technical feat. It requires that the modeller deduce, at every point in the experiment, the mental schemas (the cognitive frameworks that organize information in the mind, for example how distinct motor memories store contextual information) that the participant has at their disposal, without observing those schemas directly. This is especially tricky when contextual information is subtle (such as the sensed compliance of a vegetable) as opposed to salient (the colour of a vegetable). The model must also determine how the mental schemas at play operate — for example, how transitions between contexts are learnt, or how each memory relates to actual motor commands. To accomplish this complex form of model fitting, Heald *et al.* developed advanced mathematical tools to relate their theory directly to data from behavioural experiments using human participants. Those tools, although secondary to the main points of the paper, make key contributions to a growing body of work that enables complex models to be fitted to human behaviour[4].

Another substantial contribution of the COIN model is that it unites concepts previously developed in other fields into a coherent model of motor learning. For example, in the field of research on reward-based decision-making, the term 'contextual inference' has been used to describe a decision-maker's belief about hidden properties of the environment that might trigger the need either to reuse past choice strategies (echoing apparent learning) or to create and update new strategies (echoing proper learning)[5,6]. Heald *et al.* bring together many of these concepts in their framework, and are among the first to apply them to motor learning.

Heald and colleagues' work also builds on the idea that different forms of learning might be supported by qualitatively different cognitive mechanisms, leading to apparent variations in learning rates. For example, during simple learning tasks in which participants must learn associations between pairs of objects and rewarding actions, participants' learning rates decrease with the number of associations to be learnt[7]. This decrease is successfully explained by a shift from a strong reliance on working memory (the short-term maintenance and manipulation of information in mind) when there are fewer pairings to learn, towards increased contributions from a type of learning called reinforcement learning, in which, through trial and error, actions incrementally accrue value. Working memory thus supports rapid apparent learning, but is not a proper learning mechanism per se.

That working memory does not support proper learning is further evidenced by the fact that associations learnt through working memory are not remembered as well as are those learnt through (slower) reinforcement learning, the latter being a classic example of proper learning. As the COIN model demonstrates, similar phenomena involving interacting mechanisms are probably present in motor learning, in which the cognitive processes underlying the deliberate selection of motor actions operate alongside, and influence, the less cognitively sophisticated processes involved in calibrating movements[8].

Having established the crucial role of contextual inference in motor learning, Heald and colleagues' study raises several questions for future research. First, what are the networks in the brain that enable contextual inference? The prefrontal cortex and hippocampi are brain regions known to be sensitive to contextual information, and thus are likely candidates.

"If cutting one tomato after cutting 20 potatoes feels novel enough, it will signal a change in context."

Second, although the COIN model captures learning across distinct experiences in a given task, motor control also involves rapid, subsecond feedback corrections, for example to change gait when traversing an unseen patch of icy pavement. How do feedback-mediated control and contextual inference interact?

Third, deliberate cognitive strategies about how to move are known to have a central role in motor learning[9]. That is, motor learning is not a purely implicit process. In the COIN model, such deliberate strategies are implicated in making inferences about the state of the environment (such as the ease of cutting through a given food item). However, in addition to aiding inference about state, cognitive strategies are probably also involved in aspects of motor learning related to conscious intuitive reasoning about the physical world and the use of conceptual knowledge; future work will be needed to clarify which aspects of motor learning are explicit (deliberate) or implicit.

Heald and colleagues' COIN model marks a substantial advance in the field of motor learning. Future work could attempt to expand the model to more general-purpose forms of learning and decision-making, cashing in on the COIN model's success.

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Palaeontology

Hominin footprints reveal a walk on the wild side

Stephanie M. Melillo

Bipedalism is a defining feature of the human lineage, but not all hominin species walked in the same way. New data from a famous palaeoanthropology site reveal that at least two differently bipedal hominins roamed eastern Africa. **See p.468**

The human version of walking on two legs, known as striding bipedalism, is unique among mammals. It requires the ability to balance a tower of loosely connected body parts over a single foot, as the other foot swings forwards to complete the stride. Conventional wisdom holds that this ungainly form of locomotion had a single evolutionary origin in an ancestral hominin, followed by about six million years during which further anatomical adjustments accumulated — a linear model of evolution in which early hominin bipedalism became progressively more similar to our own over time. However, fossils discovered during the past decade show that multiple versions of bipedalism existed simultaneously during one or

more periods of hominin evolution. McNutt *et al.*[1] suggest on page 468 that evidence of locomotor diversity in hominins has been overlooked for many decades.

