Can the powerful ‘backpropagation of error’ (backprop) reinforcement learning algorithm be formulated in a manner suitable for implementation in neural circuitry? The primary challenge is to ensure that any candidate formulation uses only local information, rather than relying on global (error) signals, as in orthodox backprop. Recently several algorithms for approximating backprop using only local signals, such as predictive coding and equilibrium-prop, have been proposed. However, these algorithms typically impose other requirements which challenge biological plausibility: for example, requiring complex and precise connectivity schemes (predictive coding), or multiple sequential backwards phases with information being stored across phases (equilibrium-prop). Here, we propose a novel local algorithm, Activation Relaxation (AR), which is motivated by constructing the backpropagation gradient as the equilibrium point of a dynamical system. Our algorithm converges robustly and exactly to the correct backpropagation gradients, requires only a single type of neuron, utilises only a single backwards phase, and can perform credit assignment on arbitrary computation graphs. We illustrate these properties by training deep neural networks on visual classification tasks, and we describe simplifications to the algorithm which remove further obstacles to neurobiological implementation (for example, the weight-transport problem, and the use of nonlinear derivatives), while preserving performance.
al., 2019; Vaswani et al., 2017), unsupervised representation learning (Oord, Li, & Vinyals, 2018; Radford, Metz, & Chintala, 2015), image and audio generation (Dhariwal et al., 2020; Goodfellow et al., 2014; Jing et al., 2019; Oord et al., 2016; Salimans, Karpathy, Chen, & Kingma, 2017) and in reinforcement learning (Hafner et al., 2019; Mnih et al., 2015; Schrittwieser et al., 2019; Schulman, Wolski, Dhariwal, Radford, & Klimov, 2017; Silver et al., 2017).

We have now reached the point that the state of the art is now often at, or surpassing, the human baseline. Given a hierarchical neural network composed of multiple stacked layers of neurons, and a final output, backprop first proceeds by computing an estimated output based on network weights (forward phase), before computing the derivative of the loss with respect to the output layer, and then sequentially propagates this derivative backwards through each layer of the network, at each stage computing the derivative of the loss with respect to the activities of that layer (backward phase).

The primary reason why backprop performs so well is that it optimally solves the credit assignment problem (Lillicrap, Santoro, Marris, Akerman, & Hinton, 2020), which is the task of determining the individual contribution of each parameter (potentially one of billions in a deep neural network) to the global outcome. Given the correct credit assignments, network parameters can be straightforwardly, and independently, updated in the direction which maximally reduces the global loss. The brain also faces a formidable credit assignment problem – it must adjust many trillions of synaptic weights, which may be physically and temporally distant from the global output, so as to improve performance on downstream tasks. Given that backprop provides an optimal solution to this problem (Baldi & Sadowski, 2016), a large body or work has investigated whether synaptic plasticity in the brain could be interpreted as implementing or approximating backprop (Lillicrap et al., 2020; Whittington & Bogacz, 2019). This idea has been recently buttressed by findings that the representations learnt by backprop trained deep neural networks match closely with representations extracted from neuroimaging data across multiple cortical areas (typically multiple levels of the visual ventral stream) (Cadieu et al., 2014; Khaligh-Razavi & Kriegeskorte, 2014; Kriegeskorte, 2015).

While a direct term-for-term implementation of backprop is likely to be biologically implausible (Crick, 1989), due to the nonlocality of the required learning rules, in recent years there has been a substantial amount of work on more biologically plausible approximations to backprop which work around this issue (Bengio & Fischer, 2015; Bengio, Mesnard, Fischer, Zhang, & Wu, 2017; Guerguiev, Lillicrap, & Richards, 2017; Lee, Zhang, Fischer, & Bengio, 2015; Lillicrap, Cownden, Tweed, & Akerman, 2014; Millidge, Tschantz, & Buckley, 2020; Nøkland, 2016; Sacramento, Costa, Bengio, & Senn, 2018; Scellier & Bengio, 2017; Scellier, Goyal, Binas, Mesnard, & Bengio, 2018a, 2018b; Whittington & Bogacz, 2017). The local learning constraint requires that the update rules for each synapse utilize only information which is (in-principle) locally available at that synapse, which typically includes pre- and post- synaptic activity in addition to local point derivatives and potentially the weight of the synaptic connection itself.

The recently proposed NGRAD hypothesis (Lillicrap et al., 2020) offers a unifying view on many of these algorithms by arguing that they all approximate backprop in a similar manner. Specifically, the NGRAD hypothesis suggests that all of these algorithms approximate backprop by implicitly representing the gradients in terms of neural activity differences, either spatially between functionally distinct populations of neurons or neuron compartments (Millidge et al., 2020; Whittington & Bogacz, 2017), or temporally between different phases of network operation (Scellier & Bengio, 2017; Scellier et al., 2018b).

Another way to understand local approximations to backprop comes from the notion of the learning channel (Baldi & Sadowski, 2016). In short, as the optimal weights or parameters for the network must depend on the final outcomes or targets, any successful learning rule must somehow propagate information backwards from the targets to each individual parameter in the network that contributed to the outcome. We argue that there are two primary ways to achieve this.

