A threshold explains modulation of neural responses to opposite-contrast stereograms

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Disparity-sensitive neurons respond to contrast-inverted stereograms (aRDS) that do not evoke depth percepts. This is in conflict with the idea that such neurons are the direct correlate of depth perception. However, the output of neurons responding to aRDS may be further processed: neurons at later processing stages show weaker responses to aRDS than early stage neurons. Here, we show that such a response hierarchy emerges in a three-layered neural network. A numerical analysis demonstrates that threshold operations can largely explain the network’s behavior as well as the electrophysiological data. An extension of the energy neuron model for disparity-sensitive neurons predicts increased responses to aRDS for an identifiable sub-class of cells and can thus be tested in electrophysiological experiments.

Key words: Anti-correlated; Disparity; Energy neuron; Mechanism; Model; RDS; Stereopsis; Suppression; Threshold operation

INTRODUCTION

A very powerful depth cue comes from small differences between the images on the retinae, the binocular disparities [1]. Depth vision behavior in several species, including humans and the barn owl is influenced by binocular disparities [2].

Cats [3], monkeys [4], and owls [5] have disparity-sensitive neurons in early visual areas (V1 and visual wulst, respectively) that have been discussed as a direct neural correlate for stereoscopic vision [6]. The disparity-sensitive neurons have originally been classified as tuned (excitatory and inhibitory) and near and far, but progress in terms of a quantitative description as binocular energy detectors suggests a rather continuous distribution of response profiles with binocular phase as continuous variable being responsible for different tuning types [7,8]. Recently, doubts were cast on the perceptual relevance of these neural responses in encoding disparity because a special kind of contrast-inverted random-dot stereogram (RDS) evoked no depth percept but caused disparity-sensitive neurons in V1 to exhibit strongly tuned responses [9,10]: the stimulus where one eye’s image was contrast-inverted, i.e. black dots were substituted by white ones and vice versa, was called anti-correlated RDS (aRDS, in contrast to correlated RDS: cRDS).

It was argued that such neurons cannot be a direct neural correlate of depth perception and further neural processing of stereoscopic information was postulated [9,11]. However, in contrast to predictions of the well established energy-neuron model [12–14], tuning profiles in response to aRDS of most real neurons were shallower than tuning curves in response to cRDS, meaning that the average amplitude modulation ratio (AMR, see below) was not 1, as predicted by the energy formalism, but smaller [9,15]. Indeed, in the owl a relation between response latency and AMR was observed that led Nieder and Wagner [16] to propose a hierarchy of disparity-sensitive neurons in the owl’s visual wulst. Early-responding neurons showed AMRs close to 1, while neurons with longer latencies showed little response to aRDS and consequently small AMRs. A threshold operation has been suggested as the simplest mechanism explaining the data [17–19]. Here, we test this hypothesis with a neural network simulation and a numerical analysis.

In a previous publication [20], we have already reported that the output of a three-layered neural network model of disparity-sensitive neurons did not respond to aRDS. We demonstrate here that hidden-layer neurons were also tuned to disparity in aRDS stimuli. Thus, the three-layered network model developed a hierarchical structure similar to that found in the owl. In a numerical analysis, we demonstrate that the energy-neuron model has only to be extended by a threshold operation to reconcile it with the behavior of our network model as well as responses to aRDS of real neurons. A threshold can explain the broad distribution of relative modulation strengths for aRDS [15,16] and correlations between this modulation strength and several tuning parameters of a disparity-sensitive neuron [16] are also a direct consequence of such a threshold operation.

MATERIALS AND METHODS

The neural network model: We used standard backpropagation networks as described in detail previously [20]. The
networks consisted of three layers: an input layer with 200 units, a hidden layer with 8 units and one single output unit. The input units were divided into two groups, representing binocular input, that were fed with the responses of monocular Gabor filters (a product of a Gaussian and a cosine; Fig. 1) to half-images of random-dot stereo-pairs. The filters at each side varied in their position at the input pattern, phase of the cosine and frequency of the cosine. The spatial frequency selectivity of the Gabor filters was consistent with neurophysiological recordings [21]. The best frequencies of the filters were set to 1 cyc/deg, 2 cyc/deg, 4 cyc/deg and 8 cyc/deg. Each hidden-layer unit received input from all filters from both sides tuned to one best frequency. As a consequence, the hidden layer consisted of four pairs of binocular bandpass units. All hidden-layer neurons projected onto the output unit. Units from the hidden-layer and the output unit performed a weighted sum over their input and a threshold operation realized by a Fermi function with a constant temperature (or slope) parameter. During backpropagation training the weights and the thresholds were adjusted so that the output unit exhibited Gaussian-like excitatory responses of monocular Gabor filters (a product of a Gaussian and a cosine), here only the amplitude, the x- and y-offset, the width of the Gaussian and the frequency of the cosine are important (Fig. 1): the phase of the cosine, the quotient $\omega/\alpha$ between the width of the Gaussians and the frequency of the cosine $\omega$ that yields the side-peak suppression index (SSI). The SSI determines the height of side peaks relative to the main peak of the tuning. All other parameters only scale or shift the tuning along the two axes.

