

Does computational neuroscience need new synaptic learning paradigms?

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Computational neuroscience is dominated by a few paradigmatic models, but it remains an open question whether the existing modelling frameworks are sufficient to explain observed behavioural phenomena in terms of neural implementation. We take learning and synaptic plasticity as an example and point to open questions, such as one-shot learning and acquiring internal representations of the world for flexible planning.

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Introduction

Successful paradigms inspire the thinking of researchers and guide scientific research, yet their success may block independent thinking and hinder scientific progress [1]. Influential learning paradigms in computational neuroscience such as the Hopfield model of associative memory [2**], the Bienenstock–Cooper–Munro model for receptive field development [3**], or temporal-difference learning for reward-based action learning [4**] are of that kind. The question arises whether these and related paradigms in machine learning will be sufficient to account for the variety of learning behaviour observed in nature.

Learning paradigms and learning rules

In classic approaches to machine learning and artificial neural networks, learning from data is formalized in three different paradigms: supervised, unsupervised and reinforcement learning [5–8]. In supervised learning, each sample data point (e.g. a pixel image or measurements for multiple sensors) comes with a label such as ‘this image is a cat’, ‘this image is a dog’ (classification task) or for this

configuration of sensory data the correct output is 5.8 (regression task). The objective of supervised learning is to optimize parameters of a machine or mathematical function that takes a data point as input and predicts the output, that is, that performs a correct classification or prediction. Machine learning has developed powerful models and methods, such as support vector machines [9], Gaussian Processes [10], or stochastic gradient descent in deep neural networks [11] that allow to minimize the classification or regression error.

In contrast with the above, in unsupervised learning we just have multiple sample data points (pixel images or sensor readings), but no notion of correct or incorrect classification. The typical task of such machine learning algorithms consists of finding a representation of the data that would serve as a useful starting point for further processing. Typical objective functions include compression of the data into a low-dimensional space while maximizing the variance or independence of the data under some normalization constraints. The fields of signal processing and machine learning have developed algorithms such as principal component analysis (PCA) [5], projection pursuit [12], independent component analysis (ICA) [13,14] and sparse coding [15], that optimize these objective functions.

In reinforcement learning, data is not given, but collected by an agent which receives sparse rewards for some state-action pairs [8]. Temporal-difference (TD) learning methods [16] such as Q-learning [17] and SARSA [18], but also policy gradient methods [19,20] are the best-studied methods that enable the agent to choose actions that eventually maximize the reward.

In contrast to these purely algorithmic methods of machine learning, any learning method in computational neuroscience should ideally provide a link to the brain. In the neurosciences it is widely accepted that learning observed in humans or animals at the behavioural level corresponds, at the level of biological neural networks, to changes in the synaptic connections between neurons [21,22].

Classical stimulation protocols for long-term potentiation (LTP) [23–25], long-term depression (LTD) [26,27], or spike-timing dependent plasticity [28–30], inspired by Hebbian learning [31], combine the activation of a pre-synaptic neuron (or presynaptic pathway) with an activation, depolarization, or chemical manipulation of the postsynaptic neurons, to induce synaptic changes. Numerous synaptic plasticity rules have been developed that are

inspired by these experimental data [3^{••},32–43,44[•]]. Generically, in plasticity rules of computational neuroscience the change of a synapse from a neuron j to a neuron i is described as

$$\frac{d}{dt}w_{ij} = F(w_{ij}; s_i, a_j) \quad (1)$$

where w_{ij} is the momentary ‘weight’ of a synapse, s_i describes the state of the postsynaptic neuron (e.g. its membrane potential, calcium concentration, spike times, or firing rate) and a_j is the activity of the presynaptic neuron [45–47].

Local plasticity rules of the form 1 can be used to implement a large fraction [44[•]] of known unsupervised learning methods such as PCA [48], ICA [49], Projection pursuit [50], or map formation [33,51,52,5,36,37] as well as simple forms of supervised learning, where every neuron receives a direct teaching signal [53–55]. However, a convincing hypothesis for biologically plausible supervised learning in recurrent or multilayer (deep) spiking neural networks has yet to be proposed (but see [56–61]).

