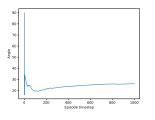
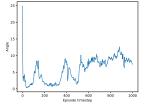
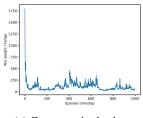
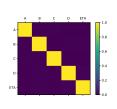
**Reviewer 1** asked if the weights are effectively learning to relax to the same steady state from random initial conditions.

- We performed an analysis to be added to the appendix (Fig. 1a,b), which shows that for two different runs the weights
- start being perpendicular –since randomly initialised– and thereafter the n-dimensional angle between the weights is not
- zero. Thus the weights are not effectively relaxing to a fixed set of values but rather change based on the environmental
- input. Additionally, the absolute weights of a particular network keep changing as well (Fig. 1c)









(a) Quadruped: weight angle

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(b) Car: weight angle

(c) Car: magnitude change

(d) Coefficient Correlations

Figure 1

Following Reviewer 1's suggestion of having both the initial condition and plasticity rules optimized, we performed 6 evolutionary runs in the car-racing environment; 3 of them converged to high-performance solutions ( $879 \pm 69$ ), and 3 of them did not  $(13 \pm 2)$ . This suggest that evolving both at the same time could be more challenging (all random+Hebbian runs always found a high-performing solution). We are currently running the same experiments for the ant, but they are unfortunately not finished yet.

Reviewer 2 noted that "it would be quite interesting if the authors could expand more their analysis of the evolved plasticity rules." We performed a correlation analysis of the evolved Hebbian coefficients and found no correlation 12 between them –neither Pearson's r nor Spearman's  $\rho$ –, suggesting that the coefficients are independent with no obvious 13 internal structure in the learning rules (Fig. 1d). We are currently investigating if frequent pattern mining methods (e.g. apriori algorithm) could reveal additional insights. 15

**Reviewer 3** said to "find it difficult to relate the Hebbian plasticity rules that are considered in this paper to rules for synaptic plasticity in the brain that have been found in neuroscience" arguing that "synaptic plasticity in the brain appears to rely often on a multitude of gating signals, and on the relative timing of pre- and postsynaptic activity." The most studied plasticity mechanism in neuroscience is spike-timing-dependent plasticity (STDP). However, STDP isn't the only plasticity mechanism that has been observed in the brain.

NNs with continuous outputs are usually interpreted as an abstraction of spiking neural networks in which the continuous output of each neuron represents a spike-rate coding average (instead of spike-timing coding) of a neuron over a long time window or, equivalent, of a subset of spiking neurons over a short time window (in this scenario, the relative timing of the pre and post-synaptic activity doesn't play a central role anymore 1. Spike-rate-dependent plasticity (SRDP) is well documented phenomena in biological brains <sup>2</sup> <sup>3</sup>. That being said, our goal is not to provide a detailed model of plasticity mechanisms in biological brains, but rather to demonstrate that evolved local rules can show adaptability and yield competitive results. Additionally, in contrast to earlier work that restricted learning rules to only four different hand-designed types (ref [30]), we evolve arbitrary synapse-specific Hebbian rules.

Reviewer 4 objected to the claim that the Hebbian approach led to greater generalization due to the fact the system was optimized for all the morphologies. Following this fair critique, we launched a new set of experiments where one of the damaged morpgologies was left out during training. While the static network only managed to solve the morphologies it had seen during the training phase, the Hebbian network -to our surprise- managed to solve all three of them in each of 3 different evolutionary runs. On the unseen morphology the Hebbian approach reached a performance of  $471\pm87$ compared to the static-network performance of  $31 \pm 46$ . We believe that this adaptation to the unseen morphological changes provides evidence of greater generalisation for the Hebbian network in relation to the static-weights one.

We ran an ablation where the Hebbian parameters are shared among neurons in one layer for the car environment: all 3 evolutionary runs resulted in poor performance (max reward  $13 \pm 2$  as opposed to  $870 \pm 13$  with individual learning rules). This suggests that a higher number of parameters is important for the agents to adapt. **Reviewer 4** argued that due to the rotational symmetry of the ant, the under-performing runs shouldn't always be the same morphology: the reported results are averages across 100 rollouts of the best solution, which had visibly evolved to favour one of the damaged morphologies; in other evolutionary trains the favoured morphology changed, which we will clarify in the paper. We finally thank the reviewers for their careful read and will subsequently correct the equation after line 149.

Brette, 2015. Philosophy of the Spike: Rate-Based vs. Spike-Based Theories of the Brain. Frontiers in Systems Neuroscience

<sup>&</sup>lt;sup>2</sup>Sjöström et al., 2001. Rate, timing, and cooperativity jointly determine cortical synaptic plasticity. Neuron

<sup>&</sup>lt;sup>3</sup>Prescott et al., 2008. Spike-Rate Coding and Spike-Time Coding. Journal of Neuroscience