

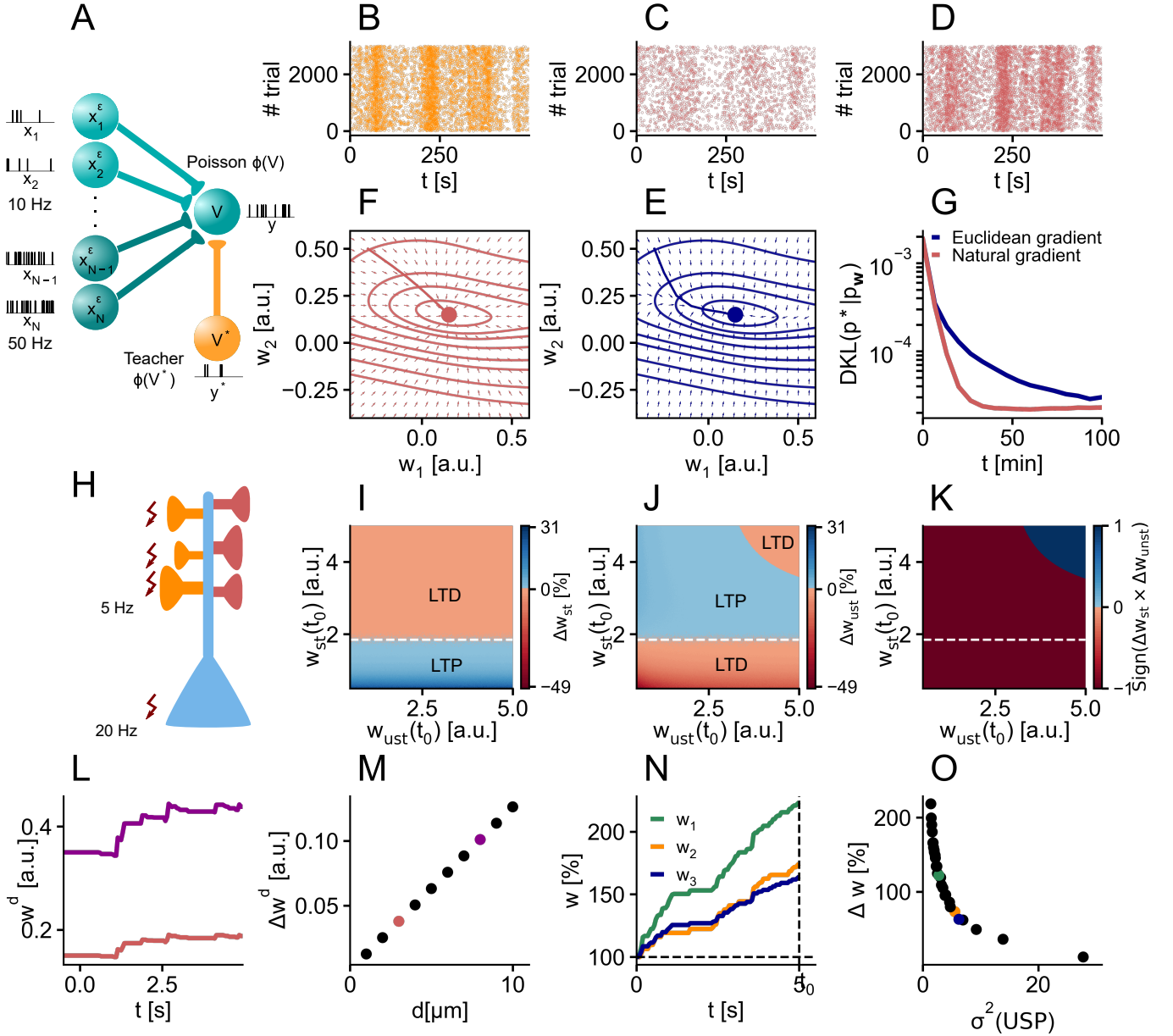
**Abstract** Gradient based plasticity rules depend, in general, on how and where the impact of a synapse is measured. Given the complexity of neuro-synaptic morphology and dynamics, this may greatly affect the predicted change in neuronal output. We argue that a consistent model leaves the latter invariant, optimizing synaptic plasticity directly in terms of neuronal output distributions. Such a plasticity rule can be obtained by applying the natural gradient framework (Amari 1998) to learning with spiking neurons. We derive the natural gradient plasticity rule and investigate it from a biological perspective, demonstrating that it exhibits faster convergence compared to classical gradient based learning. Furthermore, natural gradient predicts plasticity phenomena such as learning rate scaling in distal dendrites and provides a unified framework for both homo- and heterosynaptic plasticity. Investigating the interaction of both plasticity types in a simple learning task, we observed a counterbalancing, qualitatively similar to in-vivo experimental findings (Royer & Paré 2003).

