Pattern Orthogonalization via Channel Decorrelation by Adaptive Networks

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Abstract

The early processing of sensory information by neuronal circuits often includes a reshaping of activity patterns that may facilitate the further processing of stimulus representations in the brain. Motivated by recent studies in the olfactory system we study simple adaptive networks that aim to orthogonalize activity patterns representing similar stimuli. Biologically it is plausible that the adaptation is driven by simultaneous correlations between the input channels rather than by the similarity of input patterns that the animal experiences at different times. We demonstrate that networks can achieve effective pattern orthogonalization through channel decorrelation if they also equalize their output levels. In feedforward networks adaptation fails for even moderately similar input patterns. Recurrent networks do not have that limitation. When optimized for linear neural dynamics, they can orthogonalize the representations of highly similar input patterns quite well, even if a threshold-linear nonlinearity is retained in the neural dynamics. For complex stimulus ensembles the rectifying neural dynamics can degrade the network performance significantly. Our results provide insights into fundamental features of simplified inhibitory networks that may be relevant for pattern orthogonalization by neuronal circuits.

1 Introduction

The brain receives information from the sensory periphery in the form of activation patterns across parallel input channels, such as the photoreceptors in vision. An essential task of downstream circuits is to extract from these input patterns information that is relevant to the animal. In many sensory systems neuronal circuits at early processing stages reshape their inputs into output patterns that render the relevant information more easily accessible for the downstream circuits.

There has been extensive work on reshaping sensory information, in particular in the visual context. That work has focused, in particular, on the correlations between the output channels across a large ensemble of inputs presented to the animal (‘natural scenes’). It has been argued that an important strategy for the circuits would be to reduce the redundancy in the transmitted information ([1] but see also [2]) and it has been shown that the center-surround receptive fields of retinal ganglion cells can be viewed as resulting from the retinal circuits aiming to eliminate the pair-wise correlations between channels [3]. Along similar lines, receptive fields similar to those of simple cells in visual cortex arise as the filters of circuitry that performs independent component analysis and minimizes the statistical dependence between the channels [4].

Motivated by recent experiments on olfactory processing [5, 6], we consider here a different perspective and focus on the similarity of activity patterns representing different stimuli. The olfactory sensory neurons induce patterns of activity in the input layer of the first processing stage of the olfactory system, the olfactory bulb. The circuitry of the olfactory bulb dynamically reshapes these activity patterns: even for closely related odors, which induce very similar input patterns, the output patterns relayed on to higher brain areas typically differ significantly from each other. Thus, the olfactory bulb tends to orthogonalize the representations of similar odor stimuli. This may facilitate their discrimination, storage, and further processing in the brain.

What kind of network topology can achieve such a pattern orthogonalization? Given the complex representation of the high-dimensional odor space on the two-dimensional array of glomeruli, which constitute the input units of the olfactory bulb, it is to be expected that the optimal connectivities are more complex than the center-surround connectivity found in the retina, in which the strength of connection between two channels depends smoothly on their distance. Given the propensity of brain structures to adapt to their task we consider adaptive networks and assess their strengths and limitations.

Theoretically, the network connectivity could be optimized directly to maximize the orthogonality of the output activity patterns representing a given set of stimuli. However, such a pattern-based adaptation is difficult to implement using biologically plausible mechanisms; it would require extensive use of long-term memory, since the relevant stimuli may be presented to the animal at very different times. A biophysically reasonable algorithm exists for the network to adapt to minimize the equal-time correlation between the individual output channels [3, 7]. Based on this observation, we investigate to what extent a network is able to orthogonalize the representation of the stimuli if it successfully decorrelates the channels.

In most previous analyses of channel decorrelation [3, 4, 8] the dynamics of neuronal firing rates were assumed to be linear. Neurons and their synaptic connections are, however, highly nonlinear devices. One obvious nonlinearity is introduced by the threshold for action potential generation. As a consequence of this threshold, firing rates can only assume non-negative values and the dynamic range of firing rate changes in the negative direction is severely limited. For single channels the role of nonlinearities in optimizing the information transfer has been studied previously [9, 10]. For multiple channels, however, the influence of neuronal nonlinearities on optimal pattern orthogonalization has, to our knowledge, not been considered so far.

Here we investigate feedforward and recurrent network topologies and their ability to adapt to pattern orthogonalization. For both network types it is not sufficient to decorrelate the output channels to achieve pattern orthogonalization efficiently; in addition they need to equalize their output levels. We find that networks with feedforward inhibition are quite limited in their ability to adapt to this decorrelation and orthogonalization. For networks with recurrent inhibition no such limitation arises. The impact of a neuronal nonlinearity in the form of a linear-threshold nonlinearity depends strongly on the type of stimuli. For certain complex input ensembles it can degrade the performance of the recurrent network significantly. We discuss the potential relevance of our results for pattern processing in the olfactory system.

2 Pattern Orthogonalization via Channel Decorrelation

We consider a neural circuit with p input channels and the same number of output channels. Its inputs are drawn from an ensemble of s stimuli represented by the activities $S_{i=1\dots p, \alpha=1\dots s}$ of the input channels, which yield the output activities $P_{i=1\dots p, \alpha=1\dots s}$. In the olfactory context, for example, $S_{i\alpha}$ would give the strength of the input to glomerulus i during the stimulation with odor α , which results in the activity $P_{i\alpha}$ of the associated principal neuron. It is convenient to represent $S_{i\alpha}$ and $P_{i\alpha}$ as matrices $\mathbf{S}$ and $\mathbf{P}$, respectively.