More than 3.6 million years ago, ash fallout after a volcanic eruption blanketed the landscape at Laetoli in northern Tanzania. Animals left footprints in the ash layer as they searched for food, water and protection. Among the prints[2] of ostriches, giraffes, hyenas and chalicotheres (imagine a knuckle-walking horse with claws) are some that are instantly recognizable as hominin footprints. These traces, called site G footprints (similar footprints were also discovered later at site S at Laetoli), were left by an early hominin that had feet shaped like ours, and that walked using a biomechanical pattern very similar to our own. These iconic footprints[2] helped to prove that striding bipedalism appeared millions of years before big brains and skilled toolmaking.

Only a few experts are familiar with the enigmatic footprints found at Laetoli site A. These prints were partially excavated in the 1970s, documented and then quickly reburied to protect against erosion[2]. Unlike the footprints at sites G and S, the site A prints have an unusual shape and document a bipedal walking movement that occurred in a peculiar cross-stepping manner, in which each foot crosses over the body's midline to touch down in front of the other foot (Fig. 1). One explanation for the enigmatic site A prints was that they were made by a bear walking bipedally. An alternative proposal was that the prints from sites G and S and those of site A were made by different kinds of hominin[3,4]. Scientists were not convinced by either explanation. Ultimately, the site A prints were more easily forgotten than explained.

New excavations of the site A footprints by McNutt *et al.* reveal a combination of features diagnostic of hominins. The big toe and second toe are similar in length; the impression made on the ground by the big toe is much larger than that made by the second toe; the impressions made by the toes and the rest of the foot are continuous; and the heel is wide (Fig. 1). Still, the site A footprints are unlike those of any other hominin. The footprints themselves are oddly wide and short, and the feet responsible for their creation might have had a big toe that was capable of thumb-like grasping, similar to the big toe of apes.

The authors point out that cross-stepping is possible only thanks to unique aspects of hominin skeletal anatomy that position the feet extremely close to the body's midline, helping us to balance during walking when we are supported by a single foot. If the walker responsible for the site A prints had a foot positioned under the hip joint, as is the case for bears and other mammals, sequential footprints would be situated much more widely apart than they are in the site A tracks.

Figure 1 | Footprint analysis. a, McNutt *et al.*[1] examined an enigmatic 3.6-million-year-old footprint track, preserved in volcanic ash, at site A in Laetoli, Tanzania. The authors conclude that the tracks were made by a hominin (a member of the family tree that includes humans) using an unusual cross-stepping motion in which the foot crosses to the other side of the body at each step. **b**, Other hominin footprints (left print shown) of the same age exist at another Laetoli site (site G), but these tracks are not associated with cross-stepping. **c**, A close-up of a left footprint from site A reveals a wider and shorter footprint than that of site G prints, raising the possibility that two different hominin species were there at the same time. **d**, The authors investigated whether the site A tracks might have arisen from a bear walking bipedally. However, such bear prints (left print shown) do not match the characteristics of the site A tracks. McNutt and colleagues conclude that the angle between the big toe and second toe of the site A prints is more ape-like than like that of a typical hominin. Might this mean that the big toe had a thumb-like grasping capacity? **e**, Chimpanzees have that type of big toe, which can leave an impression that is at a notable angle to the side of the foot, as in this left print.

A bipedal bear might sound like a circus act, but the development of this proposal in the 1980s was insightful. Because of the way a bear's foot is shaped, it is possible to mistake a bear's right footprint for a primate's left footprint. This means that if the footprints were made by a bear, the site A track could have been made without cross-stepping. But if these prints were made by a hominin, as McNutt *et al.* convincingly show, then the cross-stepping mystery remains. It is difficult to imagine cross-stepping as the normal gait of a biped. Was the site A individual injured or stumbling? The number of possible scenarios is limited only by our imagination. However, the authors show that footprints made by cross-stepping humans remain recognizably human, so the unusual appearance of the site A prints is probably not due to the cross-stepping movement alone.

After heated debates in the 1970s to 1980s, most palaeoanthropologists reached a consensus that all fossil bones and footprints dated to the middle Pliocene epoch (roughly 3.7 million to 3 million years ago) represented the hominin species *Australopithecus afarensis*. This species was the earliest hominin known at that time and the presumed ancestor to all later hominin species. However, fossils discovered in the past two decades challenge the hard-won consensus[5,6].

The 3.4-million-year-old 'Burtele foot' from the Woranso-Mille project area in Ethiopia[7] is particularly difficult to reconcile with the prints from sites G and S and similarly aged fossil bones from Hadar, Ethiopia. The Burtele foot shows some features diagnostic of bipedal hominins, but they occur in combination with a short big toe that is angled away from the foot

and a second toe that curves towards the first. This arrangement indicates that the inner side of the Burtele foot would have been capable of hand-like grasping[7], which is an important adaptation to moving through trees that apes share[8]. This fossil reveals a strikingly different version of bipedalism from the one inferred for *A. afarensis*.