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1 Obviously ‘the brain’ may not optimize a single cost function, as assumed here. However even if each individual area can be thought of as optimising some combination of cost functions, the core problem of credit assignment still remains.
First, a sequential backwards pass could be utilised such that, during the backwards phase, the activations of each layer becomes a function of the layer above which propagates information about the targets backwards in a layer-wise fashion. This approach is taken by backprop, which propagates error derivatives explicitly. Other algorithms such as target-propagation \cite{Lee15} perform a backwards pass using only local information, but do not asymptotically approximate the backprop updates. Secondly, instead of a backwards pass, information could be propagated through a dynamical relaxation underwritten by recurrent dynamics, such that information about the targets slowly ‘leaks’ backwards through the networks over the course of multiple dynamical iterations. Examples of such dynamical algorithms include predictive coding \cite{Friston03, Friston05, Millidge19, Spratling08, Whittington17} and contrastive Hebbian methods such as equilibrium-prop \cite{Scellier17, Xie03}. Both of these methods asymptotically approximate the error gradients of backprop using only local learning rules.

To our knowledge, all the recurrent algorithms in the literature have utilised implicit or explicit activity differences to represent the necessary derivatives, which is in line with the NGRAD hypothesis. Here, we derive an algorithm which converges to the exact backpropagation gradients without utilising any explicit or implicit layer-wise notion of error or activity differences. Our algorithm, which we call Activation Relaxation (AR) is derived by postulating a dynamical relaxation phase in which the neural activities are treated as a dynamical system which is designed to converge to the backprop gradients. Crucially, the dynamics required to achieve this convergence are very simple, require only local information, and thus could in principle be implemented in neural circuitry. Unlike predictive coding, AR only utilises a single type of neuron (instead of two separate populations of neurons, one encoding values and one encoding errors), and unlike contrastive Hebbian methods it does not require multiple distinct backwards phases (only a feedforward sweep and a relaxation phase). This simplification is beneficial from the standpoint of neural realism, as in the case of predictive coding, there is little evidence for the presence of specialised prediction-error neurons throughout the cortex \cite{Walsh20} while in the case of contrastive Hebbian methods, the coordination and storage of information across multiple distinct backwards phases poses a substantial challenge for decentralised neural circuitry.

Moreover, we show that the energy function implicitly optimised by these dynamics is convex, and thus the backwards phase is guaranteed to converge to the global optimum corresponding to the exact backprop gradients, and in practice does so rapidly. We demonstrate that this algorithm accurately approximates the backprop gradients and can be used successfully to train deep neural networks on the MNIST and FashionMNIST tasks, where we show training performance directly comparable to backprop. Finally, we show that many of the remaining biologically implausible aspects of the algorithm, such as the weight-transport problem \cite{Crick89}, and the problem of nonlinear derivatives, can be removed, which results in an updated form of the algorithm that requires only extremely simple connectivity patterns and plasticity rules. Moreover, we show that this simplified algorithm can still be used to train deep neural networks to high levels of performance, despite no longer approximating the exact backprop gradients.

1 Methods

We consider the simple case of a fully-connected deep multi-layer perceptron (MLP) composed of \( L \) layers trained in a supervised setting. A MLP is composed of hierarchical layers of rate-coded neurons. The firing rates of these neurons are represented as a single scalar value \( x_l^i \), referred to as the neurons activation, and a vector of all activations at given

\footnote{A third method is to propagate information about the targets through a global neuromodulatory signal which affects all neurons equally, however because such learning rules do not provide precise vector feedback, the implicit gradients they compute have extremely high variance, typically leading to slow and unstable learning \cite{Lillicrap20}.}

\footnote{Although there is substantial evidence for dopaminergic reward-prediction error neurons in midbrain areas \cite{Bayer05, Glimcher11, Schultz98, Schultz00}.

\footnote{Extensions to other architectures are relatively straightforward and will be thoroughly investigated in future work. In appendix A we show that the approach can be extended to arbitrary directed acyclic graphs (DAGs), which encompasses all standard machine learning architectures such as CNNs, LSTMs, ResNets, transformers etc.}
layer is denoted as $x^l$. The activation’s of the hierarchically superordinate layer’s activations $x^{l+1} = f(W^l x^l)$ where $W^l \in \Theta$ is a set of synaptic weights and the product of activation and weights is transformed through a nonlinear activation function $f$. The final output $x^L$ of the network is compared with the desired targets $T$, according to some loss function $L(x^L, T)$. In this work, we take this loss function to be the mean-squared error $L(x^L, T) = \frac{1}{2} \sum_i (x^L_i - T_i)^2$, although the algorithm applies to any other loss function without loss of generality. We denote the gradient of the loss with respect to the output layer as $\frac{dL}{dx^L}$. In the case of the MSE loss, this gradient is just a prediction error $\epsilon^L = (x^L - T)$.