Motivated by the observations in olfaction [5, 6], we seek neural circuits that map the stimuli $S_{i\alpha}$ into outputs $P_{i\alpha}$ that are mutually orthogonal. We therefore consider the scalar product $C_{\alpha\beta}^{(patt)}$ between different output vectors,

$$C_{\alpha\beta}^{(patt)} \equiv \sum_{i=1}^p P_{i\alpha} P_{i\beta} = c^{(patt)} \delta_{\alpha\beta}, \quad (1)$$

where $\delta_{\alpha\beta}$ denotes the Kronecker symbol. In terms of the matrix $\mathbf{P}$ the matrix $C_{\alpha\beta}^{(patt)}$ of scalar products is given by

$$\mathbf{C}^{(patt)} \equiv \mathbf{P}^t \mathbf{P}. \quad (2)$$

The s outputs can only be orthogonal if the number of channels is at least as large as the number of stimuli, $p \geq s$.

Since it appears biologically difficult for a network to adapt directly to the task of orthogonalizing the outputs, we consider networks that are adapted to decorrelating their channels. This is characterized by a diagonal correlation matrix,

$$C_{ij}^{(ch)} \equiv \sum_{\alpha=1}^s P_{i\alpha} P_{j\alpha} = c_i \delta_{ij}, \quad (3)$$

i.e.

$$\mathbf{C}^{(ch)} \equiv \mathbf{P} \mathbf{P}^t = \mathbf{D} \quad (4)$$

with $\mathbf{D}$ being diagonal. Usually, channel decorrelation is considered for an infinite set of stimuli ('natural scenes'), i.e. in the limit $s \rightarrow \infty$. To establish a link between pattern orthogonalization and channel decorrelation we consider, however, a different situation in which there is only a finite number of stimuli, each of which has special significance to the animal. Thus, the s stimuli $S_{i\alpha}$ are not weakly perturbed realizations of the same stimulus, but rather different stimuli that need to be discriminated by the animal. Specifically, we take $s = p$. The situation we consider is illustrated in Fig.1. As discussed above, to orthogonalize the outputs the animal would need to compare outputs that are presented to the animal at different times; in Fig.1 the pairs of activities contributing to the scalar product (2) are indicated by red rectangles. In contrast, to compute the channel correlation only simultaneous activities of different channels need to be known; in Fig.1 the pairs of activities contributing to the scalar product (4) are indicated by green rectangles.

For $s = p$ the matrix $\mathbf{P}$ is square and if it is invertible one can express the pattern scalar product in terms of the channel correlation

$$\mathbf{C}^{(patt)} = \mathbf{P}^{-1} \mathbf{C}^{(ch)} \mathbf{P}.$$

Note that even if the input channels are perfectly decorrelated according to (4) the pattern scalar product $\mathbf{C}^{(patt)}$, which is then given by

$$\mathbf{C}^{(patt)} = \mathbf{P}^{-1} \mathbf{D} \mathbf{P}, \quad (5)$$

is in general not diagonal since the rows of $\mathbf{P}^{-1}$ and the columns of $\mathbf{P}$ are orthogonal with respect to a scalar product with uniform weights, while in (5) the matrix $\mathbf{D}$ defines in general a scalar product with non-uniform weights. Thus, in order to achieve pattern orthogonalization using channel decorrelation the network has also to equalize the activity levels of all output channels,

$$\mathbf{P} \mathbf{P}^t = \Gamma^2 \mathbf{I} \quad (6)$$

with $\mathbf{I}$ denoting the identity matrix. If that is the case, one has

$$\mathbf{C}^{(ch)} = \mathbf{P} \mathbf{P}^t = \Gamma^2 \mathbf{I} = \mathbf{P}^t \mathbf{P} = \mathbf{C}^{(patt)}, \quad (7)$$

and channel decorrelation and pattern orthogonalization are achieved simultaneously. Here Γ characterizes the level of the output activities. If the mean activity of all channels vanishes, $\sum_{\alpha=1}^s P_{i\alpha} = 0$ for all i , the equalization of the activity levels corresponds to a 'whitening' of the output [3,4].

Figure 1: Illustration of pattern orthogonalization and channel decorrelation. Each stimulus, represented by a column of the stimulus matrix $\mathbf{S}$, is mapped into the corresponding column of the output matrix $\mathbf{P}$. The matrix of scalar products $\mathbf{P}^t \mathbf{P}$ between different output vectors is shown in $\mathbf{C}^{(patt)}$, while the correlation $\mathbf{P} \mathbf{P}^t$ between channels is shown in $\mathbf{C}^{(ch)}$.

For networks with linear neural dynamics the input-output relation for stationary inputs and outputs can be written as

$$\mathbf{P} = \mathbf{K} \mathbf{S} \quad (8)$$

and the condition (6) for channel decorrelation with output equalization gives an explicit condition for the connectivity, $\mathbf{K} \mathbf{S} \mathbf{S}^t \mathbf{K}^t = \Gamma^2 \mathbf{I}$. This condition is satisfied by [3, 8]

$$\mathbf{K}^t \mathbf{K} = \Gamma^2 (\mathbf{S} \mathbf{S}^t)^{-1}. \quad (9)$$

The solutions $\mathbf{K}$ to (9) are not unique. Instead they form a large family of connectivities, which can be transformed into each other by orthogonal transformations $\mathbf{O}$ that rotate the output patterns $\mathbf{P} \rightarrow \mathbf{O} \mathbf{P}$. Two particularly well-studied cases correspond to a principal-component analysis, characterized by $\mathbf{K}^{(PCA)} (\mathbf{K}^{(PCA)})^t$ being diagonal [4], and the case of symmetric connectivity, $\mathbf{K}^{(s)} = (\mathbf{K}^{(s)})^t$, which implies [3, 4]

$$\mathbf{K}^{(s)} = \Gamma (\mathbf{S} \mathbf{S}^t)^{-\frac{1}{2}}. \quad (10)$$

For nonlinear neural dynamics in general no explicit condition for the optimal connectivity can be given.

