Recurrent neural networks that learn multi-step visual routines with reinforcement learning

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Abstract

Many problems can be decomposed into series of subproblems that are solved sequentially. When subproblems are solved, relevant intermediate results need to be stored and propagated to the next subproblem, until the overarching goal has been completed. We will here consider visual tasks, which can be decomposed into sequences of elemental visual operations. Experimental evidence suggests that intermediate results of the elemental operations are stored in working memory as an enhancement of neural activity in the visual cortex. The focus of enhanced activity is then available for subsequent operations to act upon. The main question at stake is how the elemental operations and their sequencing can emerge in neural networks that are trained with only rewards, in a reinforcement learning setting.

We propose a new recurrent neural network architecture that can learn composite visual tasks that require the application of successive elemental operations. Specifically, we selected three tasks for which electrophysiological recordings of monkeys' visual cortex are available. To train the networks, we used RELEARNN, a biologically plausible four-factor Hebbian learning rule, which is local both in time and space. We report that networks learn elemental operations, such as contour grouping and visual search, and to select sequences of operations, solely based on the characteristics of the visual stimuli and the reward structure of a task.

After training had completed, the activity of the units of the neural network resembled the activity of neurons in the visual cortex of monkeys solving the same tasks. Relevant information that needed to be exchanged between subroutines was maintained as a focus of enhanced activity and passed on to the subsequent subroutines. Our results demonstrate how a biologically plausible learning rule can train a recurrent neural network on multistep visual tasks.

Introduction

Many everyday tasks can be decomposed into subroutines that are executed sequentially. If you want to find your way on a map, for instance, you first have to search where your goal is, where your actual position is, and then you have to trace a path between those two positions. In 1984 Ullman (1984) proposed that such complex visual tasks can be solved using visual routines, neuronal programs consisting of a sequence of atomic mental steps that he called elemental operations. Curve tracing, visual search, cuing, matching or contour grouping are examples of elemental operations (Roelfsema, 2005; Roelfsema et al., 2000; Zylberberg et al., 2011).

There are at least two critical conditions for the successful implementation of visual routines: the correct elemental operations must be chosen and applied at the correct time, and information must flow between subroutines so that the output of one subroutine can be used as the input for the next one. Those two conditions are straightforward to implement in a computer program, but it remains unclear how variables are bound to subroutines in the brain. Several studies provided insights into the neural basis of elemental operations and visual routines. Jolicoeur et al. (1986) focused on curve tracing as an example elemental operation. In their task, subjects had to determine if two dots were on the same or different curves. They found that curve-tracing is a serial mental operation because the reaction time increases when subjects have to trace a longer curve (see Fig. 1 for an example curve-tracing stimulus).

Previous studies also have started to gain insight in how elemental operations are implemented in the visual cortex. The neural activity during elemental operations can be divided in several phases (Lamme & Roelfsema, 2000; Roelfsema et al., 2007). The first phase is dominated by feedforward processing. Basic features are registered in low level areas and more complex features, such as object category are registered in higher visual

areas (Roelfsema, 2006; Vanrullen, 2007). Later phases are dominated by recurrent processing, enabled by feedback and horizontal connections, allowing the early visual cortex to act as a cognitive blackboard (Roelfsema & de Lange, 2016). Higher areas may write to the blackboard in early visual cortex using feedback connections, to enhance the representation of task-relevant features and suppress the representation of distracting information. Other higher visual areas can then read from the blackboard utilizing feedforward connections to selectively process features that are task relevant.

Studies in monkeys carrying out attention-demanding tasks have supported the blackboard analogy as well as the distinction between feedforward and feedback processing. For example, Roelfsema et al., (1998) trained monkeys in a curve-tracing task while recording the activity of neurons in the primary visual cortex (area V1). The animals were trained to make an eye movement toward the end of a target curve that was connected to the fixation point, while ignoring another distractor curve (Fig. 1, Trace task). The researchers found that neurons with a receptive field (RF) on the target curve enhanced their activity compared to neurons whose RF fell on distractor curves. Later studies demonstrated that the enhanced activity spreads gradually over the V1 representation of the curve (Pooresmaeili & Roelfsema, 2014). The latency of the response enhancement was short at the start of the curve and it occurred later for neurons with RFs farther from the start of the curve. These findings demonstrate the serial nature of the contour-grouping process. Related findings have been reported for visual search, where the representation in the visual cortex of items that a monkey searches for is enhanced during a delayed phase of the neuronal responses (Chelazzi et al., 1998, 2001; Desimone & Duncan, 2003; Mirpour & Bisley, 2012; Sato et al., 2001; Zhou & Desimone, 2011) .

To examine how elemental operations are combined into visual routines, Moro et al. (2010) and Roelfsema et al. (2003) recorded from neurons in the visual cortex of monkeys trained to perform complex visual tasks. The first task was a ‘search-then-trace’ task (Fig. 1). In this task, the fixation point could be one of two colors (Fig. 1). The monkey had to register the color of the fixation point and to search for a circular marker with the same color, which demarcated the start of the target curve. The monkey then traced the target curve to its other end and planned an eye movement to a circle at that position (blue dot in Fig. 1). The search and trace operations were performed mentally, while the monkey kept its gaze on the fixation point. The eye movement was made only at the end of the trial and the monkey received a reward when he made an eye movement to the circle at the end of the target curve. The second composite task was a trace-then-search task (Fig. 1). Now the order of the two subroutines was reversed: the monkey first had to trace the target curve connected to the fixation point and register the color of a marker at the end of this curve. The monkey then then searched for a larger circle with the same color that was the target for an eye movement.

The neurophysiological studies demonstrated that it is possible to monitor the order and progress of the successive subroutines that are executed while the monkey solves the tasks by recording from area V1. The findings also illustrate how information can be transferred from one elemental operation to the next. For example, in the search-then-trace task, the initial visual search enhances the representation of the target marker as the beginning of the target curve (at a latency of 159ms, light blue circle in Fig. 1) so that the tracing operation could begin at this marker (229ms, light yellow in Fig. 1). In the trace-then-search task, trace operation caused an enhanced response of the target marker (at 180ms, Fig. 1) so that its color could be registered as the target color for the subsequent search. The visual search caused an enhanced response at the circular eye movement target at a latency of 267ms (Fig. 1).

An important finding is that the enhancement of activity in the visual cortex makes the outcome of an elemental operation available as a focus of enhanced activity that may correspond to the working memory of that feature so that it can be used as the input for the

next elemental operation (Van Kerkoerle et al., 2017). These findings also illustrate the role of early visual cortex as a cognitive blackboard (Roelfsema & de Lange, 2016). Reading and writing to the cognitive blackboard in early visual areas permits the exchange of information between elemental operations that are part of a visual routine. For example, in the search-then-trace task, the visual search operation tags the location of the target marker with enhanced activity in area V1, which corresponds to a write operation on the cognitive blackboard. This focus of enhanced activity marks the beginning of the tracing operation, which can then be traced starting at this position.

At a psychological level of description, the neuronal response modulations that occur during the later, recurrent processing phase correspond to shifts of attention, which is directed to image elements that are represented with enhanced neuronal activity (Roelfsema & Houtkamp, 2011). The sequence of mental operations is associated with a sequence of attention shifts. Visual search for a target shape or color in an array of stimuli leads to a shift of attention to the item that needs to be found (Kim & Cave, 1995). Similarly, when subjects mentally trace a curve, they gradually spread attention across all of its contour elements (Houtkamp et al., 2003).

Hence, there is substantial evidence that visual routines are implemented in the visual cortex through the propagation of enhanced activity during a recurrent processing phase. However, it remains unknown what architectures and plasticity rules permit the learning of such routines in the brain. To investigate how curve-tracing can be learned, Brosch et al (2015) developed RELEARNN. RELEARNN is a biologically plausible learning rule that uses two factors to gate Hebbian plasticity. The first factor is a reward-prediction error that is central in many approaches to biologically inspired learning (Sutton & Barto, 2018) and that is thought to be made available throughout the brain by the release of neuromodulators such as dopamine (Schultz, 2002; Schultz et al., 1997). The second factor used by RELEARNN is a feedback signal initiated by the selected action, which propagates through a dedicated set of recurrent connections in an “accessory network” that highlight the synapses that have had most influence on this action and that gate the plasticity. The combination of these two factors gives rise to a learning rule that is equivalent to the Almeida-Pineda algorithm (Almeida, 1987; Pineda, 1987), while all the information needed to control plasticity is available locally at every synapse. Furthermore, RELEARNN is based on trial-and-error learning and does not require the “teacher” of error-backpropagation, because the only feedback that the network receives is whether the response is correct or wrong.

Interestingly, Brosch et al. (2015) found that the strategy that the network learned to trace curves resembled the neurophysiological results in the visual cortex of monkeys. The target curve was tagged in an iterative manner by the spreading of enhanced neuronal activity. However, Brosch et al. (2015) only tested curve-tracing and it remains unclear if neural networks can learn to stitch elemental visual operations into visual routines using a biologically plausible learning rule that is based on trial-and-error learning. In the present study we therefore set out to examine learning of visual routines by neural networks with feedforward, feedback and lateral connections. We asked whether the network (1) would learn multiple elemental operations, (2) whether it would learn to execute the elemental operations sequentially and in the correct order and (3) how the network ensured the transfer of information of one elemental operations to the next.