Backprop computes the gradient of the loss function with respect to the weights $W^l$ through the chain rule as,

$$\frac{\partial L}{\partial W^l} = \frac{\partial L}{\partial x^{l+1}} \frac{\partial x^{l+1}}{\partial W^l} = \frac{\partial L}{\partial x^{l+1}} f'(W^l x^l) x^{LT}$$  \hspace{1cm} (1)

where $f'$ denotes the derivative of the activation function. Note: following standard machine-learning convention, we denote vector derivatives as partials so that $\frac{\partial f}{\partial x} = : \nabla_x f$. The difficulty lies in computing the $\frac{\partial L}{\partial x^{l+1}}$ term, or the derivative of the loss with respect to the activations, using only local information. Backprop computes this quantity by sequentially applying the chain rule the chain rule $\frac{\partial L}{\partial x^l} = \frac{\partial L}{\partial x^{l+1}} \frac{\partial x^{l+1}}{\partial x^l}$, which allows one to recursively compute these activation derivatives backwards from the output loss. However this procedure is not local since the update at each layer depends recursively on all the gradients of the layers above it in the hierarchy.

Here, we propose to compute the activation derivatives, $\frac{\partial L}{\partial x^l}$ using a dynamical systems approach. Specifically, we define a dynamical system where the activations of each node at equilibrium corresponds to the backpropagated gradients. This contrasts with the typical approach where the dynamical system converges to minimize the global loss. The simplest system to achieve this,

$$\frac{dx^l}{dt} = -x^l + \frac{\partial L}{\partial x^l}$$  \hspace{1cm} (2)

which, at equilibrium, converges to

$$\frac{dx_i}{dt} = 0 \implies x^*_l = \frac{\partial L}{\partial x^l}$$

These equations take the form of a leaky-integrator driven by top-down feedback, which straightforwardly implies that at convergence, $x^*$ will be equal to the backpropagated error gradient. Applying the chain rule we can Equation 2 as,

$$\frac{dx^l}{dt} = -x^l + \frac{\partial L}{\partial x^l} \frac{\partial x^{l+1}}{\partial x^l}$$

We can rewrite this in terms of the equilibrium activation of the superordinate layer as,

$$\approx -x^l + x^{l+1} \frac{\partial x^{l+1}}{\partial x^l}$$  \hspace{1cm} (3)

To achieve these dynamics in a multilayered network would require the sequential convergence of layers, as each layer must converge to equilibrium before the dynamics of the layer below can operate.

To implement this in parallel across multiple layers, we make the crucial approximation to replace the equilibrium activation of the layer above with the current activation. This allows all layers to run in parallel since only the current value of the layer above is needed.

$$\frac{dx^l}{dt} = -x^l + x^{l+1} \frac{\partial x^{l+1}}{\partial x^l}$$

$$\approx -x^l + x^{l+1} \frac{\partial x^{l+1}}{\partial x^l}$$  \hspace{1cm} (4)

$$\approx -x^l + x^{l+1} f'(W^l x^l) x^{LT}$$  \hspace{1cm} (5)
It is straightforward to reason by induction that despite the approximation, this global optimisation will find the same
minimum as if each layer was run according to the dynamics of Equation 3. Specifically, the top layer is always
provided with the stipulatively correct gradient, so it must converge. Then the penultimate layer can simply wait until
the top layer has converged when the approximation $x \approx x^*$ becomes exact, so it too will converge, and so on for all
layers sequentially. This reasoning requires that the optimisation problem for each layer not possess local minima.
Fortunately, in Appendix A, we derive the energy functional that is implicitly optimised in this procedure, and show that
under very general assumptions this is convex, effectively guaranteeing convergence to the global minimum. Moreover,
in section 2 we provide empirical results showing that it does rapidly and robustly converge in practice to the exact
numerical gradients computed by backprop.

Equation 4 forms the backbone of the activation-relaxation (AR) algorithm. The algorithm proceeds as follows. First,
a standard forward pass takes place to compute the network output, which is then compared with the target and the
top-layer error derivative $\epsilon_L$ is computed and the penultimate layer uses this error derivative in its update rule. Then,
the network enters into the relaxation phase where Equation 4 is iterated globally for all layers until convergence for
each layer. Upon convergence, the activations of each layer precisely equal the backpropagated derivatives, and then the
activations are used to update the weights (via Equation 1).

**Algorithm 1: Activation Relaxation**

**Data:** Dataset $\mathcal{D} = \{X, T\}$, parameters $\Theta = \{W^0, \ldots, W^L\}$, inference learning rate $\eta_x$, weight learning rate $\eta_\theta$.