3 Networks with Feedforward Inhibition

We first consider feedforward networks comprised of principal neurons $\mathbf{P}$ and inhibitory interneurons $\mathbf{L}$ with a network topology as sketched in Fig.2. In this network both the principal neurons $\mathbf{P}$ and the local interneurons $\mathbf{L}$ receive excitatory input from the sensory neurons, with one neuron each associated with a given input channel. The interneurons provide inhibitory input to the principal neurons with a strength given by $W_{ij}^{(ff)}$. The output is conveyed exclusively by the principal neurons.

Figure 2: Sketch of the feedforward network described by (11,12). Each channel comprises excitatory input to the associated principal neuron and an interneuron. The interneurons provide feedforward inhibition to all principal neurons with weight $\mathbf{W}^{(ff)}$.

Within the framework of firing-rate models for the individual neurons these networks are described by

$$\tau_P \frac{d}{dt} P_{i\alpha} = -P_{i\alpha} + S_{i\alpha} - \sum_{j=1}^{N_L} W_{ij}^{(ff)} [L_{j\alpha}]_+ \quad (11)$$

$$\tau_L \frac{d}{dt} L_{i\alpha} = -L_{i\alpha} + S_{i\alpha}, \quad (12)$$

where $P_{i\alpha}$ and $L_{i\alpha}$ represent the total synaptic input currents of the principal neurons and the interneurons, respectively, and the rectifying nonlinearity characterizing the firing threshold is given by

$$[x]_+ = \begin{cases} x - x_{min} & \text{for } x \geq x_{min} \\ 0 & \text{for } x < x_{min} \end{cases}. \quad (13)$$

We restrict our analysis here to $x_{min} = 0$.

We focus here on stationary stimuli, which after some transient lead to a stationary output $\mathbf{P}$. For these fixed points one obtains the input-output relationship

$$\mathbf{P} = (\mathbf{I} - \mathbf{W}^{(ff)}) \mathbf{S}, \quad \mathbf{K} = \mathbf{I} - \mathbf{W}^{(ff)}. \quad (14)$$

With our choice of the firing threshold, $x_{min} = 0$, the rectifying nonlinearity does not affect the dynamics of this network, since the sensory input $\mathbf{S}$ and with it the interneuron activity $\mathbf{L}$ is non-negative.

In the symmetric case the adapted connectivity (10) is given by

$$\mathbf{W}^{(ff)} = \mathbf{I} - \Gamma (\mathbf{S}\mathbf{S}^t)^{-1/2}. \quad (15)$$

This connectivity involves the inverse of the input correlation matrix. The strength of the connection between two neurons is therefore affected by the input correlations of *all* neurons in the network and adaptation would require a *nonlocal* learning rule. This would be difficult to implement biophysically.

If the input channels are only weakly correlated and $\mathbf{S}\mathbf{S}^t$ is close to a multiple of the identity matrix, $\mathbf{S}\mathbf{S}^t = \Gamma^2 \mathbf{I} + \epsilon \mathbf{r}$ with $\epsilon \|\mathbf{r}\| \ll \Gamma^2$, the inverse in (15) can be approximated by a Taylor expansion, leading to

$$W_{ij}^{(ff)} = \epsilon \frac{1}{2\Gamma^2} r_{ij} - \frac{3}{8\Gamma^4} \epsilon^2 \sum_k r_{ik} r_{kj} + \frac{5}{16\Gamma^6} \epsilon^3 \sum_{kl} r_{ik} r_{kl} r_{lj} + \mathcal{O}(\epsilon^4). \quad (16)$$

For sufficiently small ϵ all terms beyond the leading-order term can be ignored. This eliminates all nonlocal contributions to W_{ij} , i.e. all contributions involving channels other than i or j . The

resulting approximate connectivity is given by

$$\mathbf{W}_a^{(ff)} = \frac{1}{2} \left(\frac{1}{\Gamma^2} \mathbf{S} \mathbf{S}^t - \mathbf{I} \right). \quad (17)$$

Its weights $W_{a,ij}^{(ff)}$ depend only on the correlation between the channels i and j , which are involved in the connection.

The simple relation (17) allows an analytical treatment of the performance of the approximate feedforward connectivity for the case of two channels. It shows that this connectivity performs well only if the stimulus patterns are very close to orthogonal and if, in addition, their magnitudes are quite similar. Thus, the network is not able to equalize the output levels effectively, even if the input patterns are already orthogonal. This analysis shows also that within the class of local approximations to $\mathbf{W}^{(ff)}$ orthogonalization is improved if no output equalization is attempted. Thus, we consider $\mathbf{P} \mathbf{P}^t = \mathbf{D}$ where $\mathbf{D}$ need not be a multiple of the identity matrix but consists of the diagonal elements of $\mathbf{S} \mathbf{S}^t$. Eq.(15) is then replaced by the condition

$$\left(\mathbf{I} - \mathbf{W}^{(ff')} \right)^{-1} \mathbf{D} \left(\mathbf{I} - \mathbf{W}^{(ff')} \right)^{-1} = \mathbf{S} \mathbf{S}^t. \quad (18)$$

If the off-diagonal elements $\Delta = \mathbf{S} \mathbf{S}^t - \mathbf{D}$ are small the optimally decorrelating weights $\mathbf{W}^{(ff')}$ are small as well and one can again approximate the inverse of $\mathbf{I} - \mathbf{W}^{(ff')}$ by $\mathbf{I} + \mathbf{W}^{(ff')}$. One then obtains for the approximate connectivity $\mathbf{W}_a^{(ff')}$ the condition

$$\mathbf{W}_a^{(ff')} \mathbf{D} + \mathbf{D} \mathbf{W}_a^{(ff')} = \Delta, \quad (19)$$

or in components

$$W_{a,ij}^{(ff')} = \frac{1}{D_{ii} + D_{jj}} \Delta_{ij}. \quad (20)$$

As in the connectivity $\mathbf{W}_a^{(ff)}$ each weight is again proportional to the correlation between the neurons involved in the connection. However, in $\mathbf{W}_a^{(ff')}$ the proportionality factor differs from neuron to neuron.