The responses of an energy-neuron to aRDS are simply the responses to cRDS with a CP shifted by 180°. The whole aRDS tuning profile is the inverted version of the cRDS tuning. Thus, energy-neurons have an AMR of...
exactly 1.0 [9,20]. When an energy-neuron is extended by a threshold function applied to its output, the AMR calculated for the new model neuron differs from 1. The threshold operating on the energy-neurons output y was realized as a Fermi function \( f(y) = \frac{1}{1 + \exp(\tau(y - h_0))} \). We tested the relationship between AMR and four parameters: the CP and SSI that determine the shape of the energy-neuron’s tuning, and the height \( h_0 \) and the slope \( \tau \) of the threshold function applied to its output.

**RESULTS**

We trained a total of 75 networks, three tuned to each of 25 different disparity values between \(-0.24^\circ \) and \(+0.24^\circ \). After training we first analyzed the output units. At the output level all networks exhibited tuning to both the training cRDS patterns as well as the test cRDS patterns. The typical shape of the tuning is depicted in Fig. 2a. It resembled the Gaussian-shaped tuning of the teacher during training. By contrast, response curves of the output units to aRDS were essentially flat, thus not tuned to any disparity (Fig. 2a).

The values of the amplitude modulation are plotted as a histogram for both aRDS and cRDS (Fig. 2b). The response modulation for cRDS was much higher than for aRDS, which were almost zero, resulting in AMR values close to zero (Fig. 2e, output) as postulated for ideal disparity detectors [9].

Most hidden units showed tuned responses to test cRDS (Fig. 2c). However, the distribution of amplitude modulations was broader than for the output units (Fig. 2d). Most interestingly, hidden units also responded to aRDS, but with inverted phase (Fig. 2c) and the distribution of amplitude modulations in aRDS responses was also broad (Fig. 2d). This resulted in AMRs also differing from zero with a broad distribution up to values of 2.0 (Fig. 2e), comparable to physiological results [15].

Thus, hidden units and output units showed a response behavior that differed in a very characteristic way between the two layers and both layers’ units deviated from the energy-neuron’s prediction. Since the most significant differences between an energy-neuron and the network model’s units was the threshold function of the network units, we expected that the characteristic behavior of the two layers and their deviation from the numerical model should be a result of an interaction between the threshold operation and differing tuning parameters.

We, therefore, further investigated the difference between the two layers. One very important difference was a consequence of the network structure to mimic V1 simple cells [21], hidden units were frequency bandpasses. They received input from Gabor filters with only one spatial frequency while output units integrated over all frequencies represented in the hidden layer. In the case of an energy-neuron this would cause a difference in the width of the Gaussian and, consequently, a difference in the SSI.

Another difference was the shape of the tuning function of the hidden units. As a result of the training procedure all output unit-tuning curves were Gaussian-like (i.e. tuned-excitatory) and thus even symmetric. In the energy-neuron this would mean a CP of zero. In contrast, hidden units exhibited a continuous distribution of CPs, including all classes of physiological tuning profiles proposed by Poggio [22] (Fig. 3).