/* Iterate over dataset */

for $(x^0, t \in \mathcal{D})$ do

/* Initial feedforward sweep */

for $(x^i, W^l)$ for each layer do

$x^{l+1} = f(W^l, x^i)$
/* Begin backwards relaxation */

while not converged do

/* Compute final output error */

$\epsilon_L = T - \bar{x}_L$
$dx^L = -x^L + \epsilon_L \frac{\partial \epsilon_L}{\partial x^L}$
for $x^L, W^l, x^{l+1}$ for each layer do

/* Activation update */

$dx^l = -x^l + x^{l+1} \frac{\partial x^{l+1}}{\partial x^l}$
$x^{l+1} \leftarrow x^l + \eta_x dx^l$
/* Update weights at equilibrium */

for $W^l \in \{W^0, \ldots, W^L\}$ do

$W^{l+1} \leftarrow W^l + \eta_\theta x^l \frac{\partial x^l}{\partial W^l}$

This algorithm is extremely straightforward and only requires a single forward pass and then a backward relaxation
phase. Due to the convexity of the dynamics, the number of updates needed in the backwards relaxation phase is very
small and convergence is robust to high learning rates. Crucially, the fundamental AR update rule (Equation 4) only
utilizes local information – the activations at the current layer and the layer above, and the weights of that layer. Unlike
predictive coding or equilibrium-propagation, the AR algorithm does not use activity differences to represent gradients,
which are ultimately used to update weights. In our algorithm the update rule for the activations depends upon the

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5This top-layer error is simply a prediction error for the MSE loss, but may be more complicated and less-biologically-plausible
for arbitrary loss functions

6Although the dynamics here are integrated using gradient descent, due to the convexity of the problem, there exist substantially
more efficient algorithms in the convex optimization literature (Boyd, Boyd, & Vandenberghe, 2004) to find the optimum. It is an
interesting question whether any of these more efficient algorithms could have a direct neural analog.
difference between the activation at the current layer and the layer above, but the ultimate backprop gradient, which is used to update the network weights, is represented solely by the activations of the neurons after the relaxation phase and not by an activity difference.

## 2 Results

![Layerwise Divergences from True Gradient](image1)

![Learning Rate Comparison Layer 3](image2)

Figure 1: Numerical convergence to the exact backpropagated gradients, which were computed by automatic differentiation software. (a): convergence to backpropagated gradients for the 3 layers of the MLP. (b): the effect of the learning rate on the rate of convergence. Errors were computed by mean square error between AR and true gradient.

We demonstrate that our algorithm can train a deep neural network with equal performance to backprop. For training we utilised the MNIST and Fashion-MNIST [Xiao, Rasul, & Vollgraf 2017] datasets. The MNIST dataset consists of 60000 training and 10000 test 28x28 images of handwritten digits, while the Fashion-MNIST dataset consists of 60000 training and 10000 test 28x28 images of different clothing items. The Fashion-MNIST dataset is designed to be identical in shape and size to MNIST while being harder to solve. We used a 4-layer fully-connected multi-layer perceptron (MLP) with rectified-linear activation functions and a linear output layer. The layers consisted of 300, 300, 100, and 10 neurons respectively. In the dynamical relaxation phase, we integrate Equation 5 with a simple first-order Euler integration scheme.

\[
x^{l+1} = x^l - \eta x \frac{dx}{dt}
\]

where \(\eta\) was a learning rate which was set to 0.1. The relaxation phase lasted for 100 iterations, which we found sufficient to closely approximate the numerical backprop gradients. After the relaxation phase was complete, the weights were updated using the standard stochastic gradient descent optimizer.

\[
W^{l+1} = W^l + \eta \cdot f'(W^l x') x'^T
\]

The AR algorithm was applied to each minibatch of 64 digits sequentially. To test the network, we simply performed a forward pass and compared the outputs to the labels. The network was trained with the mean-squared-error loss between the predicted and true output labels.

Figure 1 shows that during the relaxation phase the activations converge precisely to the gradients obtained by backpropagating backwards through the computational graph of the MLP. In Figure 2 we show that the training and test performance of the network trained with activation-relaxation is nearly identical to that of the network trained with backpropagation, thus demonstrating that our algorithm can in fact be utilised to correctly perform credit assignment in deep neural networks with only local learning rules.
Figure 2: Training accuracy (left) and test accuracy (right) of the activation relaxation algorithm compared to backprop on MNIST, averaged over 5 seeds. Both backprop and activation relaxation obtain extremely high test accuracies and largely indistinguishable learning curves, showing that AR can perform credit assignment in deep hierarchical neural networks. Due to the rapid convergence of the algorithm, the ‘iterations’ are actually individual minibatches, corresponding to 10 full ‘epochs’, or sweeps through the dataset.

3 Removing Constraints

3.1 Weight Transport

Although the AR algorithm only utilises local learning rules to approximate backpropagation, there are still some remaining biological implausibilities in the algorithm. Following Millidge et al (in prep), we show how simple modifications to the algorithm can remove these implausible constraints on the algorithm while retaining high performance.