To assess the performance of the approximate connectivity $\mathbf{W}_a^{(ff')}$ we employ the stimulus set $\mathbf{S}^{(0)}$ defined by

$$S_{i\alpha}^{(0)} = (1 - \xi) \delta_{i\alpha} + \xi s_{i\alpha}, \quad 0 \leq \xi \leq 1, \quad (21)$$

which consists of p significantly different stimuli. For simplicity, we choose the $s_{i\alpha}$ uniformly distributed in the interval $[0, 1]$ and $1 \leq i, \alpha \leq p$. As ξ goes from 0 to 1 the stimuli $S_{i\alpha}^{(0)}$ transform from orthogonal vectors to random vectors in the first hyper-quadrant. To characterize the orthogonality of the output patterns we use the matrix $\mathbf{C}^{(s)}$ of scalar products of the normalized outputs,

$$C_{\alpha\beta}^{(s)} = \frac{\mathbf{P}_\alpha \cdot \mathbf{P}_\beta}{\|\mathbf{P}_\alpha\| \|\mathbf{P}_\beta\|}, \quad (22)$$

where the output $\mathbf{P}_\alpha$ is given by column α of $\mathbf{P}$. The mean of the off-diagonal elements of $\mathbf{C}_{\alpha\beta}^{(s)}$ is denoted by $\mathcal{C}^{(s)}$.

Fig.3 shows that if the stimulus patterns are close to being orthogonal, i.e. for ξ small, the network with connectivity $\mathbf{W}_a^{(ff')}$ enhances the orthogonality of the outputs (left panel). In fact, the deviation from orthogonality in the outputs depends only quadratically on the deviation from orthogonality in the inputs. This reflects the fact that $\mathbf{W}_a^{(ff')}$ satisfies the decorrelation condition (18) to leading order in the off-diagonal terms of $\mathbf{S} \mathbf{S}^t$. For less orthogonal stimulus patterns, however, the performance of the network deteriorates and for $\xi > 0.4$ the outputs are less orthogonal than the inputs and the network in fact degrades the signal (right panel).

Figure 3: Performance of the network with approximate connectivity $W_a^{(ff')}$ (cf. (20)). Left panel: input patterns for $\xi = 0.3$ (cf. (21)), matrix of scalar products of inputs, and $\mathbf{C}^{(patt)}$. Middle panel: dependence of mean scalar product $\mathcal{C}^{(s)}$ on the deviation ξ from orthogonality (cf. (21)). For $\xi > 0.4$ the outputs are less orthogonal than the inputs. Right panel: as left panel except $\xi = 0.5$.

4 Networks with Recurrent Inhibition

We now consider recurrent networks with a topology as sketched in Fig.4. Within the framework of firing-rate models the principal neurons $\mathbf{P}$ and the local neurons $\mathbf{L}$ are described by

$$\tau_P \frac{dP_{i\alpha}}{dt} = -P_{i\alpha} + S_{i\alpha} - \sum_{j=1}^l W_{ij}^{(pl)} [L_{j\alpha}]_+, \quad (23)$$

$$\tau_L \frac{dL_{i\alpha}}{dt} = -L_{i\alpha} + \sum_{j=1}^p W_{ij}^{(lp)} [P_{j\alpha}]_+. \quad (24)$$

As in the feedforward case we take the firing threshold x_{min} to be zero for both the principal neurons and the interneurons. Assuming that the interneurons follow the dynamics of the principal cells sufficiently fast, they can be eliminated adiabatically, $L_{i\alpha} = \sum_{j=1}^p W_{ij}^{(lp)} [P_{j\alpha}]_+$, resulting in a single equation for $P_{i\alpha}$,

$$\tau_P \frac{dP_{i\alpha}}{dt} = -P_{i\alpha} + S_{i\alpha} - \sum_{j=1}^p W_{ij} [P_{j\alpha}]_+ \quad (25)$$

with $W_{ij} = \sum_k W_{ik}^{(pl)} W_{kj}^{(lp)}$. We focus here on symmetric connectivities, $\mathbf{W} = \mathbf{W}^{(s)}$.

Unlike the feed-forward network, the recurrent network is affected by the rectifying nonlinearity for all values of the threshold x_{min} . One aim of our investigation is to compare the performance of the nonlinear network (25) with that of the corresponding network in which the rectifier is omitted and $[P_{j\alpha}]_+$ is simply replaced by $P_{j\alpha}$.