A link to reinforcement learning can be established by a slight modification of the Hebbian rule in Equation 1. Let us suppose that the co-activation of presynaptic and postsynaptic neurons leaves a slowly (with time constant τ_e) decaying trace e_{ij} at the synapses

$$\frac{d}{dt}e_{ij} = F(w_{ij}; s_i, a_j) - \frac{e_{ij}}{\tau_e} \quad (2)$$

which is transformed into a permanent weight change only if a modulatory signal $M(t)$ confirms the change

$$\frac{d}{dt}w_{ij} = e_{ij}(t)M(t) \quad (3)$$

The two-step learning process described in Equations 2 and 3 is consistent with experimental data of synaptic plasticity under the influence of neuromodulators [62–66] as well as with the concepts of synaptic tagging, capture, and consolidation [67–69]. Interestingly, most, if not all, of the reinforcement learning algorithms in the class of TD-learning and in the class of policy gradient rules can be cast in the form of Equations 2 and 3 [53,70–77,78[•]]. An excellent candidate for the modulating factor M in Equation 3 is the neuromodulator dopamine, since its activity is correlated with reward signals [4^{••},79].

Associative memory models [2^{••},80–83] have been one of the most influential paradigms of learning and memory in computational neuroscience and inspired numerous theoretical studies, for example, [84–90]. Their classification in terms of supervised, unsupervised, or reward-based learning is not straightforward. The reason is that in all the cited studies, learning is supposed to have happened somewhere in the past, while the retrieval of previously learned memories is studied under the assumption of *fixed* synaptic weights. Thus, implicitly this paradigm suggests

a modulating factor, similar to M in Equation 3 that determines whether learning is switched off (for retrieval of existing memories) or on (in the case of novel patterns that need to be learned) [91–93,78[•]]. If such a novelty-related modulating factor is missing, the creation of new memories with Hebbian learning rules is difficult [94–97,98[•]]. Novelty-related factors combined with a Hebb-like STDP rule have also been studied in models of autoencoders or sequence generators with spiking neurons [99,100].

The existing paradigms in computational neuroscience continue to trigger interesting research that relates synaptic plasticity to learning behaviour. For example, plasticity rules of the form 1 explain the formation of receptive fields in early sensory processing stages like V1 [101[•],44[•]]. Models with modulated Hebbian plasticity as in Equations 2 and 3 can explain habitual learning as observed for example in the Morris water maze task [77,78[•]]. And associative memory models explain some behaviour that depend on episodic memory [98[•],102[•]].

Limits of learning rules in computational neuroscience

With the standard paradigms of learning in computational neuroscience reviewed above in mind, we return to the question of whether these paradigms are sufficient to account for the variety of observed learning behaviour, in particular, one-shot learning and updating acquired representations of the world.

Let us consider the following example. When we hear about a traffic jam on the route from home to work, we can easily adapt our behaviour and take an alternative route. Knowing the cause of the traffic jam, for example, a road construction site, allows us to decide hours later which route to choose on the way back. In this example, the internal representation consists, first, of possible routes between home and work, second, the position and the cause of the traffic jam, and third, cause-dependent expectations about the duration of traffic jams, for example, a few hours in case of a small accident, at least a day for a road construction site. These three pieces of information are typically acquired at different moments in life and, presumably, all cause lasting synaptic changes that affect behaviour. Importantly, some events are experienced only once, for example, the news about the traffic jam, but are sufficient to cause long-lasting memories (‘one-shot learning’ or ‘one-shot memorization’).