The most pressing difficulty is the weight-transport problem (Crick, 1989), which has long been noted as a major hurdle in any biologically plausible implementation of backprop. The weight transport problem concerns the $\theta^T$ term in Equation 5. In effect, the update rule for the activations during the relaxation phase consists of the activity of the layer above propagated backwards through the transpose of the forwards weights. However, in a neural circuit this would require either being able to transmit information both forwards and backwards symmetrically across synapses, which has generally been held to be implausible, or else that the brain must maintain an identical copy of ‘backwards weights’ which are kept in sync with the forwards weights throughout training, which would require an extremely precise connectivity scheme as well as a lot of supporting machinery to keep the weights aligned. However, in recent years, there has been much work showing that the precise equality of forward and backwards weights that underlies the weight transport problem is simply not required. Surprisingly, Lillicrap, Cownden, Tweed, and Akerman (2016)
showed that fixed random feedback weights are sufficient to drive learning in simple MLP networks, as the forward weights learn to align with the fixed backwards weights to convey useful feedback signals, in a phenomenon called feedback alignment. Later work (Akrout, Wilson, Humphreys, Lillicrap, & Tweed, 2019; Amit, 2019) has shown that it is also possible and more effective to learn the backwards weights from a random initialisation, where learning can take place with a local and Hebbian learning rule.

In sum, feedback alignment replaces the $\theta^T$ in Equation 5 with fixed random backwards weights $\psi$. The updated Equation 5 reads

$$\frac{dx^l}{dt} = x^l - x^{l+1} f'(W^l x^l) \psi^l$$

The (initially random) backwards weights can be additionally trained with the local and Hebbian learning rule which is a simple Hebbian update between the activations of the layer and the layer above.

$$\frac{d\psi^l}{dt} = x^{l+1}^T f'(W^l x^l) x^l$$ (6)

In Figure 3.a we show that strong performance is obtained with the learnt backwards weights. We found that using random feedback weights without learning (i.e. feedback alignment), typically converged to a lower accuracy and was also unstable and had a tendency to diverge, which may be due to a simple Gaussian weight initialization used here compared to the original paper. Nevertheless, when the backwards weights are learnt, we find that the algorithm is stable and can obtain performance comparable with using the exact weight transposes. This approach of using learnable backwards weights to solve the weight transport problem has been similarly investigated in (Akrout et al., 2019; Amit, 2019), however these papers simply implement backprop with the learnt backwards weights. Here we show that learnable backwards weights can be combined with a fundamentally local learning rule, while maintaining training performance.

Figure 3: Test accuracies for the AR algorithm with a.) backwards weights, b.) no nonlinear derivatives and c.) both simplifications at once. Top row is MNIST, bottom row is Fashion-MNIST. Generally the simplifications make effectively no difference to the performance of the algorithm, except perhaps when combined which produces a slightly higher variance score.
3.2 Nonlinearity Derivatives

The second potential biological implausibility in the algorithm is the requirement to multiply the weight and activation updates with the derivative of the activation function. While in theory this only requires a derivative to be calculated locally for each neuron, whether biological neurons could compute this derivative is an open question. We experiment with simply removing the nonlinear derivatives in question from the update so that the updated Equation 5 now simply reads

\[
\frac{dx^l}{dt} = x^l - x^{l+1} W^{lT}
\]  

(7)

Although the gradients are now incorrect, we show in Figure 3.b that learning performance against the standard model is relatively unaffected, showing that the influence of the nonlinear derivative is small. We hypothesise that by removing the nonlinear derivative, we are effectively projecting the backprop update onto the closest linear subspace, since the backpropagated rule is now linear, which is still very close in terms of angle to the correct rule, and thus can support learning.

Moreover, and importantly, we can combine these two changes of the algorithm such that there is both no nonlinear derivative and also learnable backwards weights. Surprisingly, we see that in Figure 3.c by combining these improvements the combined algorithm both performs equivalently to the correct algorithm, and thus backprop, while also retaining an extremely simple and biologically plausible form. The activation update equation for the combined algorithm is:

\[
\frac{dx^l}{dt} = x^l - x^{l+1} \psi
\]  

(8)

which requires only locally available information and is mathematically very simple. In effect, each layer is only updated using its own activations and the activations of the layer above mapped backwards through the feedback connections, which are themselves learned through a local and Hebbian learning rule. This rule both maintains high training performance while being incredibly robust and, at least in theory, relatively straightforward to implement in neural circuitry.

4 Discussion

We have shown that by taking a relatively novel perspective on the problem of approximating backprop through recurrent dynamics – by explicitly designing a dynamical system to converge on the gradients we wish to approximate – it is possible to straightforwardly derive from first principles an extremely simple algorithm which asymptotically approximates backprop using only recurrent dynamics with local learning rules. This algorithm, which we call activation-relaxation (AR), requires only a feedforward pass and then a dynamical relaxation phase which converges quickly and robustly to the exact numerical gradients computed by backprop due to the convexity of the dynamics (Appendix A). We show empirically that this is the case in practice, that this convergence is maintained across training, and that the algorithm can be used to train deep MLPs to obtain identical performance to backprop.

We then show that two key remaining biological implausibilities of the algorithm – the weight transport problem, and the need for nonlinear derivatives – can be removed without apparent harm to performance. The weight transport problem can be seemingly solved by postulating a second set of independent backwards weights which can be trained in parallel with the forward weights with a Hebbian update rule. Meanwhile, perhaps surprisingly, we have found that the nonlinear derivatives can be simply dropped from the learning rules which and this step, although it renders the update rules incorrect, does not appear to significantly harm learning performance. Future work should test whether performance is still maintained on more challenging architectures. When these adjustments to the algorithm are combined, we obtain the extremely simple and elegant update rule shown in Equation 7.