If the neural dynamics were linear and all eigenvalues of $\mathbf{I} + \mathbf{W}^{(s)}$ positive, stationary stimuli would lead after some transient to stationary outputs $\mathbf{P}$ given by

$$\mathbf{P} = \mathbf{K} \mathbf{S} \quad \text{with} \quad \mathbf{K} = (\mathbf{I} + \mathbf{W}^{(s)})^{-1}. \quad (26)$$

In that case the symmetric channel-decorrelating connectivity would be given by

$$\mathbf{W}^{(s)} = \Gamma (\mathbf{S} \mathbf{S}^t)^{\frac{1}{2}} - \mathbf{I}. \quad (27)$$

This connectivity can be learned by a *local* learning algorithm; the weight $W_{ij}^{(s)}$ depends only on information that is available at the neurons i and j : the algorithm involves the correlations between

Figure 4: Sketch of the recurrent network described by (23,24). In each channel the stimulus provides excitatory input to the associated principal neuron. The interneurons are driven by the principal neurons and provide recurrent inhibition to all principal neurons.

the excitatory feedforward input and the inhibitory recurrent inputs to the same neuron [3, 7]. For linear neuronal dynamics the representation $\mathbf{P}$ of any set of p linearly independent stimuli $\mathbf{S}$ can therefore be orthogonalized perfectly.

Quite commonly, however, the neural firing-rate dynamics cannot be assumed to be linear [5, 11–13] and at the very least the firing threshold of the neurons has to be taken into account. We model the dependence of the firing rate on the neural activity $\mathbf{P}$ in a minimal fashion using the piecewise linear rectifying nonlinearity (13). The adapted connectivity can then not be given explicitly in terms of the input correlations $\mathbf{S}\mathbf{S}^t$. Rather than determining the adapted connectivity by a numerical optimization procedure we investigate the performance of the connectivity (27) and how it is affected by the rectifying nonlinearity.

So far it has been assumed that the connectivity of the network allows an arbitrary matrix $\mathbf{K}$ in the input-output relation $\mathbf{P} = \mathbf{K}\mathbf{S}$. Here we focus on purely inhibitory recurrent interactions, which imply $W_{ij} \geq 0$. Because $\mathbf{W} = \mathbf{K}^{-1} - \mathbf{I}$ the diagonal elements of $\mathbf{W}$ are most prone to be negative. They describe self-inhibition or self-excitation and are therefore closely related to the magnitude of the output activity levels relative to those of the inputs. If the output activity levels, which are set by Γ , are too high for a given input ensemble the network has to act as an amplifier. This is not possible in a purely inhibitory network satisfying $W_{ij} \geq 0$. To avoid the need for self-excitation, we choose therefore Γ to be equal to the inverse of the smallest diagonal element of $(\mathbf{S}\mathbf{S}^t)^{1/2}$. In the resulting weights matrix $\mathbf{W}^{(s)} = \Gamma(\mathbf{S}\mathbf{S}^t)^{1/2} - \mathbf{I}$ all diagonal element $W_{ii}^{(s)}$ are then non-negative. Typically, the off-diagonal elements of $(\mathbf{S}\mathbf{S}^t)^{1/2}$ turn out to be non-negative as well or at most very few of them are weakly negative. Setting them to 0 has therefore only a very small effect and we do so in all of our simulations.

To measure the performance of the network we employ two types of similarity measures. The scalar product between the normalized outputs, $\mathbf{C}^{(s)}$, as defined in (22), is a simple and widely used measure, but may not be the best measure of pattern similarity for neuronal networks. Since the information passed on to subsequent brain areas is the firing rate $[\mathbf{P}_\alpha]_+$ rather than $\mathbf{P}_\alpha$ itself we employ also the measure

$$C_{\alpha\beta}^{(p)} = \frac{\hat{\mathbf{P}}_\alpha \cdot \hat{\mathbf{P}}_\beta}{\|\hat{\mathbf{P}}_\alpha\| \|\hat{\mathbf{P}}_\beta\|} \quad (28)$$

with

$$\hat{P}_{i\alpha} = [P_{i\alpha}]_+ - \bar{P}_\alpha, \quad \bar{P}_\alpha = \frac{1}{p} \sum_{i=1}^p [P_{i\alpha}]_+.$$

In analogy to $\mathcal{C}^{(s)}$, the mean $\mathcal{C}^{(p)}$ includes only the off-diagonal elements of $\mathbf{C}^{(p)}$. Note that in the following $\mathcal{C}^{(p)}$ will always be based on the rectified output $[\mathbf{P}]_+$. The measure $\mathcal{C}^{(p)}$ may provide a suitable characterization of the difference in the output patterns as viewed from the perspective of a higher brain area that also receives gain control depending on the mean activity of the output patterns.

Figure 5: Performance of the recurrent connectivity $\mathbf{W}^{(s)}$ with rectifying nonlinearity for stimulus ensemble $\mathbf{S}^{(1)}$ ($\sigma = 2$, $p = s = 9$, cf. (29)). Top panels: input $\mathbf{S}$ and output $\mathbf{P}$ for $\eta = 0.1$. Bottom panel: dependence of the similarity measures $\mathcal{C}^{(s,p)}$ on the dissimilarity η averaged over 5 realizations of $s_{i\alpha}$. The one-sided error bar indicates the standard deviation of $\mathcal{C}^{(p)}$ across the different realizations $s_{i\alpha}$ of $\mathbf{S}^{(1)}$. The similarity of the input patterns is given in terms of $\mathcal{C}^{(s)}$ (unmarked solid line) and $\mathcal{C}^{(p)}$ (unmarked dashed-dotted line).