One view on the traffic jam example is that it requires episodic memory that links the ‘what, where and when’ of specific events. Many models of episodic memory rely on recurrently connected neural networks that implement an associative memory [102[•],103,104] where specific input cues (e.g. position of an object or event) recall certain object representations. The association of ‘what’ (e.g.

traffic jam caused by a road construction site) with ‘where’ could be learned by strengthening the connections between the corresponding neurons by up-regulation of ‘Hebbian’ plasticity under neuromodulation. A temporal ordering (when) of what-where associations could be learned by strengthening connections between subsequently active neurons [86,102*]. In these recurrent neural networks, ‘one-shot memorization’ has been studied in models of palimpsest memory [105–111], where the last few patterns in a continuous stream of patterns can be recalled and no catastrophic forgetting is observed.

Such models give a conceptual account for the recall of what-where-when associations given a cue. But are they sufficient to explain the behaviour in the traffic jam example? Maybe partially. Experiencing different types of traffic jams, travelling different routes from home to work, the news about the traffic jam: all these experiences could form ‘what, where and when’ associations. But key questions remain. How does our brain generate internal cues to recall all relevant information about the specific traffic jam, the possible routes and the typical durations? How does it combine the recalled patterns to decide which route to take? Without an answer to these question it seems that models of associative memory explain only half of a behaviour that requires episodic memory.

An alternative view on the traffic jam example relies on an acquired representation of space. With unsupervised learning in form of competitive Hebbian synaptic plasticity, navigating agents can learn the receptive fields of place cells [70,112,113], such that these cells fire exclusively when the agent is at certain positions [114]. Given these place cells, TD-learning allows to learn position-dependent optimal actions to reach a goal [71,70,112]. In these models, the learning time to find the optimal actions is comparable to behavioural learning times, if the agent explores a novel and stationary environment (e.g. the standard reference memory watermaze task [71]). But if a well known environment changes abruptly, as in the traffic jam example, learning in these models is much slower than behavioural learning. In order to match the behavioural learning times, the agent needs to acquire a map of the environment that adds metric or topological information to the internal representation and allows planning (see e.g. the delayed-matching-to-place task in [71]).

Learning a map of the environment is just one example of acquiring domain-specific structure to quickly learn novel tasks. Many more examples exist. People that know to read and write can learn from a single presentation of an unseen character to correctly classify and generate new examples [115*]. Having learned the rules of grammar or the hierarchical organization of biological species, people can easily generalize from sparse data, like forming the plural of a novel word or inferring from the fact that ‘jays are birds’ that ‘jays are animals’ and that ‘jays are not mammals’.

Acquiring internal representations that incorporate such domain-specific structures is possible with abstract algorithmic models in machine learning and artificial intelligence, like model-based reinforcement learning [8,116] hierarchical Bayesian methods [115*,117*] or inductive logic programming [118]. It is, in general, not straightforward to translate these models into neural implementations, but for the specific case of learning maps of the environment, there are interesting propositions [71,119–124,125*] that could serve to learn the different routes in the traffic jam example and potentially also the expectations about durations of traffic jams, for example, with models inspired by dynamic programming [125*].

We as computational neuroscientists should aim for an explanation of one-shot learning or the acquisition of internal representations that are tightly constrained by both behavioural and physiological data. Currently it seems out of reach to obtain suitable physiological data from humans. But impressive learning behaviour is also observed in food-storing animals [126–128,129**]. Western scrub-jays encounter a problem very similar to the one in the traffic-jam example: they hide different types of food at different places in their environment, and update their search behaviour based on their expectations about the perishability rates of the different types of food [130]. Furthermore, corvids were observed to be rule learners in simple matching and oddity tasks [131], they use transitive inference to predict social dominance [132] and re-cache hidden food to prevent pilfering, by remembering which individual watched them during particular caching events [133].

In summary, one-shot learning and the acquisition of internal representations for flexible planning do not yet seem to be satisfactorily explained by the dominant paradigms of learning in computational neuroscience. To make progress in our understanding of such flexible learning behaviour, abstract models on an algorithmic level could give hints for novel models of synaptic learning that then, in turn, need to be constrained by physiological and behavioural data.

Conflict of interest statement

Nothing declared.

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