The AR algorithm does away with much of the complexity of competing schemes. Unlike contrastive Hebbian approaches such as equilibrium-prop, it does not require multiple distinct backwards dynamical phases such as the ’free
phase’ and the ‘clamped phase’ and the storage of information across phases. Unlike predictive coding approaches (Millidge et al., 2020; Whittington & Bogacz 2017), error-dendrite methods (Guerguev et al., 2017; Lillicrap & Santoro 2019; Sacramento et al. 2018), or ‘ghost units’ (Mesnard, Vignoud, Sacramento, Senn, & Bengio 2019), AR does not require multiple distinct neural populations with separate update rules and dynamics. Instead, the connectivity scheme in AR is identical to that of a standard MLP with only one type of neuron required. Furthermore, unlike target-prop and related methods, AR exactly approximates the backpropagated gradients and thus performs stochastic gradient descent, while target-prop instead performs an approximate second-order Gauss-Newton update (Meulemans, Carzaniga, Suykens, Sacramento, & Grewe 2020). Although in theory second order methods have several advantages over first order methods like backprop, due to taking into account the information contained in the curvature of the local loss surface (Martens 2016), empirically first order methods such as backprop have demonstrated substantially better scaling potential.

Since it can approximate backprop without any implicit or explicit representation of activity differences across time or space, the AR algorithm thus provides a counterexample to the NGRAD hypothesis, suggesting that it requires some nuancing. Although the gradients themselves are not represented or computed through any kind of activity or temporal difference, the activation derivative update rule (Equation 5 and 7) can be interpreted as a kind of prediction error between the current activity and the activity of the layer above mapped through the backwards weights. In fact, this rule is strongly reminiscent of the target-prop updates, suggesting some points of commonality which would be interesting to investigate in future work. However, the NGRAD hypothesis as currently stated in (Lillicrap et al., 2020) requires that gradients be encoded directly in differences, our method shows that this is not necessary and that instead inter-layer errors can be used to drive dynamics which converge asymptotically to the correct gradients, thus suggesting perhaps an extension of the NGRAD formalism is warranted.

Although the AR algorithm (especially the simplified version) takes a strong step towards biological realism, it still possesses several weaknesses which may render a naive implementation of the algorithm in neural circuitry challenging. The primary difficulty is the necessity of two distinct phases – a feedforward phase where the activations are set directly by bottom-up connectivity, and a dynamical relaxation phase where the activations are then slowly adjusted using local learning rules until they converge to the backpropagated gradients. In effect, the algorithm uses the ‘activation’ units for two distinct purposes – to represent both the activations and their gradients – at different times. While this is not a problem in the sequential presentation paradigm used in standard machine learning, where i.i.d items from a dataset are presented sequentially to the network, for a biological brain enmeshed in constant sensory exchange with the outside world in continuous time, the requirement for a dynamical relaxation adjusting the firing rates of all neurons for learning, before the next sensory stimulus can be processed would be a significant challenge. This problem is made especially acute by the fact that the dynamical relaxation phase requires multiple iterations to converge, although not many due to the convexity of the dynamics. In effect, by reusing the activations for two different tasks, the brain must either rigidly stick to two separate phases – an ‘inference’ phase and a ‘learning phase’ to be carried out sequentially, or else must be able to correctly multiplex the different phases together adaptively to perform the correct updates. This difficult is compounded when considering the weight updates which require the presence of both the gradient and the original activation simultaneously, thus necessitating the storage of the original activation information across the backwards relaxation phase.

One potential solution to the multiplexing problem and the related problem of storing the original activations is through the use of multicompartment models of neurons with segregated dendrites. A number of proposed algorithms have shown to be able to approximate backpropagation using the useful properties of apical dendrites to keep separate representations of the activity and the error (Guerguev et al., 2017; Sacramento et al., 2018; Urbanczik & Senn 2014). Moreover, the apical dendrites of pyramidal neurons have a number of useful properties in this regard – they are known to receive a substantial amount of top-down feedback from other cortical and thalamic areas (Ohno et al. 2012; Rockland & Virga 1989), they are electronically distant from the soma (M. Larkum 2013; M. E. Larkum, Waters, Sakmann, & Helmchen 2007; Megias, Emri, Freund, & Gulyas 2001), and through NMDA spiking they are thought
to be able to operate as a ‘third factor’ in synaptic plasticity rules (Körding & König, 2001). Translating this model to a multicompartmental dendritic model will be a fascinating area of future work, although beyond the scope of this paper. Another potential solution to the multiplexing problem is that the different phases could be coordinated by the regular oscillatory rhythms of activity such as alpha or gamma band activity which are observed in EEG studies (Buzsaki, 2006). These oscillations could then separate inference and relaxation into different phases which the system to maintain the required separation between them while also handling a continuously changing external environment.