We first test the performance of the recurrent connectivity $\mathbf{W}^{(s)}$ using the stimulus ensemble $\mathbf{S}^{(1)}$,

$$S_{i\alpha}^{(1)} = Ae^{-(i-6)^2/\sigma^2} + \eta s_{i\alpha}, \quad 0 \leq s_{i\alpha} \leq 1. \quad (29)$$

The stimuli in this ensemble share a Gaussian profile. The difference between them is characterized by the dissimilarity parameter η . For simplicity the $s_{i\alpha}$ are drawn from a uniform distribution. Throughout, we use $A = 1$. As in ensemble $\mathbf{S}^{(0)}$, the input patterns in $\mathbf{S}^{(1)}$ are meant to represent significantly different stimuli and the task of the network is to render the corresponding outputs mutually orthogonal to aid their discrimination by down-stream brain areas. To test the limitations of the recurrent network we include ensembles with highly similar stimuli (small η). Note that the spatial arrangement of the channels is arbitrary; physically, the weakly excited channels in the tails of the Gaussian profile could be interspersed with the strongly excited ones. The stimulus ensemble $\mathbf{S}^{(1)}$ is meant to mimic to some extent the focal character of the olfactory stimulus patterns [11, 14].

Fig.5 shows that even with the rectifier retained in (25) the network orthogonalizes the stimulus representations $\mathbf{P}$ very well, both in terms of $\mathcal{C}^{(s)}$ and $\mathcal{C}^{(p)}$, even for very small values of the dissimilarity parameter η for which the input patterns are highly similar as indicated in the top left panel of Fig.5.

To pose a greater challenge to the network we use now a third stimulus ensemble, $\mathbf{S}^{(2)}$, which is comprised of two classes of similar stimuli (top left panel of Fig.6),

$$S_{i\alpha}^{(2)} = Ae^{-(i-2)^2/\sigma^2} + \quad (30)$$

$$+ Ae^{-(i-6)^2/\sigma^2} + \eta s_{i\alpha}, \quad 1 \leq \alpha < 4,$$

$$S_{i\alpha}^{(2)} = Ae^{-(i-6)^2/\sigma^2} + \eta s_{i\alpha}, \quad 5 \leq \alpha \leq 9. \quad (31)$$

The stimuli of the first class, $5 \leq \alpha \leq 9$, are as in ensemble $\mathbf{S}^{(1)}$ (cf. (29)) and share a Gaussian profile of excitation across the input channels. The stimuli of the second class strongly excite in addition a second group of input channels. These stimuli might be thought of as mixtures of two

types of stimuli, with each exciting predominantly one of two sets of channels. Note that as in stimulus ensemble $\mathbf{S}^{(1)}$ some inputs are consistently less active than others.

Figure 6: Performance of the recurrent connectivity $\mathbf{W}^{(s)}$ with rectifying nonlinearity for stimulus ensemble $\mathbf{S}^{(2)}$ ($\sigma = 2$, $p = s = 9$, cf. (29)). Top panels: input $\mathbf{S}$ and output $\mathbf{P}$ for $\eta = 0.1$. Bottom panel: dependence of the similarity measures $C^{(s,p)}$ for the outputs $\mathbf{P}_{\alpha=5..9}$ on the dissimilarity η averaged over 5 realizations of $s_{i\alpha}$. The similarity of the input patterns is given in terms of $C^{(s)}$ (unmarked solid line) and $C^{(p)}$ (unmarked dashed-dotted line).

As can be seen from the local learning algorithm for $\mathbf{W}^{(s)}$ [3], the two separate groups of strongly excited channels in stimuli $S_{i\alpha}$, $1 \leq \alpha \leq 4$ (cf. (30)) establish substantial inhibition of principal cells with index near $i = 2$ by the principal cells near $i = 6$. This inhibition drives the activity of cells near $i = 2$ to strongly negative values when the stimuli are presented that comprise only a single strong group of input channels ($5 \leq \alpha \leq 9$). Without rectifying nonlinearity the magnitude of their negative activity would be reduced by the self-inhibition W_{ii} . With rectifier, however, the self-inhibition is not active for $P_{i\alpha} < 0$ and the principal cells near $i = 2$ exhibit a common, strongly negative activity as is apparent in the top right panel of Fig.6.

The common negative activity in the output resulting from the second class of stimuli leads to a strong increase in $C^{(s)}$ when the dissimilarity η is small (bottom panel of Fig.6). Note that without the rectifying nonlinearity $C^{(s)}$ would be identically 0 for all η . Since for small η the similarity between the outputs is mostly in the negative components, the outputs are significantly more orthogonal in terms of $C^{(p)}$, which is based on the rectified output patterns. Nevertheless, the rectifying nonlinearity in (25) significantly compromises the ability of the network to orthogonalize the output patterns resulting from these highly similar inputs.

Overall, even in this difficult orthogonalization task, which was designed to enhance the impact of the rectifying nonlinearity, the adapted recurrent network performs quite well in terms of $C^{(p)}$ as long as the patterns are not too similar.

5 The Importance of Output Equalization

As discussed in Sec.2, perfect channel decorrelation implies perfect pattern orthogonalization only if the output levels are equalized (cf. (7)). To assess quantitatively how much a lack of output equalization degrades the performance of the network we now investigate recurrent networks using connectivities $\mathbf{W}^{(s')}$ that decorrelate the input channels perfectly, but equalize the output levels

only to a degree. Thus, $\mathbf{P}\mathbf{P}^t$ is diagonal, but not necessarily proportional to the identity matrix (cf. (3)). In analogy to (18) the weights matrix $\mathbf{W}^{(s')}$ satisfies then the equation

$$(\mathbf{I} + \mathbf{W}^{(s')}) \begin{pmatrix} c_1 & 0 & \dots & 0 \\ 0 & c_2 & \dots & 0 \\ \dots & \dots & \dots & \dots \\ 0 & \dots & 0 & c_m \end{pmatrix} (\mathbf{I} + \mathbf{W}^{(s')})^t = \mathbf{S}\mathbf{S}^t. \quad (32)$$

One possible choice for the c_i is to set them equal to the input activity levels, $c_i^{(0)} = D_{ii}$. Then the output and input levels are the same for each channel. To assess the impact of output equalization we continuously vary the c_i between the values $c_i^{(0)}$ and a uniform value c_w ,

$$c_i = (1 - \mu) c_i^{(0)} + \mu c_w \quad 0 \leq \mu \leq 1. \quad (33)$$

Thus, for networks with linear neuronal dynamics perfect equalization is obtained for $\mu = 1$.