We trained the networks on three visual routines for which electrophysiological recording of monkeys performing the same routines exist: a trace task, a search-then-trace and a trace-then-search task (Moro et al., 2010), using RELEARNN (Brosch et al., 2015). We found that the networks were able to learn all three tasks. Interestingly, the activation of units of the networks resembled to spatiotemporal patterns of activity observed in the visual cortex of monkeys. The networks learned to propagate enhanced activity along curves and to

enhance activity in retinotopic areas to transfer information between subroutines. Our model shows how a recurrent neural network trained with a biologically plausible learning rule can learn to propagate enhanced activity to solve complex visual tasks.

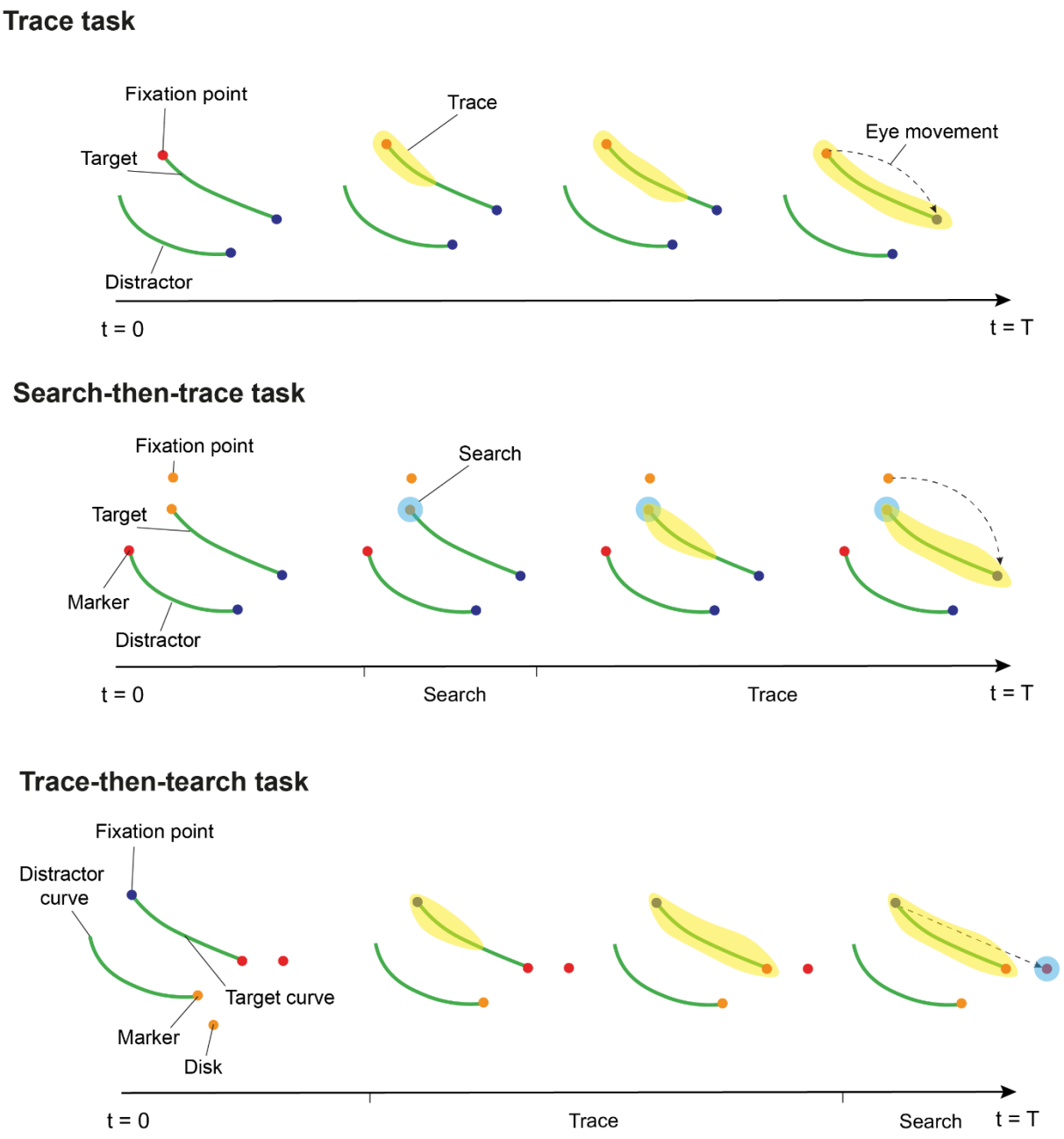

Fig. 1. Example stimuli for the three tasks. Trace task. In this task, the monkey or model makes an eye movement toward the blue dot connected to the red fixation point. During curve-tracing, the representation of the target curve in the visual cortex is enhanced (spread of activity in light yellow corresponding to the trace operation). **Search-then-trace task**. Here, the monkey or model makes searches for a marker that is one of two colors and then traced the curve that starts at this marker to its other end to make an eye movement to the blue dot. This task requires a search operation followed by a tracing operation . In the visual cortex, first the search operation labels the target marker with enhanced activity (light blue circle), which can be used as the starting position of the tracing operation which then propagates over the target curve (light yellow)**. Trace-then-search task**. In this task, the monkey or model first has to trace the target curve connected to the fixation point and identifies the target color at the end of this curve. It then has to search for a disk with the same color, which is the target for an eye movement. In the visual cortex, enhanced activity first propagates across the target curve and identifies the target color (trace operation, light yellow), which can is used during the subsequent search (search operation, light blue circle).

The tasks for the model

We trained networks on three tasks for which electrophysiological data of monkeys are available (Moro et al., 2010; Roelfsema et al., 2003). The first task is a version of the curve tracing task (Fig. 1, trace task). This task requires only one of the elemental operations, which is curve tracing (Ullman, 1984). To solve it, the model had to learn to group a set of connected pixels on a grid of 15 by 15 pixels. The network had to locate the end of the curve that was a blue pixel, which was connected to a red pixels that marked the start of the relevant curve. At every retinotopic location of the input layer, there were four units, one for each of the possible colors of the pixels (red, orange, blue and green). We trained the model to report the blue pixel at the other end of the curve starting with the red pixel, by selecting this location for an eye movement.

The second task was the search-then-trace task (Fig. 1, search-then-trace task). In the version of the search-then-trace task for the model, we cued the color that was the target of search by activating one of two additional input units, which coded for yellow and red (Fig. 2). The model had to locate the pixel with the same color in the visual stimulus and trace the curve starting at this pixel to its other end to locate a blue pixel that was the target for an eye movement.

The third task was the trace-then-search task (Fig. 1, trace-then-search). In the version of the task for the model, the target curve started with a blue pixel. The model had to identify the color at the other end of the target curve and to select the same color at a location outside the pixel frame. Specifically, it could choose between a red and yellow response pixel.

Contrary to the version of the tasks for monkeys, where a trial started with a fixation point and the full stimulus appeared later on, in the version of the tasks for the model each trial started with the full stimulus, irrespective of the model's gaze position.

The search-then-trace and the trace-then-search tasks can be solved by visual routines, composed of visual search and curve tracing as elemental operations, but in different orders. These tasks illustrate that the output of one operation needs to be carried over as input for the next operation. For example, the output of the search operation of the search-then-trace task is the location of the marker with the right color, which is the starting point for the subsequent tracing operation.

Model

We will first describe the network architecture and RELEARNN, the biologically plausible reinforcement learning rule. We will then compare the network simulations with neuronal activity in the visual cortex of monkeys that were trained on the same tasks.

Structure of the network

We trained convolutional neural networks with an input layer, two hidden layers and an output layer. In each layer there was a group of feedforward units that only propagated information to the next layer and to other feedforward units. These feedforward units also gated the activity of neurons in the other, recurrent group with a RF at the same position (Fig. 2, "horizontal gating"). Units in the recurrent group could propagate information to the next or previous layer and to units with different receptive fields within the same layer. As a result, neurons in the recurrent group could be modulated by activity outside their RF. The gating by neurons in the feedforward group with the same RF (Fig. 2) ensured that the response modulation could not spread to recurrent units that represent features that are not present in the image.