To test whether the interaction between different CP and SSI values on the one hand and different threshold parameters on the other hand could be responsible for the AMR distributions described above, we performed a numerical analysis with an energy-neuron and a threshold with varying parameters: first, we fixed the SSI to 1/3 and the slope \( \tau \) of the Fermi function to 9 per amplitude of the energy-neuron output. We now varied CP from 0 to 0.5 periods for four threshold heights \( h_0 \): 1.0, 0.8, 0.6, 0.4 times the amplitude of the Gabor function. This variation of CP generates all possible tuning types described for physiological neurons and the hidden layer (Fig. 4a). Note that CP values between 0.5 and 1.0 do not have to be treated for reasons of cyclic symmetry. As expected for a pure energy-neuron, for a low threshold \( h_0 \) of 0.4 amplitudes the AMR did not differ very much from 1, independent of the CP value. For higher thresholds the AMR showed a systematic dependence on CP: For CPs < 0.25 periods AMR was always smaller than 1.0, while for CPs > 0.25 AMRs became bigger than 1.0. AMR increases strictly monotonically with increasing CP. All curves intersected 1.0 AMR at a CP of 0.25. Thus, two sub-classes of neurons may be identified with respect to AMR. Those with CP < 0.25 have an AMR < 1, and those with CP > 0.25 have AMR > 1. The deviation from 1 increases with threshold height.

In the next test, the height of the threshold was fixed to 0.5 amplitudes and the slope was varied (Fig. 4b). For small threshold slopes the behavior was similar to the pure energy-neuron. For a small slope the threshold has a broad dynamic range where it behaves almost linearly. When slopes increased the AMR function became steeper and, again, responses to aRDS were suppressed for CPs < 0.25 periods and enhanced for bigger CPs.

When we kept the slope and height of the Fermi function constant and varied the SSI (Fig. 4c), the AMR function...
became steeper for bigger SSI. This variation of the SSI resembles the difference between the hidden units and the output units. While the latter have high SSI (but zero CP) the hidden units have small SSI (and all possible CP values).

**DISCUSSION**

The discrepancy between tuned responses of disparity-sensitive neurons to aRDS and the absence of depth percepts in the same stimulus has led to the postulation of a hierarchy of disparity processing [9,11]. Neurons that do not respond to aRDS were supposed to constitute the top of this path of sensory processing. Recently, Nieder and Wagner [16] have reported such a hierarchy in the owl. They suggested that non-linear threshold operation and inhibition might generate this hierarchy. Threshold operation and inhibition have also been proposed to eliminate coding ambiguities in V1 orientation tuning [17,18].

Here, we present data from a hierarchical neural network model that support the idea of a simple threshold mechanism. While they do not exclude more elaborate mechanisms, including for example inhibition, our data show that a threshold operation can largely explain known experimental facts. The hidden and output layers of our hierarchical network produced low-level and high-order disparity detectors, respectively. While output units did not respond to aRDS, hidden-layer units showed tuned responses to this class of stimuli. The difference in the behavior of hidden and output units could be explained by the narrower spatial frequency band-pass characteristics of the hidden units and the shape of their tuning curves, two tuning properties that can be parameterized by the SSI and the CP. A numerical analysis of the effect of a threshold applied to the outputs of an energy-neuron showed that the AMR’s deviation from unity increased with increasing SSI and slope and height of the threshold function. The CP of the tuning decided whether this deviation led to a suppression or amplification of responses to aRDS relative to cRDS responses. For neurons with CPs < 0.25 (traditionally classified as tuned-excitatory [22]) aRDS responses were suppressed. For neurons with CPs > 0.25 (tuned-inhibitory) aRDS responses were amplified.

A threshold operation is thus a candidate for a causal explanation of the correlations between AMR and SSI reported by Nieder and Wagner [16]. They, however, did not find a correlation between AMR and CP (as implied by the extended energy-neuron model); this may partly be due to the abundance of tuned-excitatory cells in their sample but also to other mechanisms (e.g., inhibition) involved in stereo-processing.

Since we only consider responses of single neurons, our approach is not suited to investigate more complex phenomena of stereoscopic vision like transparency or smoothness of depth percepts. These would be expected to be a result of population coding and have already been treated by other authors [23,24]. Our modeling applies to the behavior of single neurons to a well-defined class of stimuli. The extended energy-neuron model can be tested in electrophysiological experiments. It predicts a suppression of responses to aRDS for neurons with tuning curves of the excitatory type and an amplification of responses to aRDS for inhibitory type neurons. An analysis especially in the cat should be promising since cat disparity-sensitive neurons show a broad distribution of CP values [7] and a non-negligible amount of neurons with AMRs > 1.0 [16].

**CONCLUSION**

We show that thresholding allows a simple interpretation of the suppression of responses to aRDS, recently reported by Nieder and Wagner [16]. The standard energy-neuron model extended by only one threshold operation applied to its output largely explains the tuning found in the network simulations as well as physiological data. This simple model makes a prediction for the behavior of neurons with different tuning types and can be tested in electrophysiological experiments.

**REFERENCES**


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