4.1 Conclusion

We have derived a novel algorithm which converges rapidly and robustly to the exact error gradients computed by backprop using only local learning rules. This algorithm requires only a single backwards phase and one type of neuron, thus shedding much of the complexity implicit in related models in the literature. Moreover, we have shown that two key remaining biological implausibilities of the model – that of weight symmetry and nonlinear derivatives can be removed from the algorithm without apparent ill-effect, resulting in a final algorithm which is both extremely robust and competitive with backprop while also possessing a compelling simplicity and straightforward biological interpretation.

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Appendix A: Energy function, extension to arbitrary DAGs and the convexity of the dynamics

In this appendix we elaborate on the mathematical background of the AR algorithm. We present a.) A candidate energy function that the dynamics appear to optimize, and discuss its limitations, b.) An extension of the AR algorithm to arbitrary computation graphs, which allow, in theory, for the AR algorithm to be used to perform automatic differentiation and optimisation along arbitrary programs, including modern machine learning methods, c.) We demonstrate that under the assumption of maintaining a memory of the original feedforward pass activations, the energy function is convex and thus the dynamics are guaranteed to converge rapidly and reliably to the global optimum, which corresponds to the correct gradients. To show convexity, it is necessary to first define an energy function (subsection 1), and then for convenience we extend the algorithm to arbitrary graphs (subsection 2). This provides a convenient formalism for understanding the convexity of the global optimisation problem in terms of the adjacency matrix. Finally we demonstrate the convexity of the global problem through an examination of the Hessian. Importantly, the MLP case considered in the paper is subsumed under the general graph formalism with an adjacency matrix which is simply an upper diagonal row of 1s.

The Energy Function

We first define the implicit energy function $\mathcal{E}$ that the dynamics can be thought of as implementing. Given a hierarchical MLP structure with activations $x^l$, and activation function $f$ and parameters $\theta_i$ at each layer. This energy function is:

$$\mathcal{E} = \sum_{i=0}^{L} \frac{1}{2} x^i x^i + \frac{1}{2} f(W^l, x^l)^2$$  \hspace{1cm} (9)

Given this energy, function we can derive the dynamics as a gradient descent on $\mathcal{E}$

$$\frac{dx^l}{dt} = - \frac{\partial \mathcal{E}}{\partial x^l} = -x^l + f(W^l, x^l) \frac{\partial f(W^l, x^l)}{\partial x^l}$$  \hspace{1cm} (10)

$$= -x^l + x^{l+1} \frac{\partial f(W^l, x^l)}{\partial x^l}$$  \hspace{1cm} (11)

where the second step uses the fact that in the forward pass $x^{l+1} = f(W^l, x^l)$. While this energy function can derive the required dynamics it possesses several limitations. At the initial forward pass, it is 0 for all layers except potentially the output layer, and moreover it does not define a standard loss function (such as the mean-squared error) at the output. Thus the AR algorithm requires a special case to deal with the final output layer, as the ‘natural’ final layer loss is simply $T^2 - f(W^L, x^L)^2$ which is not a standard loss. Secondly, the value of the loss is not bounded above or below, for instance it cannot easily be interpreted as a prediction error, which can go to 0. Minimizing the energy function thus
effectively requires trying to push \( f(W^l, x^l) \) to be greater than \( x^l \) as much as possible, rather than trying to equilibrate the two. Finally, the replacement of \( f(W^l, x^l) \) with \( x^{l+1} \) is a subtle issue due to the way the AR algorithm treats the activations in two separate ways. During the forward pass, this substitution is valid, however during the backward relaxation, the activations are changed away from their initial forward-pass values, and thus this substitution is not valid in this case.

**Extension to DAGs**

Here we consider the extension of the AR scheme described in the paper to more complex architectures. Specifically we are interested in any function which can be expressed as a computation graph of elementary differentiable functions. This class includes essentially all modern machine learning architectures. A computation graph represents a complex function (such as the forward pass of a complex NN architecture like a transformer [Vaswani et al., 2017], or an LSTM [Hochreiter & Schmidhuber, 1997]) as a graph of simpler functions. Each function corresponds to a vertex of the graph while there is a directed edge between two vertices if the parent vertex is an argument to the function represented by the child vertex. Because we only study finite feedforward architectures (and since it is assumed finite we can ‘unroll’ any recurrent network into a long feedforward graph), we can represent any machine learning architecture as a directed acyclic graph (DAG). Automatic Differentiation (AD) techniques, which are at the heart of modern machine learning (Griewank et al., 1989; Margossian, 2019; Van Merriënboer, Breuleux, Bergeron, & Lamblin, 2018), can then be used to compute gradients with respect to the parameters of any almost arbitrarily complex architecture automatically. This allows machine-learning practitioners to derive models which encode complex inductive biases about the structure of the problem domain, without having to be manually derive the expressions for the derivatives required to train the models. Here we show that the AR algorithm can also be used to compute these derivatives along arbitrary DAGs, using only local information in the dynamics, and requiring only the knowledge of the inter-layer derivatives.