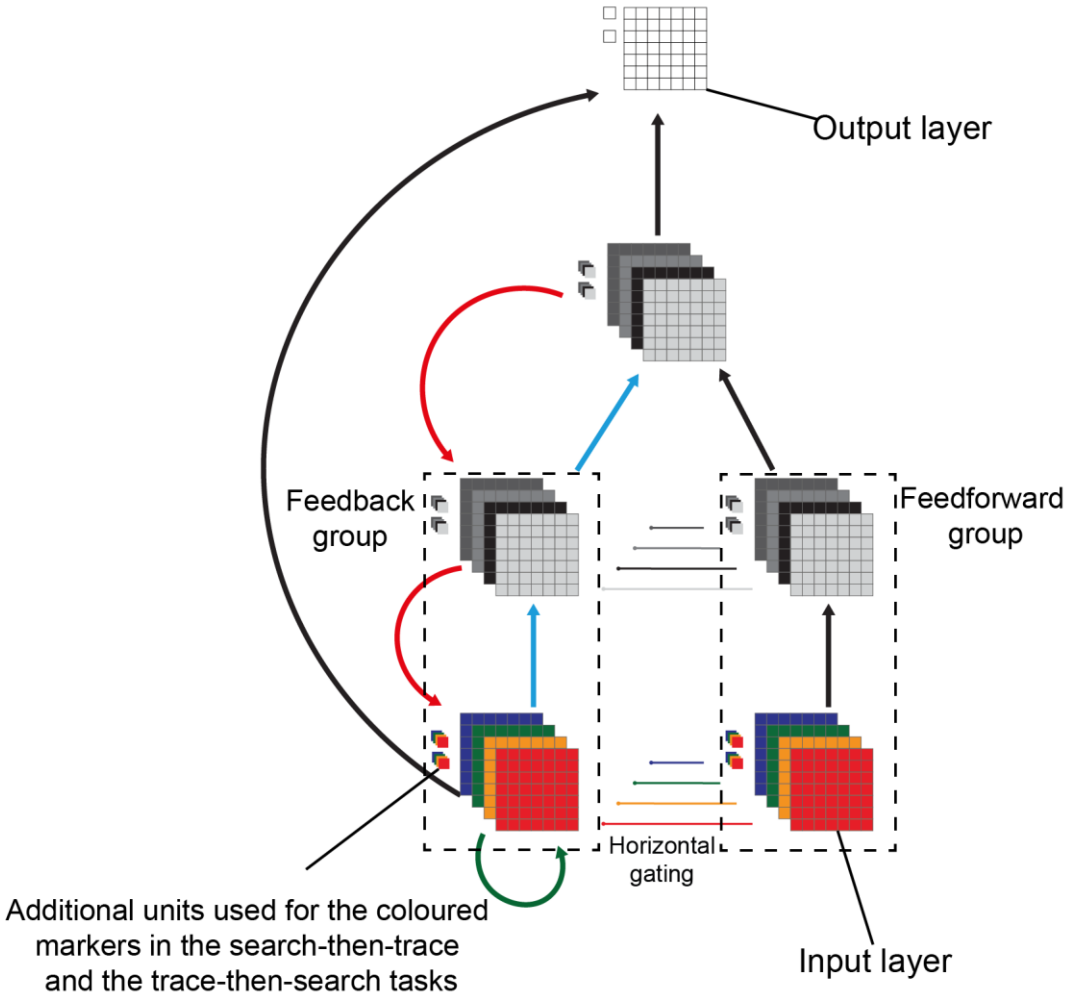

Fig. 2. Architecture of the network. The network comprises one input layer, two hidden layers and one output layer. The input and hidden layers have 4 features each. In each layer, neurons can belong either to the feedforward or to the recurrent group. The activity of units in the recurrent group is gated by horizontally input of neurons in the feedforward group so that they can not participate in the spread of activity in case the corresponding feedforward unit is inactive.

The activities of neurons in the feedforward group in layer *i* at timestep *t* were determined by activities of feedforward neurons in the lower layer at the same timestep. If *X* represents the activity of neurons in the feedforward group, *Y* the activity of neurons in the recurrent group, *i* the layer index (we call the input layer 'layer 0'), then the activity of neurons was determined by:

$$X^l(t) = \sigma\left(V \otimes X^{l-1}(t)\right) \tag{1}$$

$$Y^l(t) = \begin{cases} \sigma\left(\varphi(X^0(t)) \odot (U^1 \otimes Y^1(t-1) + H^0 \otimes Y^0(t-1))\right), & if\ l = 0 \\ \sigma\left(\varphi(X^l(t)) \odot \left(U^{l+1} \otimes Y^{l+1}(t-1) + T^{l+1} \otimes Y^{l-1}(t)\right)\right), & otherwise \end{cases} \tag{2}$$

Here σ is a nonlinear activation function and φ a gating function (see bellow), ⊙ represents an element-wise product between the activity of feedback and feedforward units and ⊗ indicates a convolution.

In the recurrent group, neurons in the input layer get horizontal input from the same layer at the previous timestep through H, while neurons in hidden layers get feedforward input from the preceding layer at the same timestep through T. The horizontal connections in the input layer carry color information and facilitate the learning of the search component in the search-then-trace and the trace-then-search tasks.

For connections between hidden layers, we used 3x3 convolution kernel, and enforced that neurons could only make connections to their Von Neumann neighbourhood (4-neighbourhood). As in convolutional neural networks the kernels were replicated across the entire input map which requires weight sharing, a property not present in biological neural networks (Pogodin et al., 2021). When we used weight sharing to train networks on the curve tracing tasks, networks learnt the task after an average of 19,000 trials, while without weight sharing, meaning that each kernel corresponded to one receptive field only on the input map, networks learnt the task in an average of 140,000 trials.To reduce the computation time we therefore trained networks while using weight sharing, and all results reported are obtained by training networks with weight sharing.

The last hidden layer was fully connected with the output layer and the recurrent input layer with weights linking units with the same RF initialized with positive values and between units with different RFs initialized with negative values, thereby biasing the winner-takes-all mechanism of the last layer, which stabilized learning.

The activity of neurons in the output layer was determined as:

$$Q = W^3 \otimes X^3(T) + W^0 \otimes X^0(T) \tag{3}$$

Where T is the timestep at which the network reached a stable state.

The output layer was organised retinopically. Units were uniquely associated with a saccade to one of the pixels of the stimulus grid and they learned to represent the also called Q-value (Sutton & Barto, 2018), which is the expected reward when the networks selected this position for an eye movement.

During training, the model chose the eye movement with the highest Q-value with probability $1 - \epsilon$. With probability ϵ the network explored other actions and sampled a random action from the Boltzmann distribution P_B:

$$P_B(a) = \frac{exp(q_a)}{\sum_k exp(q_k)} \tag{4}$$

ϵ was set to 0.05 across tasks and networks.

We trained the networks with RELEARNN (Brosch et al., 2015), which is a biologically plausible implementation of Q-learning that can be broken down in three phases. Upon presentation of the stimulus, the activity of the input neurons remains constant and activity propagates trough the recurrent connections of the network. If the activity of the units settled at a constant activity level, the action was selected, but we did not wait longer than 50 timesteps if the activity had not yet stabilized. When an action was selected, an “attentional” signal originating from the winning action was propagated through an accessory network to determine the influence of each neuron on the selected action. The network then gets a reward r from the environment and computes a reward prediction error δ that is determined by

$$\delta = r - Q_a \tag{5}$$

Where Q_a is the Q-value of the selected action.
This reward prediction error δ is broadcasted in the whole network by a neuromodulatory signal, such as dopamine (Schultz et al., 1997) and is thus available at all synapses. δ and the "attentional" feedback signal are combined to update the weights of the network, as will described below in the RELEARNN section.

Activation and gating functions

A popular activation function to train recurrent neural networks is the ReLU function because it alleviates the problem of the vanishing gradient (Glorot et al., 2011). However, ReLU functions offer no guarantees that the network will reach a stable state (Simard et al., 1989), which is a necessary condition for learning rules such as RELEARNN. On the other hand, squashing nonlinearities like sigmoid or tanh functions guarantee that the network reaches a stable state (Liao et al., 2018), but may suffer from the vanishing gradient problem, which might hurt performance (Linsley et al., 2020). To guarantee that our network reaches a stable state while mitigating the vanishing gradient problem, we used a ReLU-like function with a slope that decreases after a threshold:

$$\sigma(x) = \begin{cases} max(0, x), & x \leq 6 \\ log(1.5 \cdot x + 1) + c, & otherwise \end{cases} \tag{6}$$

Where c is set to $6 - log(10)$ to ensure that σ is continuous. We will describe below how the networks learn to label the target with a response enhancement. However, we observed that this process was hampered if the activation function was bounded from above if the curves were long. In that situation, units coding for all pixels reached the bound and the networks could not differentiate between the target and the distractor curve. The new activation function ensure that the network could also differentiate between long target and distractor curves.

The horizontal gating of feedback units by feedforward units, was also governed by a non-linear function. The activity of neurons of the feedforward units was passed through a continuous approximation of a step-function:

$$\phi(x) = \frac{100.x}{\sqrt{1 + (100.x)^2}} \tag{7}$$

RELEARNN

One of the most popular algorithms to train recurrent neural network is backpropagation trough time (Werbos, 1988, 1990). During the forward pass, the consecutive states of each neuron are memorized because they are needed to update the weights during the feedback pass. This algorithm is non-biological because it is neither local in time nor in space (Lillicrap & Santoro, 2019). The information needed to update the synaptic weights is not available at the relevant synapses and each neuron would need access to the history of previous activation levels. We therefore used RELEARNN (Brosch et al., 2015), which is a learning rule that is local in time and in space and equivalent to backpropagation in a reinforcement learning paradigm (Almeida, 1987; Pineda, 1987). RELEARNN uses a separate accessory "attentional" network with one accessory unit for every regular network unit (Fig. 3). On each trial, the output layer chooses one of the possible actions. The accessory units represent the influence of the corresponding regular units on this chosen action. Once an action has been chosen, the winning unit in the output layer activates a number accessory

units and thereby initiates the propagation of activity through the rest of the accessory network. The strength of a connection from unit A to unit B in the accessory network is proportional to the strength of the connection from unit B to unit A in the regular network so that the activity in the accessory network (dotted arrows in Fig. 3) equals the influence of regular units on the chosen action, once the accessory network converged to a stable state (Fig. 3, third phase, see Brosch et al., 2015 for details). Accessory units corresponding to regular units with a strong influence on the Q-value of the chosen action are very active and those that correspond to regular units that did not influence this Q-value are silent. The network of accessory units can thereby assign credit (or blame) to the regular units that are responsible for the outcome of the action. Changing the synapses between the regular units with a strongly active accessory unit will have the largest influence on the Q-value of the chosen action on later trials.

