

News & views

Computational neuroscience

Context is key for motor learning

Anne G. E. Collins & Samuel D. McDougle

A sophisticated theory for learning motor skills places emphasis on the need for inferring context – drawing conclusions about the structure of the environment – for efficiently storing and expressing motor memories. **See p.489**

Humans can develop a wide variety of motor skills, from speaking and riding bicycles, to manipulating complex objects such as computer keyboards and musical instruments. Having a robust portfolio of motor skills encoded as motor memories is crucial to everyday life, but the neural and psychological principles of motor learning and memory are in many ways still a mystery. On page 489, Heald *et al.*¹ examine the computational principles of motor-memory formation and modification. By placing context centre stage in motor learning, the authors account for various behavioural phenomena in a single, elegant computational framework.

Consider a budding cook who, knowing only how to chop potatoes, encounters a new food. The motor program – the set of commands issued by the brain to the muscles – that the cook uses to chop potatoes should easily apply to chopping, say, a yam. By contrast, the cook might infer that they need to acquire a new chopping technique when faced with a tomato (Fig. 1). How our brain stores motor memories separately so that they can be engaged in later appropriate scenarios has not been clear.

Indeed, conventional models of motor learning² do not usually account for the existence of multiple motor memories that serve similar task goals. Returning to the knife-skills example, a conventional view would be that, on experiencing a surprisingly compliant tomato, the motor program that is engaged to chop any similarly sized object would be altered through a single learning process, independently of the context (seeing a tomato or potato). Although efficient, such a learning scheme has a major limitation: why adapt a single memory when instead you could store multiple memories and infer which one is currently most appropriate?

The authors' contextual inference (COIN) model lays out a theory of motor learning in different contexts, in precise quantitative terms. The model proposes that contextual inference – the drawing of conclusions about an environment's properties, state and dynamics – controls how motor memories are segmented, stored and expressed, with individual motor memories being stored with inferences about their associated context. The theory posits that motor learning can occur through two distinct and interacting mechanisms that

depend on contextual inference: 'proper learning' (the creation and modification of memories) and 'apparent learning' (the differential expression of competing memories). Heald *et al.* test their theory in new experiments as well as against previously published data sets. Overall, the COIN model explains an impressive range of previous findings, and makes intriguing predictions that are borne out in the authors' behavioural experiments.

For instance, one classic (and puzzling) finding in motor learning is the phenomenon of 'savings': the faster relearning of a previously acquired motor behaviour after it has apparently been forgotten³. Proper learning alone does not satisfyingly explain this effect (why should one's learning rate spontaneously increase?). According to the COIN model, however, savings instead implies a sort of 'quarantining' of separate motor memories – apparent learning brought on by contextual inference (Fig. 1). If cutting one tomato after cutting 20 potatoes feels novel enough, it will signal a change in context and perhaps the formation of a distinct new motor memory. Returning to the familiar potato (or even a yam) would then trigger the rapid re-expression of the separate memory of how to chop potatoes.

Relating the COIN model to individual participants' motor behaviour is no minor

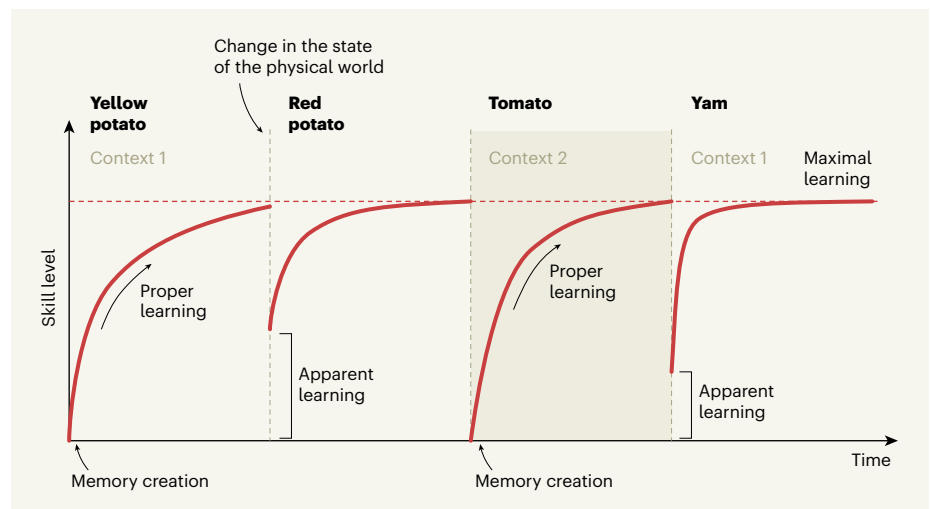


Figure 1 | A theory of motor learning relies on context. Heald *et al.*¹ emphasize the importance of drawing conclusions about an environment's properties, state and dynamics – a computation known as contextual inference – in a theory of motor learning. Contextual inference is needed for both 'proper learning' (the creation and modification of memories) and 'apparent learning' (the differential expression of competing memories). In this example, a budding chef first learns how to chop a yellow potato. The context associated with chopping a potato – a relatively hard food item – is stored with the newly created memory, and the chef's skill improves over time. When faced with a change in the state of the physical world – switching to a red potato – the chef's performance shows benefits (savings) from the previous learning with the yellow potato. Chopping a soft food item such as a tomato represents a new context, requiring proper learning. Apparent learning then underlies savings when the chef learns to chop another hard item – a yam.

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 behaviour⁴.

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 learnt⁷. 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 movements⁸.

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.

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Second, although the COIN model captures learning across distinct experiences in a given task, motor control also involves rapid, sub-second 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 learning⁹. 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

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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