**Additional Detail** Due to their simplicity and their success in machine learning tasks (Rumelhart, Hinton, Williams 1986), gradient based learning rules represent a popular choice for synaptic plasticity models. While they have been linked to biological phenomena such as STDP (Pfister 2006), it is often ignored that their predictions generally depend on a specific representation of the synaptic strength (Amari 1998). Unlike in an artificial neural network, where the weight of a synaptic input is just an abstract variable, in a neuron, the impact of a synapse corresponds simultaneously to the state of many physical quantities inside the cell. Which one we choose to derive a gradient descent learning rule can have a remarkable effect in terms of model prediction (Surace and Brea 2018). This is dissatisfying both from the viewpoint of optimal output adaptation, as well as from a conceptual angle. Clearly, the aim of learning is to adapt the output statistics rather than an internal parameter, and plasticity should strive to adjust it in an optimal fashion. Moreover, we argue that from an evolutionary perspective the contribution of local synaptic changes to the change in output should be independent of the synapse’s random location on the dendritic tree. The framework of natural gradient descent (Amari 1998) provides a solution to both problems, combining the intuition of gradient descent with the elegance of an output change that is invariant under a change of representation in terms of synaptic weights. More specifically, the synaptic updates follow the gradient directly on the manifold of the neuron’s firing probabilities, retranslated into their own state space. While the computational and theoretical advantages of natural gradient are well-studied (Amari 1998, Park 2000, Pascanu 2014, Ollivier 2015), its predictive power as a model for in-vivo synaptic plasticity has not been assessed. We study natural gradient descent from a biological perspective by applying it to learning with Poisson spiking neurons. Unlike most machine learning applications, following an approach of Amari, we calculate an explicit formula for the synaptic weight update in the context of a supervised learning task with Poisson spiking neurons. In terms of somatic EPSP amplitudes it is given as

$$\dot{\mathbf{w}} = \eta \gamma_s (Y^* - \phi(V)) \frac{\phi'(V)}{\phi(V)} \left( \frac{c_\epsilon \mathbf{x}^\epsilon}{\mathbf{r}} - \gamma_u + \gamma_w \mathbf{w} \right). \quad (1)$$

**EXPLAIN VARIABLES.** The coefficients  $\gamma_s, \gamma_u, \gamma_w$  are in general functions of the membrane potential, its first and second moment, as well as the total input. However, our simulations reveal that in many cases,  $\gamma_u, \gamma_w$  may be replaced by constants, while  $\gamma_s$  yields a global scaling dependent on the properties of the spiking-nonlinearity. A closer look at formula one reveals, that just as classical gradient descent based learning rules, natural gradient plasticity follows the postsynaptic error. Additionally, a presynaptic contribution adjusts synapses that received input close to the current point in time. However, unlike for classical error learning, this homosynaptic weight update is complemented by two forms of heterosynaptic changes, a uniform adaptation of all synapses, as well as a weight proportional contribution. This is in line with experimental findings that show that also currently unstimulated synapses undergo plasticity if their neighbours receive input (Lynch 1977, Chistiakova 2009, Royer Pare 2003, Wöhrle 2007, White et al. 1990), as well as with computational studies that list heterosynaptic plasticity as a necessary component of stable learning (Zenke 2017). To investigate the interaction of homo- and heterosynaptic plasticity induced by natural gradient learning, we conducted simulation where we monitored how changes at unstimulated synapses differed from changes at sites that received input under a simple stimulation protocol. Qualitatively similar to experimental findings in different parts of the brain (Lynch 1977, White 1990, Royer Pare 2003 Wöhrle 2007), we found that changes at unstimulated synapses exhibited