It is useful to distinguish between three phases on each trial (Fig 3). In the first phase, the stimulus is presented as a pattern of activity across the input neurons. Activity propagates trough the feedforward, horizontal and feedback connections among regular units until it converges to a stable state. At the end of this phase a presynaptic neuron *i* and a postsynaptic neuron *j* will have activity x_i^{∞} and y_j^{∞}. At the start of the second phase, an action is selected, which is represented by one of the regular units in the output layer. The corresponding unit in the motor layer of the accessory network is activated and activity is propagated within the accessory network until a stable state is reached (in our experience this phase can be terminated after a fixed number of timesteps; Liao et al., 2018). At the end of the second phase, neurons *i* and *j* in the accessory network have activity x_i^{acc} and y_j^{acc}, which is proportional to the influence of the corresponding regular units on the chosen action value (see Brosch et al., 2015 for a proof):

$$x_i^{acc} \propto \frac{\partial Q_a}{\partial x_i^{\infty}} \tag{8}$$

In the third phase, the network receives a reward if the correct action was selected, and no reward in case of an erroneous response. The reward prediction error is broadcasted trough the network using a neuromodulator and weights are modified according to a four-factor Hebbian learning rule:

$$\Delta w_{ij} = \delta \cdot x_i^{\infty} \cdot y_j^{acc} \cdot \sigma'\left(y_j^{\infty}\right) \tag{9}$$

It can be seen that the weight update of RELEARNN is local in space, as weights are modified using only pre and postsynaptic information, and local in time, as it's not necessary to keep a history of all the subsequent activities of a neuron, only the activity at the last timestep.

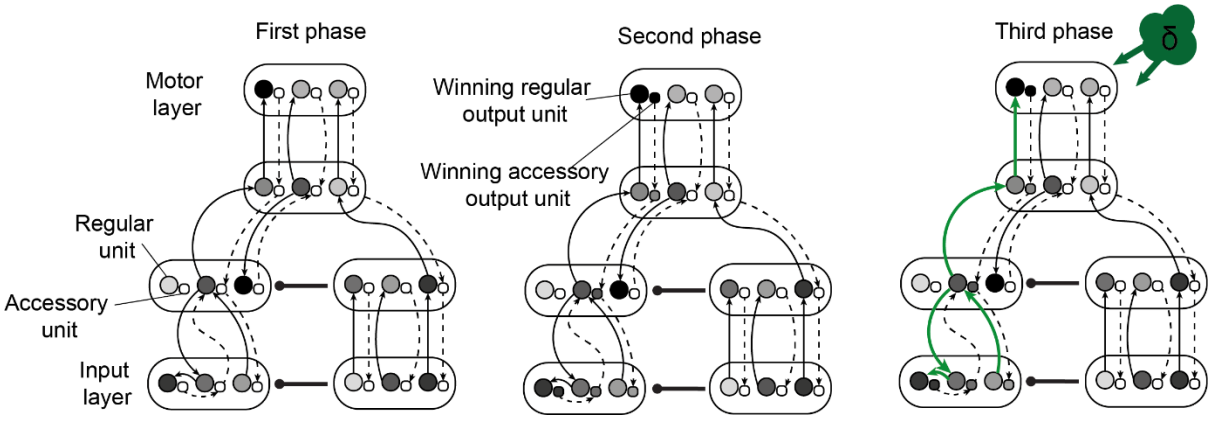

Fig. 3. RELEARNN in the network. In the first phase, activity propagates in the regular network that has both feedforward and recurrent connections (medium squares and plain arrows) until this network reaches a stable state. In the second phase, a winning unit is selected (black square in the motor layer) and activates the corresponding unit of the accessory network (small black square in the motor layer). From there, activity propagates in the accessory network (small squares and dotted arrows) to tag the connections that are responsible for the outcome in the first phase. After a few timesteps, activity in the accessory unit x_i^{acc} becomes proportional to the influence of the activity of the corresponding regular unit x_i^{∞} on the chosen output unit Q_a. In the third phase, a reward is given if the action was correct (or not in case of error) and a globally available neuromodulator (green cloud, d) broadcasts the reward prediction error to the network. Weights are changed according to a four-factor Hebbian learning rule.

Results

Curve-tracing task

We trained the networks with a curriculum to perform the curve-tracing task, a strategy that is also used to train monkeys. We first presented a stimulus with one blue and one red pixel, which were placed randomly on the grid, to train the network to select blue pixels as target for an eye movement. If the network achieved an accuracy of 85% during a test phase with 500 trials, fixed weights and without exploration, the network was trained with a target and a distractor curve with a length of three pixels. When the network achieved an accuracy of 85%, we added one pixel to the curves until the length of the curves was 9 pixels. Using this curriculum, we trained 24 networks and judged that they had learned the task if they achieved an accuracy larger than 85% for curves that were 9 pixels long.

We next aimed to gain insight into the strategy of the networks. The curves were drawn randomly at each trial (see Fig. 4A for an example stimulus). The number of possible curves grows exponentially with their length, and we therefore conjectured that it might be impossible to memorize all possible input patterns (Roelfsema et al., 1999). Instead, we hypothesized that the networks learned a general rule, which could be based on applying an elemental operations. To test this hypothesis, we exposed the networks to curves that were longer than those shown during training. When a network achieved an accuracy larger than 85% for curves of length N, we switched off exploration and tested curves with lengths ranging from N+1 to N+4. We found that the networks' accuracy was above chance levels for curves that were longer than the curves in the training set (Fig. 4B). For example, networks trained on curves up to a length of 9 pixels generalized to curves with a length of 13 pixels (red in Fig. 4B) ($p<10^{-6}$, Wilcoxon signed-rank test). This generalization emerged during training, indicating that networks learned to trace curves as an elemental operation that can be used to detect connected pixels for any stimulus (Roelfsema et al., 1999).

We next examined the activity of units of trained networks and compared it to the activity in the visual cortex of monkeys that had been trained on a similar curve tracing task (Roelfsema et al., 1998). We first compared the activity of networks units whose receptive field fell on the target curve to the activity of units whose receptive field fell on the distractor curve. By design,

the representation of the stimulus by units of the feedforward group is not modulated by curve-tracing, whereas units of the recurrent group can propagate enhanced activity (Fig. 4C). We examined the time course of the response modulation by comparing the activity of recurrent units elicited by pixels of the target (orange in Fig. 4C) and distractor curve (blue in Fig. 4C) at the same distance from the start of the curves. The time-point at which this difference becomes positive signals the moment at which the enhanced activity reached the representation of a particular pixel. After a delay the activity of units whose RF fall on the target curve is enhanced compared to units whose RF fall on the distractor curve.This result is quantitively similar to what is observed in the visual cortex of monkeys solving a similar curve-tracing task. Fig. 4D shows the average activity of V1 neurons in the visual cortex of monkeys elicited by a target curve (orange) and a distractor curve (blue). Initially, the neurons were activated by the appearance of a contour element in their RF, and this feedforward response was the same for the target and distractor curves. However, recurrent processing caused the V1 representation of the target curve to be enhanced over the representation of the distractor curve, after a delay of 130ms, adapted from (Roelfsema et al., 2003)

We quantified the magnitude of the response enhancement across 345,000 stimuli and the 24 networks that were trained successfully with a modulation index (Roelfsema et al., 1998), which is the difference between the response evoked by the target and distractor curve divided by the average response:

$$MI = \frac{Target - Distractor}{(Target + Distractor)/2} \tag{10}$$

A positive modulation index signifies an enhancement of activity evoked by the target curve relative to that evoked by the distractor curve. We observed that the recurrent units representing target pixels had a higher activity than those representing distractor pixels. The mean modulation index was 1.18, corresponding to an activity enhancement of 292% (Fig. 4E). This result is qualitatively similar to what has been observed in monkeys, although the increase in the representation of the target curve in area V1 of monkeys was weaker (Fig 4F, see also Roelfsema et al., 1998). It is of interest that the neural network replicated the spread of the enhancement of the activity across image elements of the target curve that is observed in the visual cortex.

In the visual cortex of monkeys, the enhanced activity spread iteratively, starting at the red cue at the beginning of the curve until it reached the end. Accordingly, units in the model representing pixels close to the beginning of the target curve enhanced their activity before units representing pixels that were farther away. To quantify the time-point of modulation, we used the moment when the difference between the activity elicited by the target and distractor curve became larger than 70% of its maximum (Fig. 4G). The distribution of modulation latencies across units confirmed that the onset of modulation was significantly later for pixels farther from the fixation point ($p<10^{-15}$, Mann-Whitney U test). Interestingly, the time course of modulation for units in the output layer of the network was similar with a gradual propagation of enhanced activity over the target curve (Fig. S1).

The modeling results resemble observations in the visual cortex of monkeys, where neurons with receptive fields farther along the target curve enhanced their activity later than neurons with RFs closer to the start (Fig 4H). Furthermore, the latency of the response modulation in the frontal eye fields of monkeys, which is an area involved in the planning and generation of eye movements, was also similar to the latency of the response modulation in the visual cortex (Khayat et al., 2009; Pooresmaeili et al., 2014). Our results show that the neural network learned a strategy that is also implemented in the visual and frontal cortex of monkeys, spreading enhanced neuronal activity along the entire target curve. In the model, spreading is iterative and relies on horizontal and feedback connections, which makes the

process generalizable across stimuli and curve lengths, in spite of the limited network depth. The results are also in line with the results by Jolicoeur et al. (1986) showing that the reaction times of human observer in a curve-tracing task increase linearly with the length of the curve that needs to be traced.