We test the performance of the connectivity $\mathbf{W}^{(s')}$ using stimulus ensemble $\mathbf{S}^{(1)}$ with and without rectifying nonlinearity. In Fig.7 we express the dependence on the equalization parameter μ in terms of the relative standard deviation $\Delta c/c_{mean}$ of the coefficients c_i . As expected, with decreasing degree of equalization, i.e. with increasing $\Delta c/c_{mean}$, the mean scalar product $\mathcal{C}^{(s)}$ rises even without rectifying nonlinearity, although for all values of $\Delta c/c_{mean}$ the channels remain uncorrelated, i.e. $\mathbf{C}^{(ch)}$ is diagonal. Within the resolution of Fig.7 the results for $c_w = \min_i c_i^{(0)}$ and for $c_w = \max_i c_i^{(0)}$ are indistinguishable without rectifier. With the rectifying nonlinearity retained the outputs are substantially less orthogonal in terms of $\mathcal{C}^{(s)}$ for $c_w = \max_i c_i$ since the rectifier limits the ability of the network to amplify its output. For $c_w = \min_i c_i$ the mean scalar product $\mathcal{C}^{(s)}$ is much lower (not shown). In terms of $\mathcal{C}^{(p)}$ the performance of the network is less affected by the rectifying nonlinearity.

Figure 7: Dependence of the network performance on the equalization of the output levels as characterized by the relative standard deviation $\Delta c/c_{mean}$ of the coefficients c_i for $c_w = \max_i c_i$ (cf. (33); $\Delta c/c_{mean} = 0$ for $\mu = 1$ and $\Delta c/c_{mean} = 1.65$ for $\mu = 0$). Without rectifier ('NR') the performance is very similar in terms of $\mathcal{C}^{(s)}$ and $\mathcal{C}^{(p)}$. With rectifier ('R') orthogonalization is impaired significantly in terms of $\mathcal{C}^{(s)}$. The inputs are given by ensemble $\mathbf{S}^{(1)}$ with $\sigma = 1$ and dissimilarity $\eta = 0.1$ yielding $\mathcal{C}^{(s)} = 0.997$.

The significance of the equalization depends on the heterogeneity in the activity levels of the channels. Decreasing the width σ of the stimuli in ensemble $\mathbf{S}^{(1)}$ (cf. (29)) from $\sigma = 3$ to $\sigma = 0.5$ increases the ratio $(c_{max}/c_{min})^{(1/2)}$ from 3.6 to 28.9. Without output equalization this leads to a drastic increase in the similarity of the output patterns (Fig.8). For $\sigma = 0.5$ the network is not able to increase the orthogonality of its output at all if it does not equalize its output levels.

Thus, a network that is adapted to decorrelate co-active input channels does not perform good pattern orthogonalization unless it achieves a sufficient level of output equalization.

Figure 8: Without output equalization ($\mu = 0$), the mean scalar products $\mathcal{C}^{(s)}$ and $\mathcal{C}^{(p)}$ increase significantly with the heterogeneity in the input levels, i.e. with decreasing width σ of the stimuli in $\mathbf{S}^{(1)}$ (cf. eq.(29)). Results are with rectifier retained and averaged over 5 realizations.

6 Discussion

Using simulations and analytical approaches, we examined general features that influence the ability of adaptive inhibitory networks to orthogonalize the activity patterns representing different sensory stimuli. The direct adaptation to this task would require the comparison of representations of stimuli that are presented to the animal at different times. This would imply a substantial use of long-term memory and appears difficult to implement biophysically in peripheral sensory systems. We have therefore investigated to what extent pattern orthogonalization can be achieved if the network adapts to minimize the correlation between individual channels. Networks can learn to decorrelate channels employing mechanisms that require only the comparison of simultaneously available information. Channel decorrelation itself has been studied extensively from various perspectives in the past [1, 3, 4, 7, 8, 15]. However, its connection with pattern orthogonalization and issues like the influence of nonlinearities in the neuronal input-output function and the role of output equalization have not been clarified in detail. Our results address some of these issues and provide insights into general network features that influence pattern orthogonalization.

i) We found that channel-decorrelating networks typically achieve efficient pattern orthogonalization only if they also equalize their output levels.

ii) For inhibitory networks with feedforward architecture the optimal connectivity depends non-locally on the correlations between the input channels, i.e. the strength of the connection between two neurons depends on the correlations between all input channels. Such a connectivity would require an adaptation mechanism that is biophysically difficult to implement. For input patterns that are close to orthogonal the optimal connectivity can be approximated by one in which the strength of the connection between two neurons depends only on the input correlations between the associated channels. These feedforward networks fail, however, to orthogonalize the representations of even moderately similar stimuli. Networks with recurrent inhibitory architecture do not suffer from these difficulties. This difference between the two network architectures may have significant consequences for the function of neuronal circuits.

iii) Most previous analyses of optimally decorrelating connectivities have been based on firing-rate models with linear neural dynamics [3, 4, 8]. To explore the effect of the firing threshold of neurons, we introduced a rectifying nonlinearity after optimizing the connectivity for pattern orthogonalization in the linear regime. We found that the impact of the rectifying nonlinearity strongly depends on the type of stimulus ensemble to which the network is adapted. Overall, networks with nonlinear dynamics performed well on simple decorrelation tasks but the performance degraded for more complex stimulus ensembles. Hence, care has to be taken when insights into the function of neuronal circuits are derived from the analysis of linear models. It would now be interesting to compare these networks to adaptive networks that are optimized taking the nonlinear neural dynamics into account. Instead of employing the explicit expression (7) the connectivity would have to be determined by a numerical optimization procedure. A further interesting extension would be to explore how changes in the firing threshold, which was kept at zero in our study (cf. (13)), influence network performance.