an opposite sign compared to the plasticity at stimulated synapses. This is also in line with the possible computational benefits of heterosynaptic plasticity as a stabilizer of homosynaptic changes. (True for sv learning?) Additionally to the presence of heterosynaptic changes, our learning rule also includes a scaling of the homosynaptic contribution by the input rate. A similar rescaling is observed in the Bayesian framework of Aitchison et al. (Aitchison 2014?), where the authors state that a higher rate provides the synapse with more chances to update, thus the stepsize should be decreased. From the derivation of our learning rule, it becomes clear that this rate rescaling arises from a rescaling by the USP variance, which for Poisson input is linearly related to the input rate. A follow-up simulation revealed that under a simple stimulation protocol, the learning rate of the full natural gradient rule was inversely related to the USP variance when the mean was kept fixed. Furthermore, another rescaling (not visible in the equation) followed directly from our approach of invariant output changes. Since synaptic changes are attenuated on their way to the soma, in order to evoke the same effect in terms of adapting the neuron’s firing behavior, changes at distal synapses must be upscaled compared to plasticity at proximal synapses with a similar (desired) impact on output firing. While this phenomenon of democratic plasticity reminds of the dendritic democracy concept (Häusser 2001, Magee and Cook 2000), it can exist independent from the latter, since it only concerns synaptic changes, but not the absolute target weight of a synapse. We explored the biological implications of natural gradient descent learning for Poisson spiking neurons. Our results demonstrate that apart from a consistent plasticity framework that is optimal in terms of output adaptation, natural gradient descent learning provides several experimentally testable predictions, and in particular a unified framework for both homo- and heterosynaptic changes. Therefore: ACCEPT OUR ABSTRACT.



**Figure 1:** **A** Learning task. Receiving Poisson spike trains from afferent nerve cells, a neuron had to respond by firing spikes according to a target distribution. The latter was delivered via spikes from a teacher neuron that received the same input. The firing rate of the student neuron depended via a transfer function  $\phi$  on the somatic membrane potential  $V$ , whose elevation above rest was determined by the sum of the synaptic inputs. **(B-D)** Spike trains, for teacher (orange) and student (red) neuron. **(B)** before learning, **(C)** after learning with the natural gradient rule. **(E-G)** Contour lines of the  $D_{KL}$  between output and target distribution and normalized vector plots for Euclidean gradient vectors **(E)** and natural gradient vectors **(F)** together with weight path during learning. The classical error learning rule based on Euclidean gradient descent follows the contour lines of the error function, whereas the natural gradient rule updates synapses in direction of the target. **(G)** Learning curves for natural and Euclidean descent learning, averaged over 500 trials with initial and target weights randomly chosen. The natural gradient shows faster learning compared to the classical error learning rule. Fixed learning rates were tuned for each algorithm separately to exhibit the fastest possible convergence. **(H)** Direction of homo- and heterosynaptic plasticity in a simple experiment with variable excitatory input and tonic inhibition. We stimulated 5 out of ten afferents providing excitatory Poisson input at 5 Hz to a neuron, while simultaneously delivering tonic inhibition and a teacher spike train at 20 Hz. We investigated the direction of synaptic changes at stimulated and unstimulated synapses as a function of the initial weights. **(I)** Weight change of stimulated weights. While varying the size of the unstimulated weights has no effect, increasing the initial weight of the simulated synapses results in a change from potentiation to depression, once the postsynaptic error term becomes negative. **(J)** Weight change of the unstimulated weights. Heterosynaptic plasticity decreased the unstimulated weights in regions where the stimulated weights underwent LTP. Increasing the size of initial stimulated weights resulted in a change to potentiation at the same point where homosynaptic LTP turned into LTD. Further increase of either unstimulated or stimulated weights resulted eventually lead to depression of the unstimulated synapses. **(K)** Example traces of absolute EPSP amplitude change at the dendrite, for  $d = 3\mu\text{m}$  and  $d = 7\mu\text{m}$ . **(L)** Absolute dendritic amplitude change as a function of distance from soma is linearly increasing. The synaptic weight traces in **(M)** show a higher weight change for low variance input compared to high USP variance scenarios. **(N)** Synaptic weight change on the interval as a function of USP variance. **(O)** Synaptic weight change on the interval as a function of USP variance.