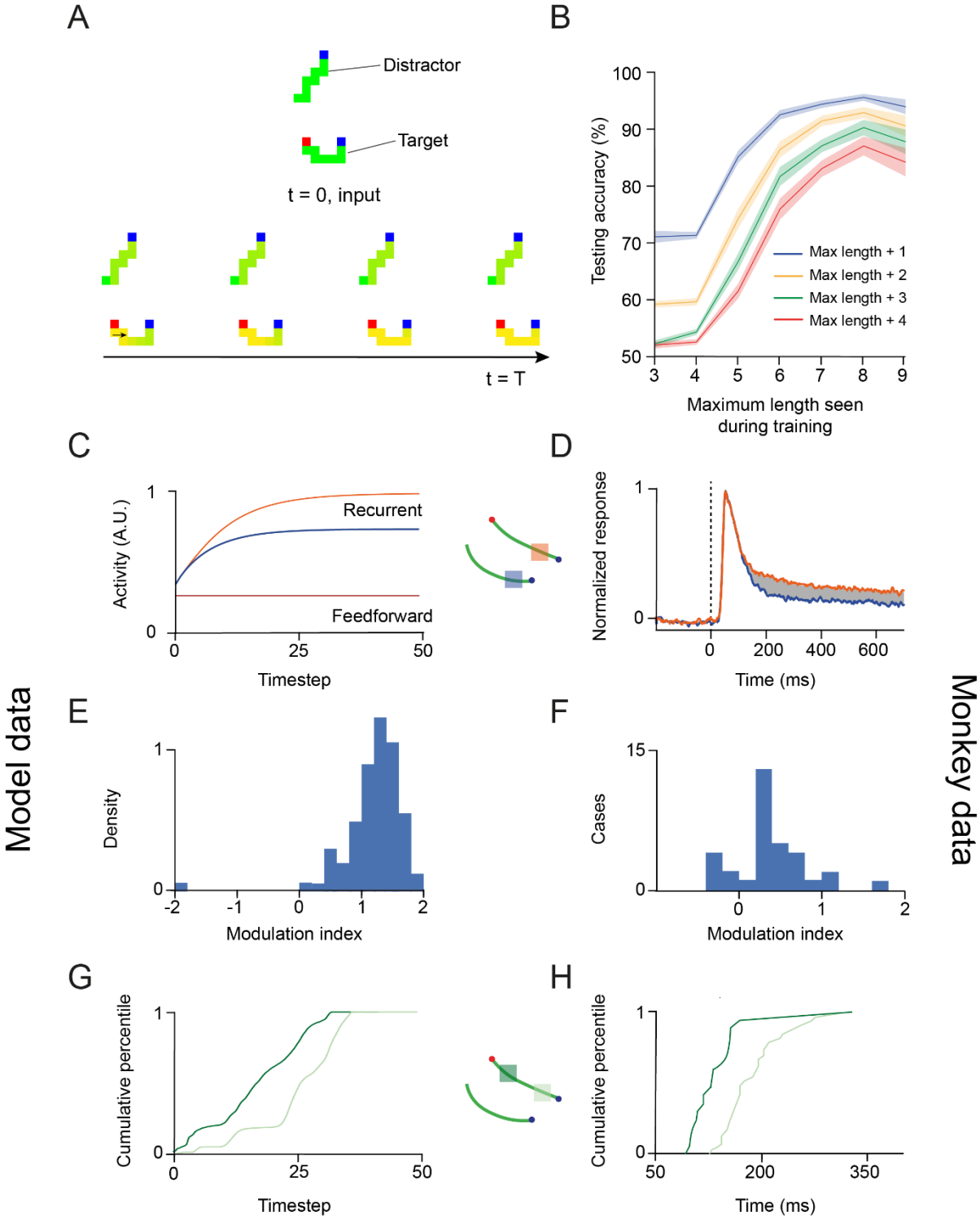

Fig. 4. Propagation of enhanced activity across the representation of the target curve during curve-tracing.). **A**. Example stimulus shown to an example network. Overlayed in yellow is the activity of neurons in the recurrent input layer across time. Note how the activity of neurons whose receptive field fall on the target curve is higher than the activity of neurons whose receptive field fall on the distractor curve, and how it spreads from the red cue. **B**. Testing accuracy for curves of length up to N+4 pixels where N is the maximum length that has been seen during training. At the beginning of training, the agent cannot generalise to longer curve. At the end of training, even though the agent has been trained on curves up to 9 pixels long, it could solve the tasks with curves up to 13 pixels with above chance accuracy. The agent has learnt an abstract, general rule that can be applied irrespectively of the parameters used ($p<10e-6$, at the end of training for 13 pixels long curves, Wilcoxon signed-rank test). **C**. Activity of an example unit in the recurrent group elicited by the target (orange) or distractor curve (blue), and activity of the corresponding unit in the feedforward group (brown). Note that the activity elicited by the target curve is enhanced compared to that elicited by the distractor curve**. D**. Average activity of neurons in the visual cortex during a curve tracing task, when their receptive field fall on the target curve (orange) or on the distractor curve (blue). Adapted from (Roelfsema et al., 2003) **E.** Distribution of the modulation index across recurrent units of the neural networks. A positive value indicates an enhanced response to the target curve. **F**. Distribution of modulation index in area V1 of the visual cortex of monkeys (from Roelfsema et al., 1998) **G**. Distribution of the modulation latency across units of the network. The onset of modulation is delayed for units representing pixels that are farther from the beginning of the curve ($p<10^{-15}$, Mann-Whitney U test). **H**. Distribution of the modulation latency across recording sites in monkeys performing the curve-tracing task, adapted from Pooresmaeili & Roelfsema, 2014.

How does the network learn to trace, i.e. to group pixels into curves, when the only feedback after each trial is the presence or absence of a reward? To understand the learning process enabled by RELEARNN, we examined the activity of the accessory network units that influence learning. Figure 5A illustrates how the activity propagates among the accessory units that represent the selected curve, starting from the selected eye movement and then across the representation of other pixels of this curve. This strength of this accessory signal represents the influence of the units of the regular network on the selected action. If the network happens to select the target curve, the connections between regular units are strengthened in proportion to the reward-prediction error δ. If the network erroneously selects the distractor curve, the credit assignment signal ensures that that the recurrent connections among units representing this curve are weakened. The unique and distinguishing feature of the target curve is that it starts with a red pixel, and the credit assignment signal of the accessory network ensures that the representation of this red pixel becomes the source of activity propagation in well-trained networks during learning.

An analysis of the spread of activity within the accessory network also provides insight in the role of the curriculum. If the network has been trained with curves up to a certain length N, and is tested with curves that have N+1 pixels, the credit assignment signal reaches the fixation point if the model selects the appropriate eye movement and the relevant connections increase in strength (Fig. 5B, left). However, when we presented curves with N+5 pixels, the signal at the beginning of the curve did not discriminate between the target and distractor curves and learning did not occur (Fig. 5B, right). Hence, training was more efficient with a curriculum in which we gradually increased the length of the curves.

Let us briefly summarize how the network learns to solve the curve-tracing task. Upon presentation of the stimulus, the network starts with a feedforward processing phase which does not discriminate between the target and the distractor curve. This early activity pattern has been called ‘base representation’ (Roelfsema, 2006). During the later, recurrent processing phase, recurrent units learn to propagate enhanced activity along the representation of the target curve, starting at the fixation point, with its unique color. This enhancement of activity cannot spill over from the target curve to nearby curves because feedforward neurons that respond to image locations that are not occupied by a pixel are silent. The activation of these feedforward neurons is necessary before the recurrent units can activate. In other words, the gating process of the base representation ensures that recurrent activity can only spread along the representation of connected pixels.