Such changes would simulate changes in the spontaneous firing rate or the resting potential of the neurons.

iv) The assessment of network performance depends strongly on the orthogonality measure employed, which reflects general properties of the readout strategy. To what extent a network achieves orthogonalization depends therefore also on the readout mechanisms employed by higher-order networks.

Although our firing-rate models contain extreme simplifications some results may be of relevance to real neuronal circuits. We therefore discuss below possible implications of our results for neuronal circuits, with emphasis on the olfactory system.

Our analysis identified an important role of output equalization for the orthogonalization of activity patterns representing similar stimuli. This may be particularly relevant for natural olfactory systems as well as artificial noses [16, 17]. In such systems, different types of olfactory receptor neurons or chemical sensors detect different spectra of compounds. Thus, each type of receptor has its own identify. This is to be contrasted with the achromatic visual system where all photoreceptors are essentially equivalent. As a consequence, in olfaction the mean input activity levels of the channels are expected to differ from each other, even when averaged across a large number of natural odor scenes. Equalization of output activity may be achieved by adaptive gain control mechanisms that are known to exist in the first olfactory processing centers of insects and vertebrates. In *Drosophila*, gain control is achieved by a nonlinear transfer function at the first synapse in the olfactory pathway [10]. In the insect antennal lobe and in the olfactory bulb, the average output firing rate remains relatively stable even if the input intensity varies over a wide range, presumably as a consequence of distributed inhibitory feedback onto the output neurons [18–20]. Hence, gain control in the first olfactory processing center may equalize the output activity and thereby contribute to the orthogonalization of activity patterns.

Neurons in the first olfactory processing centers of vertebrates and invertebrates respond to odors with dynamic firing rate variations that often include periods of complete silence [21]. Similar silencing of activity is common also in other sensory modalities [12, 13], indicating that rectification is a prominent feature of neuronal output during sensory responses. This rectification usually deteriorates pattern orthogonalization by models optimized for the linear regime. However, we found that the rectifying nonlinearity renders pattern orthogonalization more resistant against changes in input intensity (data not shown). The rectifying nonlinearity is therefore an important feature of neurons that has to be considered in most network models.

Various adaptive mechanisms can be envisioned to contribute to bulbar pattern orthogonalization. One possible mechanism is synaptic long-term plasticity at the excitatory synapse between principal neurons and granule cells, which constitute the major population of inhibitory interneurons [22–24]. In addition, new inhibitory interneurons are generated in the olfactory bulb throughout the life of the animal. This persistent rewiring of the network through adult neurogenesis may permit an efficient adaptation of neuronal circuits to the animal’s odor environment [25].

In the olfactory bulb there are at least two inhibitory networks of interneurons, which are associated with the peri-glomerular cells and with the granule cells. Since the peri-glomerular cells receive direct input from the sensory neurons, their inhibition to the mitral cells has a feedforward character. We have found that purely feedforward networks that adapt to input correlations via *local* learning rules orthogonalize the activity patterns associated with even moderately similar stimuli only very poorly. This may shed light on the fact that the peri-glomerular cells also receive excitatory input from the mitral cells, which adds a recurrent character to this network. We have not investigated the performance of such a network of mixed type.

Purely feedforward networks have been investigated previously in the context of the insect olfactory system [26] and of the classification of chemical data [27]. The connection strengths were taken proportional to the input correlations as in the approximately adapted connectivity $\mathbf{W}_a^{(ff)}$ satisfying (17). However, while the overall coupling strength is fixed by (17), it was treated as a free fitting parameter in [26, 27]. We found that $\mathbf{W}_a^{(ff)}$ performs only very poorly for very similar stimuli. Allowing the overall coupling strength to be a fitting parameter does improve the performance. However, we find that the optimal value of the fitting parameter depends on how similar

the input patterns are (data not shown). This suggests that within the local approximation $\mathbf{W}_a^{(ff)}$ the optimal coupling strengths would depend nonlinearly rather than linearly on the input correlations. We found that the approximate connectivity $\mathbf{W}_a^{(ff')}$, which does not attempt to equalize the outputs, achieves considerably better orthogonalization than $\mathbf{W}_a^{(ff)}$. As is apparent from (20), its coupling strengths depend not only on the correlations between the channels but also on the input activity levels of the respective neurons. It would be interesting to see whether the performance of the network studied in [27] could be improved by implementing connectivity $\mathbf{W}_a^{(ff')}$ instead of $\mathbf{W}_a^{(ff)}$.

Owing to simplifications inherent in our approach, some prominent features of real biological systems have not been represented in our models. For example, neurons downstream of a decorrelating network may selectively focus on a subset of output neurons, which, moreover, could depend on the stimulus presented. This could change the constraints on pattern pre-processing and allow the system to discriminate stimuli even if the corresponding overall activity patterns are not very well orthogonalized. In addition, neuronal responses in the olfactory and other sensory systems exhibit pronounced non-trivial dynamics with transients that seem to carry information about the triggering stimulus. It would therefore be interesting to investigate how the connectivities may be optimized to allow pattern orthogonalization already during the transient evolution of the output [28].

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