R., Rico-Guevara, A. & Webster, M. S. *Proc. R. Soc. B* **289**, 20220332 (2022).
4. Ford, E. B. *Biol. Rev.* **20**, 73–88 (1945).
5. Hedrick, P. W. *Annu. Rev. Ecol. Syst.* **17**, 535–566 (1986).
6. Hedrick, P. W. *Trends Ecol. Evol.* **27**, 698–704 (2012).
7. Roulin, A. *Biol. Rev. Camb. Phil. Soc.* **79**, 815–848 (2004).
8. Bond, A. B. *Annu. Rev. Ecol. Syst.* **38**, 489–514 (2007).
9. Prum, R. O. *Zool. J. Linn. Soc.* **172**, 910–941 (2014).
10. Falk, J. J., Webster, M. S. & Rubenstein, D. R. *Curr. Biol.* **31**, 4381–4387 (2021).
11. Shuster, S. M. in *Evolutionary Behavioral Ecology* (eds Fox, C. & Westneat, D. F.) 434–450 (Oxford Univ. Press, 2010).
12. Kjærnsmo, K. *et al.* *Curr. Biol.* **30**, 551–555 (2020).
13. Davis, A. L. *et al.* *Curr. Biol.* **30**, 3470–3476 (2020).
14. Zheng, K. *et al.* *Proc. R. Soc. B* **289**, 20220678 (2022).
15. Wallace, A. R. *Trans. Linn. Soc. Lond.* **1**, 1–71 (1865).

The author declares no competing interests.

Robotics

A walk in the wild helps to tailor leg exoskeletons

Carlos Rodriguez-Guerrero

An innovative approach to controlling wearable robots takes the optimization process out of the laboratory. The method uses a data-driven model to infer a user's energy consumption and to personalize the assistance it provides. **See p.277**

Wearable robots can improve a person's quality of life by alleviating physical disabilities or augmenting their existing capabilities (or both). But differences between humans require these robots to adapt their behaviour to each user's needs in a personalized way. The optimization methods typically used to achieve this rely on lengthy and cumbersome tests performed under laboratory conditions that don't encourage natural movement in a user. Now, on page 277, Slade *et al.*¹ report a data-driven approach to controlling wearable robots that can be carried out rapidly and under real-world conditions, bringing

the promise of assistive technologies a step closer to widespread adoption.

Robotic exoskeletons are assistive devices that are worn over all or part of the human body, and are often designed to improve the performance of a specific task. An example of an exoskeleton is a robot that assists leg movement – for instance, during rehabilitation from injury. Precisely timed electrical motors are usually used to control the robot so that it can impart a torque at the leg joint (or joints) it is assisting.

As well as aiding rehabilitation, leg exoskeletons can reduce the energy cost of walking.

To achieve this goal, the system must decide when and how much to assist the leg. A person's walking speed varies widely over the course of a day, so the first challenge is to understand how to time the assistance to match the current walking speed. A second problem is that every gait is unique, so the robot needs to be able to adapt to the user, and assistance must be calculated in a way that is specific to each individual. The amount of assistance required of the robot at any given moment must therefore be computed efficiently and accurately.

These challenges, and the techniques for addressing them, must be further modified when a person's movement is constrained by their interaction with the robot^{2,3} or by a neurological disorder. Understanding the adaptation mechanisms that humans use in such scenarios is therefore crucial to minimizing negative effects. One of the most successful ways to tackle this problem is a method known as human-in-the-loop (HIL) optimization^{4,5}. It uses real-time physiological measurements as feedback to control when and how the device assists the wearer, thus minimizing the user's energy use while walking.

HIL optimization techniques usually estimate metabolic cost by taking copious measurements of the volume of oxygen and carbon dioxide exchanged by the user, and data on their motion while walking on a treadmill in laboratory sessions involving specialized equipment (Fig. 1a). This process is typically long, complicated and expensive, and Slade and colleagues took a more pragmatic approach. They used data from a previous experiment⁶ to train a model that can extract the metabolic energy expended from subtle changes in the user's motion as they walk with the aid of an exoskeleton.

The authors used this model to compare different ways in which an ankle exoskeleton could assist a user walking in real-world situations (Fig. 1b). They then optimized control of the device iteratively to minimize energy consumption. This approach simplifies the HIL optimization problem by removing the need for respiratory measurements that are time-consuming and difficult to acquire. The information captured by inexpensive sensors in the exoskeleton is used to personalize the assistance offered by the device.

Slade and colleagues' exoskeleton, designed using this HIL approach, incorporates an adaptive controller that calculates the assistance required at a given walking speed by interpolating between assistance parameters optimized for different speeds. This feature allows the device to respond to the natural variation in a user's gait over the course of the day.