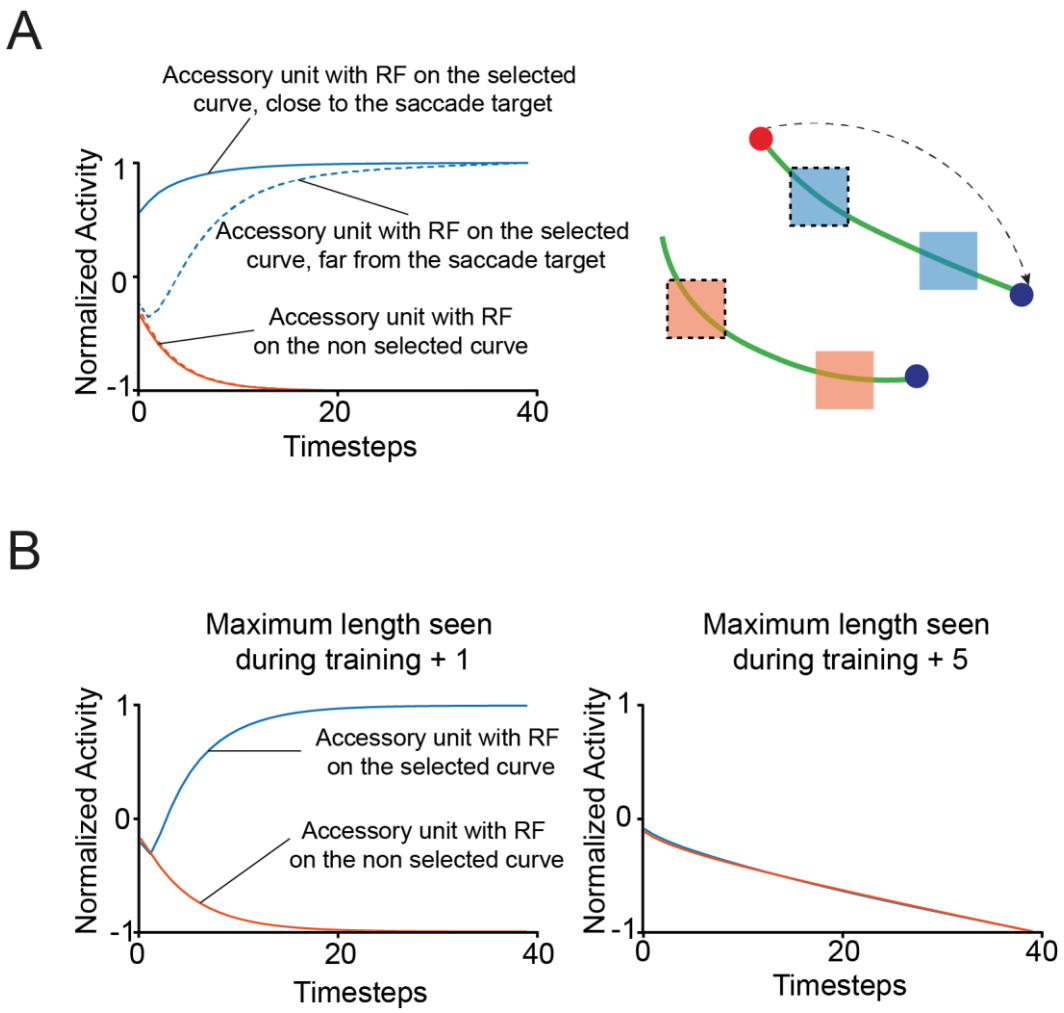

Fig. 5. Activity in the accessory network. A. Activity of neurons in the accessory network whose receptive field fall on the selected curve (blue lines) or the non-selected one (orange lines), at different distances from the blue pixel that is target of the eye movement (continuous and dotted traces show the activity of accessory units representing pixel nearer and farther to the saccade target, respectively). Hence, the credit assignment signal propagates in the opposite direction compared to the enhanced activity, starting from the selected eye-movement target. This credit assignment signal is absent from the representation of the distractor curve. **B.** Activity of neurons corresponding to the beginning of the selected and non-selected curves in the accessory network, for curves that were one (left panel) or five pixels longer (right) than the curves used in training. If the length of the curve was similar to the curriculum that was used, the credit assignment signal propagates to the beginning of the target curve and training is effective. However, if the target curve is much longer, the credit assignment signal does not reach other pixels of the target curve and training fails.

Search-then-trace task

Having established that the networks learned to trace curves, we sought to explore more complex multistep visual routines that require the succession of multiple elemental operations, and the transfer of information between them. The search-then-trace task required a visual search for a colored marker followed by curve-tracing. In the task for the model, the color of relevant markers was orange or red and its color cued by activating one of two input units (color cue in Fig. 6A). The network had to trace the target curve starting at the relevant marker and to select an eye movement to the blue pixel at the other end of this curve.

We trained the network using a curriculum that was similar to the one used for the trace task. First, we presented a stimulus of one blue pixel and one red pixel randomly placed on the grid. If the network achieved 85% accuracy during a 500 trials test phase with weights fixed and no exploration, we presented a target and a distractor curve with a length of three

pixels, where one of the two curves started with an orange pixel and the other one with a red pixel. If the network achieved 85% accuracy during the test phase, we added one pixel to the curves and repeated the operation until the curves were 9 pixels long.

We trained 24 networks and 79% of them learned the task within an average of 40,000 trials. Just as in the curve-tracing task, the networks learned a solution in which they generalized across different shapes of the curves and for two colors that had to be searched. Trained networks generalized to curves that were 4 pixels longer than the ones presented during training (Fig. 6B, red curve, $p<10^{-4}$, Wilcoxon signed-rank test).

How does the network learn to transfer information between elemental operations such that the output of an elemental operation becomes the input of the next one? In the visual cortex of monkeys, this information transfer appears to take place by the persistence of enhanced neuronal activity between the elemental operations. In the search-then-trace task, the visual search for the marker with the cued color enhances the activity of neurons with a RF at this marker (Fig. 1, search-then-trace task), as if it is ‘written' to the cognitive blackboard of early visual cortex. The subsequent tracing operation can ‘read’ this position and use it as the start the curve-tracing operation.

Interestingly, the model discovered a similar method to transfer information between the successive search and trace operations. In the model, recurrent processing started with an enhancement of the representation of the target marker (see Fig.6A for the spread of activity across time in the recurrent input layer of an example network for an example stimulus, red trace in Fig. 6C). This search operation was made possible by the horizontal connections in the recurrent input layer (Fig. 2). Color-selective connections between the 2 additional units and the rest of the grid enabled the network to transfer information between the curves and the color cue. Without the horizontal connections in the recurrent input layer, the networks could not learn the search-then-trace task. After the search operation, the enhanced activity propagated across the representation of the target curve (Fig. 6A, green traces in Fig. 6C). The time course of activity propagation in the output layer was similar to that in the visual layers of the model (Fig. S1). We next examined the onset of enhanced activity of the units across 260000 stimuli and 19 networks. This analysis revealed that the early enhancement of units with a RF on the target marker (red in Fig. 6E), followed by the propagation of enhanced activity across the target curve (green in Fig. 6E) was a general feature. Fig. 6F shows similar results that were observed in area V1 of the visual cortex of monkeys (Moro et al., 2010). Also in the monkey visual cortex, the marker with the relevant curve is first labeled with enhanced activity, before activity spread across the V1 representation of the target curve.

These results, taken together, indicate how RELEARNN, which is biologically plausible reinforcement learning rule, can train networks to execute a visual routine composed of multiple elemental operations and to use persistent enhanced activity to transfer information from one element operation to the next.

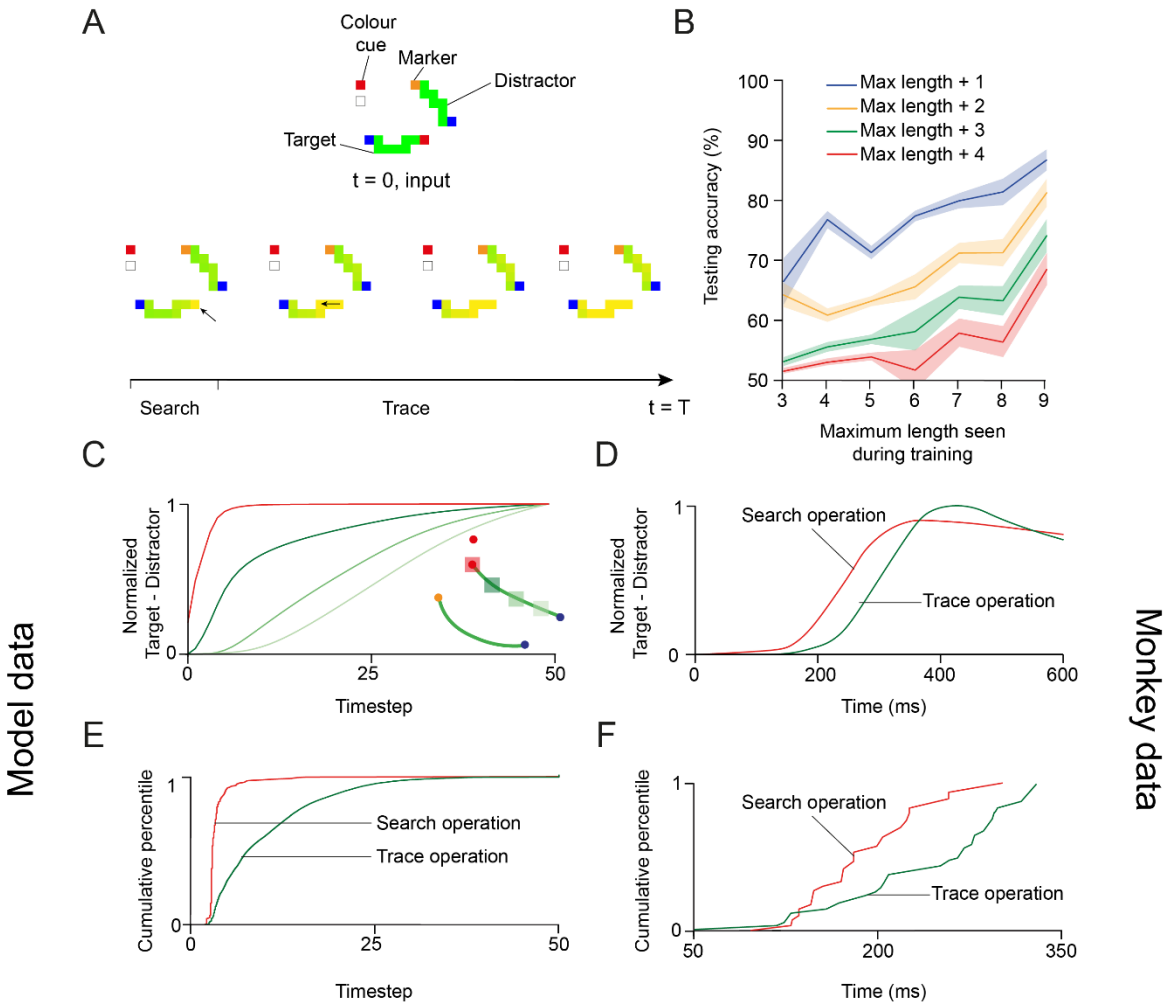

Fig. 6. Search-then-trace task. A. Example stimulus shown to an example network. Overlayed in yellow is the activity of neurons in the recurrent input layer across time. The enhancement of activity first reach the red marker, which corresponds to the search operation, before spreading along the curve, which corresponds to the trace operation. **B.** We tested how well the models generalized to curves that were longer than those used during training. Generalization was better for networks that had been trained on longer curves (x-axis). E.g. networks trained on curves up to a length of 9 pixels generalized to curves with 13 pixels ($p<10^{-6}$, Wilcoxon signed-rank test). **C**. Normalized response enhancement for the target marker and target curve. Each curve is normalized by its maximum over time. First the activity of the unit with a RF at the location of the target marker was enhanced (search operation, red curve). Thereafter, enhanced activity propagated across the target curve connected to it (trace operation, green curves). **D**. In the visual cortex of monkeys, the representation of the target marker is enhanced (red) before the enhanced activity spreads over the V1 representation of the target curve (green; adapted from Moro et al. 2010). **E**. Distribution of the latency of the response enhancement across 260 000 stimuli and 19 networks. The latency of the modulation related to the search operation was shorter than that related to curve-tracing ($p<10^{-15}$, Mann-Whitney U test). **F**. Distribution of the latency of response enhancements across V1 neurons in monkeys solving the search-then-trace task (adapted from Pooresmaeili & Roelfsema, 2014).