Could the site A footprints and the Burtele foot represent the same hominin species — one that is distinct from *A. afarensis*? This would be the simplest explanation. These fossils come from a similar place and time, and both provide evidence of a foot that is more ape-like than is that of *A. afarensis*. However, differences between the Burtele foot and the site A prints appear when the details are examined closely. Most notably, the first and second toes in the site A footprints are of similar lengths, whereas the Burtele foot's big toe is relatively short compared with its second toe. It is unclear whether differences such as this could exist among individuals of the same species. No living animal has a combination grasping–bipedal foot, so we have no reference for the kind of print such a foot would make.

It seems that two possibilities remain as probable explanations for the site A prints. They could have been created by a hominin species other than *A. afarensis* (perhaps the same as that represented by the Burtele foot). Alternatively, they could have been created by an *A. afarensis* individual walking in an atypical manner other than that tested in the study by McNutt and colleagues. Virtual approaches that simulate the process of footprint creation in extinct species might help us to decide between these options in the future.

If the footprints at sites G and S and those at site A were made by different species, then the Laetoli footprint tuff (rock made of volcanic ash) captures multiple hominin species living in the same habitat and at the same geological instant. This level of precision is exceedingly rare in the fossil record. It would demonstrate species coexistence in a way that implies competition for ecological resources, and it would provide a new view of the evolutionary forces at play during the early periods of human evolution.

But which hominin species existed alongside *A. afarensis*? The site A footprints and the Burtele foot provide evidence that another species was present, but these fossils are floating in a taxonomic limbo because foot bones and footprints are not conventionally used to define species. A number of species names are directly attached to skulls, jaws and teeth from middle Pliocene sites in eastern Africa, but researchers have questioned whether some or all of these fossils are distinct enough from *A. afarensis* to be considered different species. Palaeoanthropologists have debated how to link footprints, foot bones and species names ever since early hominins were discovered in eastern Africa. The state of the current fossil record ensures that this debate will continue for years to come.

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Coronavirus

Genetic clues to COVID susceptibility and severity

Samira Asgari & Lionel A. Pousaz

An individual's genetics can influence their risk of infection and the severity of disease symptoms. A large international study has identified parts of the human genome that can affect the risk of severe COVID-19. **See p.472**

For more than a year now, scientists and clinicians have been trying to understand why some people develop severe COVID-19 whereas others barely show any symptoms. Risk factors such as age and underlying medical conditions[1], and environmental factors including socio-economic determinants of health[2], are known to have roles in determining disease severity. However, variations in the human genome are a less-investigated source of variability. On page 472, members of the COVID-19 Host Genetics Initiative[3] (www.covid19hg.org) report results of a large human genetic study of SARS-CoV-2 infection. The researchers identify 13 locations (or loci) in the human genome that affect COVID-19 susceptibility and severity.

Scientists already knew that human genetic variants can influence the severity of infectious diseases, including infection with SARS-CoV-2 (refs 4–6). The effects of genetic factors range from those of rare, high-impact mutations that can make the difference between an individual developing mild symptoms and life-threatening illness[7], to more-common genetic variants that only moderately affect symptom severity[5].

Even so, human genomic studies of infectious diseases remain scarce compared with those of other immune-mediated conditions, such as autoimmune disorders. There are several reasons for that. Chief among them is that infectious diseases are typically studied with a focus on the disease-causing microorganism, rather than the host. Moreover, human genetic variants usually have relatively small effects on infection outcomes compared with the effects of socio-demographic factors such as age or access to health care[8]. Identifying these generally modest effects requires studies of large, well-characterized groups of people to produce sufficient statistical power to reveal the relevant genetic factors. Finally, unlike for chronic diseases, the window for characterizing the severity and outcomes of infectious diseases is often limited to a short period during which individuals are symptomatic.

The authors overcame these challenges by rapidly setting up a large, international collaboration when the pandemic started. This collaboration of around 3,000 researchers and clinicians includes data from 46 studies involving more than 49,000 individuals with COVID-19 and 2 million control individuals, with participants recruited from 6 ancestry groups and 19 countries. By acting swiftly, the authors could recruit symptomatic patients, and, by setting up international collaborations, were able to include enough participants to overcome statistical-power limitations. In addition, they tried to account for the role of socio-demographic factors by collecting data on some of the known risk factors, such as age and sex, and including this information in their statistical analyses.

To obtain comparable results across all 46 study groups, the authors defined 3 categories of analysis: infection, which