Core to AD is the multivariate chain-rule of calculus. Given a node \( x^l \) on a DAG, the derivative with respect to some final output of the graph can be computed recursively with the relation

\[
\frac{\partial L}{\partial x^i} = \sum_{x^j \in \text{Chi}(x^i)} \frac{\partial L}{\partial x^j} \frac{\partial x^j}{\partial x^i} \tag{12}
\]

Where \( \text{Chi}(x^i) \) represents all the nodes which are children of \( x^i \). In effect, this recursive rule states that the derivative with respect to the loss of a point is equal to the sum of the derivatives coming from all paths from that node to the output. We now derive the AR energy function and dynamical update rule on a DAG. Specifically, we have in the forward pass that \( x^i = f(W^i, x^j) \in \text{Par}(x^i) \) (where \( \text{Par}(x) \) denotes the parents of \( x \)) so that each activation is some function of its parent nodes. We can thus write out the energy function and dynamics, and compute the equilibrium to obtain:

\[
E = \sum_{i=0}^{L} \frac{1}{2} x^i - \frac{1}{2} f(W^i, x^j) \in \text{Par}(x^j)^2 \tag{13}
\]

\[
\frac{dx^i}{dt} = -\frac{\partial E}{\partial x^i} = x^i - \sum_{x^j \in \text{Chi}(x^i)} f(W^i, x^j) \in \text{Par}(x^j) \frac{\partial f(W^i, x^j)}{\partial x^i} \tag{14}
\]

\[
= x^i - \sum_{x^j \in \text{Chi}(x^i)} x^j \frac{\partial x^j}{\partial x^i} \tag{15}
\]

\[
\frac{dx^i}{dt} = 0 \implies x^i = \sum_{x^j \in \text{Chi}(x^i)} x^j \frac{\partial x^j}{\partial x^i} \tag{16}
\]

Crucially, this recursion satisfies the same relationship as the multivariable chain-rule (Equation 11), and thus if the output nodes are equal to the gradient at the top-level such that \( x^L = \frac{\partial L}{\partial x^L} \), at equilibrium the correct gradients will
be computed at every node in the graph. Thus AR can be converted into a general-purpose AD algorithm which utilises only local information. Neurally, this only requires the dynamics in the relaxation phase to respond to the sum of top-down input, which is very plausible, and thus perhaps suggests that it is possible the brain could be utilizing substantially more complex architectures than feedforward MLPs.

Convexity in the Relaxation Phase

Here we show that the optimisation problem posed by this energy function is convex for a general DAG, and thus the dynamics are guaranteed to converge to the global optimum which corresponds to the correct backprop gradient. Moreover, this convergence is rapid and robust to high learning rates. We demonstrate this empirically in Figure 1 of the main text.

We first formally define the computation graph $G = \{E, V\}$ as a DAG with edges $E = \{f^i \ldots f^L\}$ and vertices (or nodes) $V = \{x^i \ldots x^L\}$. The adjacency matrix $A$ of $G$ is defined such that $A[i, j] = 1$ if and only if $x^j \in \text{Chi}(x^i)$, i.e. that node $x^j$ is a child of $x^i$. An energy function is convex if its Hessian $H$ is positive-definite everywhere. A sufficient condition for positive-definiteness is that all the eigenvalues of the matrix are positive. We demonstrate that the Hessian $H(\mathcal{E})$ of the energy function fulfills this criterion. We compute the elements of the Hessian as follows:

$$H[i, j] = \frac{\partial^2 \mathcal{E}}{\partial x^i \partial x^j} = \frac{\partial}{\partial x^j} \left[ \frac{\partial \mathcal{E}}{\partial x^i} \right]$$

$$= \frac{\partial}{\partial x^j} \left[ x^i - \sum_{x^j \in \text{Chi}(x^i)} x^j \frac{\partial x^j}{\partial x^i} \right]$$

$$= \begin{cases} 
1, & \text{if } i = j \\
-f'(W^i, x^i)W^iT, & \text{if } A[i, j] = 1 \\
0, & \text{Otherwise} 
\end{cases}$$

Since the computation graph $G$ is a DAG, it is possible to permute the vertices of the adjacency matrix $A$ such that it becomes upper-triangular with 0s on the diagonal. The Hessian $H$ is thus upper-triangular with 1s on the diagonal. The eigenvalues of an upper-triangular matrix are simply the diagonal elements which are all $1 > 0$, and thus the Hessian is positive definite, rendering the energy function convex. Importantly this unusual upper triangular form of the Hessian is caused by the assumption of the two separate phases – the first forward phase where the forward activations are computed and stored and the second relaxation phase where the activations are updated through a gradient descent until they reach the backprop gradients. Crucially in this backwards phase the derivative $\frac{\partial x^{i+1}}{\partial x^i}$ is assumed constant, since it requires the use of the old (forward) $x^i$. However this constant assumption is not made in the first differentiation of the energy function to obtain the equation in the first place, thus since the assumption ‘kicks in’ only after the first differentiation, the Hessian takes on a non-symmetric upper-triangular form.