Trace-then-search task

We next examined if the network could learn a different visual routine to solve the trace-then-search task. This task requires the same elemental operations as in the search-then-trace task, but they now need to be applied in the opposite order. First, the agent has to trace the curve connected to the fixation point, which was blue. This target curve ended with a marker that was either red or orange and indicated the color that the model had to search for. The model had to select the pixel with the same color as the target marker, which was visible on the side of the grid (Fig. 1, trace-then-search task).

We adapted the curriculum by first training the networks on simple curve-tracing tasks in which the target curve started with a blue pixel, and the two curves ending with a red and an orange marker. When the networks had learned to trace curves with a length of 9 pixels, we added the two colored pixels outside the grid and required the model to select the pixel with the same color as the target marker for an eye movement.

We trained 24 networks on this task and 66% learned the task after an average of 37,000 trials. As in the previous tasks, the networks learned a general solution, which did not depend on the position and color of the marker and the shape of the curve. Trained networks also performed the task for curves that were 4 pixels longer than the stimuli that were part of the curriculum (Fig. 7B, $p=1.4\cdot10^{-4}$ for curves with a length of 13 pixels, Wilcoxon signed-rank test).

Trained networks first spread activity along the target curve until its end was reached (see Fig. 7A for the spread of activity across time in the recurrent input layer of an example network for n example stimulus, Fig. 7C green traces) and the target color could be identified. The enhanced activity then spread to colored eye movement target, as the outcome of the search operation. (Fig. 7A, Fig. 7C red trace). Hence the networks learned to first perform a trace operation, followed by a search operation. As in the previous tasks, the time course of modulation in the output layer followed a similar pattern (Fig. S1). The progression of activity was also evident when we examined the activity across 230 000 stimuli in the 16 networks that were trained successfully. The green trace in Figure 7E illustrates the time-point in which the activity of the representation of the last, colored pixel of the curve was enhanced, which corresponds to the output of the curve-trace operation (green curve). Thereafter, the representation of the colored eye-movement target was enhanced, corresponding to the realization of the search operation (red curve in Fig. 7E). The results are qualitatively similar to those in the visual cortex of monkeys trained on the trace-then-search tasks, where the enhanced neuronal activity first spread along the target curve (Fig. 7F, green trace), before the V1-representation of the colored disk that was the target of the eye movement was enhanced (Fig. 7F, red curve).

These results indicate that RELEARNN can train networks to carry out elemental operations in different orders depending on the task at hand, which is remarkable for a biologically inspired learning rule in which the only feedback that the networks receive is a reward upon a correct choice.

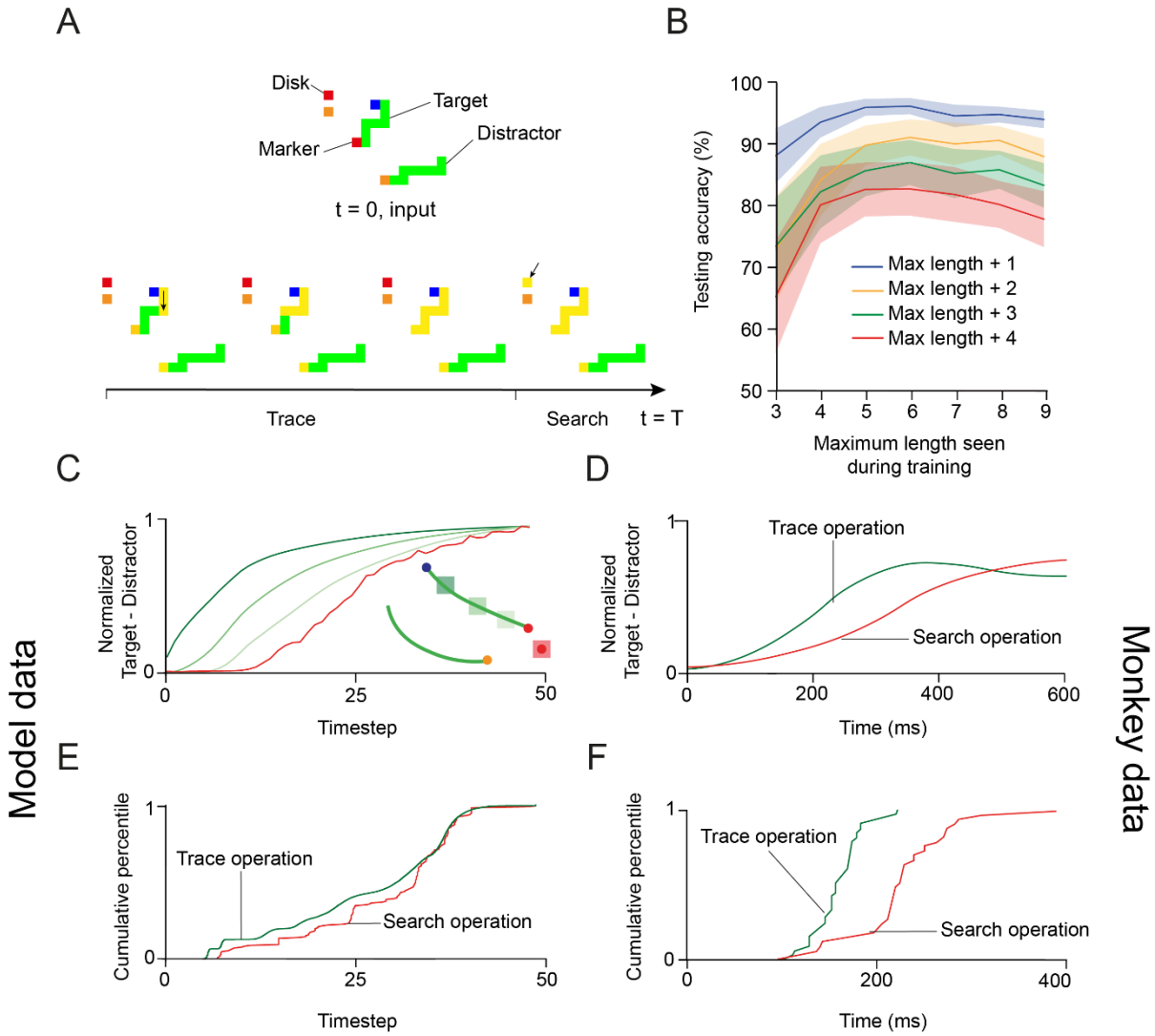

Fig. 7. Model performance in the trace-then-search task. . A. Example stimulus shown to an example network. Overlayed in yellow is the activity of neurons in the recurrent input layer across time. The enhancement of activity first spreads to the curve connected to the blue cue, which corresponds to the trace operation, before spreading to the read disks, which corresponds to the search operation. **B.** Testing accuracy for curves of length up to N+4 pixels where N is the maximum length that was part of the curriculum. The generalization performance improves when the network learns to trace longer curves, indicating that it learned a general rule ($p=1.5\cdot10^{-4}$ for curves of 13 pixels, Wilcoxon signed-rank test). **C**. Normalized response enhancement for target pixels, averaged across units. Each curve is normalized by its maximum over time. First the curve connected to the fixation point is labeled with enhanced activity (trace operation, green curves) and then the units that represent the correct eye movement target, i.e. with has the same color as the target marker, enhanced their activity (search operation, red trace). **D**. In the visual cortex of monkeys, the response enhancement also first labels the segments of the target curve (green trace), before it labels the position of the eye movement target (red trace; adapted from Moro et al., 2010). **E**. Distribution of the modulation latency across model units (230 000 stimuli and 16 networks). The response modulation of trace operation precedes that of the search operation ($p=1.5\cdot10^{-5}$, Mann-Whitney U test). **F**. Distribution of the modulation latency across recording sites in monkeys solving the search-then-trace task, adapted from Moro et al., 2010.