The boost in simplicity that Slade and colleagues' method offers is an inspiring step

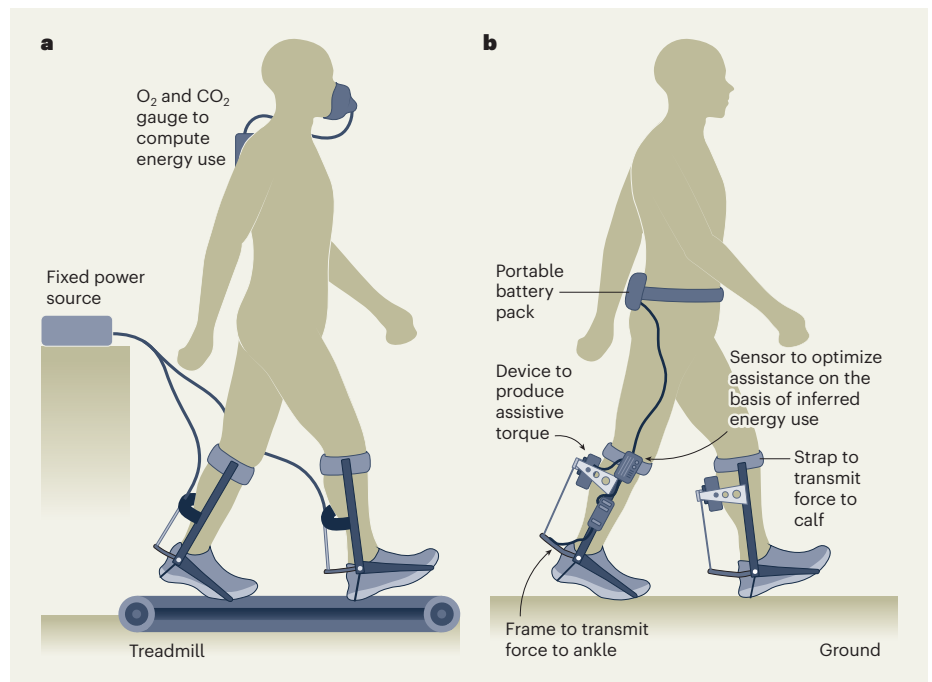


Figure 1 | A leg exoskeleton that can be trained in the real world. **a**, Wearable robots that are designed to rehabilitate or enhance performance are typically optimized by making many measurements of the oxygen and carbon dioxide exchanged while the user walks on a treadmill at a steady pace in a laboratory setting. This process is lengthy and expensive. **b**, Slade *et al.*¹ designed a device with a portable power source that does not require extensive respiratory measurements. It can therefore be worn and tailored for the user through training in real-world settings. The device transmits torque and forces to the leg, and a built-in sensor array infers the energy use from a data-driven model. (Adapted from Figs 1a and 2a of ref. 1.)

forwards in the field of wearable robotics. But, so far, HIL strategies seem to be limited to walking, a cyclical pattern of movement that can be generalized, without too much trouble, using classic regression techniques or machine-learning algorithms. It remains to be seen whether the authors' approach can be applied to more complex movements, such as reaching – a task that is far less predictable

“Every gait is unique, so the robot needs to be able to adapt to the user.”

than walking – with an exoskeleton built to enhance a human arm.

Future studies could go even further than this by optimizing robotic assistance for a range of tasks in daily life, including climbing stairs and navigating irregular terrain. Slade and colleagues' source data are available with the paper, and the source code and raw data⁶ have also been made accessible (see go.nature.com/3ev4f3h), so there is hope that progress on this front will be rapid, and that other groups will find uses for this data set and methodology.

The dream of exoskeletons helping people to achieve superhuman feats in a perfectly seamless way is still far beyond our current

technical capabilities. And although the use of HIL optimization techniques is an attractive methodology, it shares the shortcomings of any other data-driven approach, namely, it solves a problem but it doesn't tell us how it achieves this. For a deeper understanding, researchers need new multidisciplinary methods that systematically evaluate the intrinsic causal relationship between human and machine. But until those methods are available, the emergence of a technology that is simpler and more effective than existing approaches is to be celebrated.

Carlos Rodriguez-Guerrero is in the Department of Mechanical Engineering, KU Leuven, 3001 Heverlee Leuven, Belgium. e-mail: carlos.rodriguez@kuleuven.be

1. Slade, P., Kochenderfer, M. J., Delp, S. L. & Collins, S. H. *Nature* **610**, 277–282 (2022).
2. Jackson, R. W. & Collins, S. H. *IEEE Trans. Neural Syst. Rehabil. Eng.* **27**, 2059–2069 (2019).
3. Shirota, C., Tucker, M. R., Lamercy, O. & Gassert, R. 2017 *Int. Conf. Rehabil. Robot.* 430–434 (IEEE, 2017).
4. Tudor-Locke, C., Leonardi, C., Johnson, W. D. & Katzmarzyk, P. T. *J. Occup. Environ. Med.* **53**, 1382–1387 (2011).
5. Awad, L. N., Kudzia, P., Revi, D. A., Ellis, T. D. & Walsh, C. J. *IEEE Open J. Eng. Med. Biol.* **1**, 108–115 (2020).
6. Poggensee, K. L. & Collins, S. H. *Sci. Robot.* **6**, eabf1078 (2021).

The author declares no competing interests.

Correction

"The original version of this article said that Slade and colleagues' raw data were not publicly available. In fact, they were made available at go.nature.com/3ev4f3h when they were published in ref. 6. The source code was not included at the time of publication, but is available now (see go.nature.com/3ev4f3w)."