Discussion

We studied how visual reasoning tasks can be learned by trial and error, using a biologically plausible learning rule. We took inspiration from previous work on visual routines, which are built from elemental operations (Ullman, 1984). Studies of the visual cortex revealed that the elemental operations, like curve-tracing and visual search, are associated with the

enhancement of neuronal activity elicited by target elements over distractor elements. Specifically, curve-tracing is associated with the spread of enhanced activity across a target curve and visual search results in an activity enhancement of the representation of the target of search. We found that the neural network that were trained on curve-tracing and on visual routines that required search and curve-tracing developed a similar strategy of successive labeling task-relevant image elements with enhanced neuronal activity. We also studied how these networks learned to transfer information between one elemental operation and the next and observed that the strategy of labeling image elements with enhanced activity also provided the necessary information transfer, because the focus of enhanced activity was used to start the next elemental operation, providing a mechanisms that is equivalent to the transfer and the binding of parameters to subroutines in a computer program.

The model architecture incorporated a feedforward group of units that is only sensitive to input from lower layers, and a recurrent group that also receives feedback connections from higher layers and from horizontal connections from units in the same layer. Non-zero activity of units in the feedforward group allows the corresponding recurrent units to be also active, implementing a form of gating of units of the recurrent group. This gating process prevents that recurrent activity can spill over to units that represent the blank screen, helping with the sensitivity of the propagation of activity among the units that represent connected image elements. A comparable division of labor has been observed in the visual cortex, where some neurons are influenced by curve-tracing and other neurons are not (Pooresmaeili et al., 2010). The neurons that are and are not sensitive to recurrent processing are clustered in the different layers of cortex, as has been observed during curve-tracing and figure-ground segregation tasks (Self et al., 2013; Van Kerkoerle et al., 2017). Neurons that are most sensitive to the feedforward input are enriched in layers 4 and 6, whereas the influence of figure-ground segregation and visual attention are more pronounced in the superficial layers 2 and 3 and in layer 5 (Self et al., 2013; Van Kerkoerle et al., 2017). Thus, the feedforward group could correspond to neurons in layers 4 and 6 while the recurrent group could correspond to neurons in layer 2, 3 and 5. This view is supported by recent experimental evidences for the existence of separate channels for feedforward and feedback processing, suggesting that these influences might be mediated by partially non-overlapping neuronal circuits (Semedo et al., 2022)

We used RELEARNN to train the networks. RELEARNN is a biologically plausible learning rule that is equivalent to the Almeida-Pineda algorithm, but it is local both in space and in time so that all the information that is necessary for the synaptic changes are available at the synapse. The learning rule relies on two networks. The first network is active during inference when activity propagates through feedforward and recurrent connections, during the processing of the stimulus. The second network is an accessory network, dedicated to help with the learning process. The activity is initiated by the action that is selected in the output layer and it then propagated through the network, emphasizing the synapses that have a strong influence on the activity of the winning output unit. When the activity in the main and accessory networks is combined with the reward prediction error, which can be mediated by a globally released neuromodulator such as dopamine, all the information for the synaptic update is available locally at the synapse. In previous work RELEARN was shown to train networks in the curve-tracing task (Brosch et al., 2015) and here we showed that it is powerful enough to train networks on more complex, multistep tasks.

It is of interest that the networks developed strategies that are similar to those observed in the visual cortex of monkeys. During the curve-tracing recurrent units in the lower and higher layers propagated enhanced activity along the representation of the target curve. This finding resembles how curve-tracing is implemented in the visual cortex of monkeys, where the neurons with RFs on the target curve successively enhance their activity, starting at the beginning of the curve and the spreading process continues until the response enhancement

reaches the end of the curve. These responses enhancements occur in multiple cortical areas including the frontal cortex, where the correct eye movement is selected (Pooresmaeili et al., 2014). Furthermore, the model implemented visual search by enhancing the activity of units coding for the relevant color, which then ultimately led to an enhanced representation of the location where this color was found, just as is observed in the visual cortex responses (Chelazzi et al., 1998, 2001; Desimone & Duncan, 2003; Mirpour & Bisley, 2012; Sato et al., 2001; Zhou & Desimone, 2011). Finally, this propagation of enhanced activity was used by the model to transfer information from one elemental operation to the next, just as is observed in the visual cortex of monkeys.

The present study builds on results from previous studies that used artificial neural networks to solve sequential visual tasks. Marić & Domijan (2019) configured a model to trace curves and they also combined feedforward and recurrent network units. They examined the activity propagation along curves but they did not examine learning of the curve-tracing task. In their network, tracing could proceed faster for target curves that were farther from a distractor curve than for target curves that were near to a distractor. This result reproduced psychophysical and neurophysiological data showing that tracing speed increases in proportion to the distance between curves (Jolicoeur et al., 1991; Pooresmaeili & Roelfsema, 2014). Such a scale dependence could rely on the hierarchical organization of the visual cortex where neurons in higher areas have larger receptive fields. If curves are far apart, activity can propagate with the involvement of neurons at higher levels with larger RFs, whereas if the curves are nearby, activity could propagate at a lower level, where the spatial resolution is higher, but at the cost of increased processing times (Roelfsema & Houtkamp, 2011).

Linsley et al. (2019) trained recurrent neural network on a pathfinder task, which resembles curve-tracing, but now the curves consists of shorter, disconnected line elements. Their network had to determine whether two dots were on the same curve. The authors demonstrated that a recurrent unit, called h-GRU (Mély et al., 2018), which activates based on feedforward connections but also integrates horizontal input, was useful to solve the task. Unlike the present study, the authors used backpropagation through time, which is a non-local learning rule that requires a teacher. Instead, in the present work we used RELEARNN, which is a biologically plausible learning rule. In addition, we analyzed the strategies that emerged after training and trained networks on visual routines, in which curve-tracing was combined with visual search. Although we focused on curve-tracing, future modeling studies may also examine other tasks in which objects surfaces need to be grouped in perception. For example, Jeurissen et al. (2016) found that the time it takes to determine whether two dots are on the same surface increases with the distance between the dots. The same principle that enables our network to trace curves could be expanded to enable networks to group 2D image regions, which are important in real-life scenarios, and they might even be generalized to more complex situation that require semantic segmentation.

In conclusion, the new model architecture illustrates the versatility of networks that spread enhanced activity to solve elemental operations and to glue them together into visual routines, ensuring the transfer of the relevant parameters. The similarity between the network activity and neurons in the visual cortex indicate that the approach provides insight into how the circuits in the visual brain can configure themselves during the learning, based on biological plausible learning rules that combine attentional feedback and neuromodulatory signals. Future studies could expand this approach to further elucidate how feedforward, feedback, horizontal and lateral connections are used to enhance the cognitive capabilities of brain networks.

Methods

Data Analysis

We trained 24 networks for each task. For the analysis, we only kept networks that learned the tasks for curves up to 9 pixels long. We froze the weights after training and set the exploration rate ϵ to 0. We presented 15,000 randomly generated stimuli to each network and analyzed the activations of the units for these stimuli, including only correct trials in the analysis.

Parameters

All networks were initialized and trained with the same parameters. They are summarized in the following table

Parameter	Value
Learning rate δ	0.02
Exploration rate ϵ	0.05
Weights between hidden layers	Sampled from U(0,0.1)
Weights between the last hidden and the output layers, same receptive field	Sampled from U(0,0.1)
Weights between the last hidden and the output layers, different receptive field	Sampled from U(-0.01,0)

Here U(x,y) refers to the uniform distribution on the interval [x,y].

Code availability

All the code used to train the networks and to analyze the data is available on the following GitHub address: https://github.com/samimol/Visual-Routines

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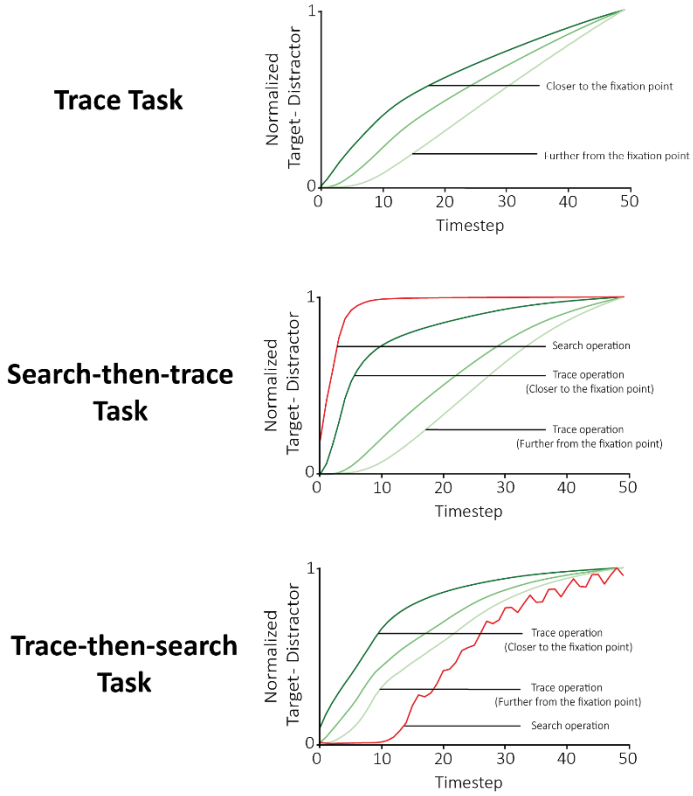

Fig. S1. **Time course of activity modulation in the output layer.** In the output layer, the enhancement of activity of units with RFs on the target curve followed the same time course as neurons in the lower layers. Hence, the time required for spreading activity in the visual layers predicts the reaction time. These results are compatible with the reaction time measurements in humans by Jolicoeur et al. (1986. They demonstrated that the reaction time increases in proportion to the length of the curve that needs to be traced.