Recurrent Long-Range Interactions in Early Vision

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Abstract. A general principle of cortical architecture is the bidirectional flow of information along feedforward and feedback connections. In the feedforward path, converging connections mainly define the feature detection characteristics of cells. The computational role of feedback connections, on the contrary, is largely unknown. Based on empirical findings we suggest that top-down feedback projections modulate activity of target cells in a context dependent manner. The context is represented by the spatial extension and direction of long-range connections. In this scheme, bottom-up activity which is consistent in a more global context is enhanced, inconsistent activity is suppressed. We present two instantiations of this general scheme having complementary functionality, namely a model of *cortico-cortical V1–V2* interactions and a model of recurrent *intracortical V1* interactions. The models both have long-range interactions for the representation of contour shapes and modulating feedback in common. They differ in their response properties to illusory contours and corners, and in the details of computing the bipole filter which models the long-range connections. We demonstrate that the models are capable of basic processing tasks in vision, such as, e.g., contour enhancement, noise suppression and corner detection. Also, a variety of perceptual phenomena such as grouping of fragmented shape outline and interpolation of illusory contours can be explained.

1 Motivation: Functionality and Architecture

How does the brain manage to form invariant representations of the environment that are relevant for the current behavioral task? The sensory system is steadily confronted with a massive information flow that arrives via different channels. In vision, spatio-temporal pattern arrangements that signal coherent surface arrangements must be somehow reliably detected and grouped into elementary items even in changing situations and under variable environmental conditions. Such a grouping enables the segregation of figural components from cluttered background as well as the adaptive focusing of processing capacities, while suppressing parts of the input activity pattern that are less relevant to support the behavioral goal or task [14,28]. Grouping and segregation requires the interaction of several representations and activity distributions generated by different processing streams. Here we focus on the detection of contour features

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such as smooth boundary patterns as well as corner and junction configurations by adaptive neural mechanisms.

A characteristic feature of cortical architecture is that the majority of visual cortical areas are linked bidirectionally by feedforward and feedback fiber projections to form cortico-cortical loops. So far, the precise computational role of the descending feedback pathways at different processing stages remains largely unknown. Empirical evidence suggests that top-down projections primarily serve to *modulate* the responsiveness of cells at previous stages of the processing hierarchy (e.g., [20]). We particularly investigated the recurrent interaction of areas V1 and V2. The results of this investigation suggest a novel interpretation of the role of contour grouping and subjective contour interpolation at V2 such that observable effects relate to the task of surface segmentation. This information is used to evaluate and selectively enhance initial measurements at the earlier stage of V1 processing of oriented contrasts.

Other architectural principles encountered in cortical architecture are long-range horizontal connections and intracortical feedback loops [9], among others. Via horizontal connections cells of like-orientation couple and thus cell responses are selectively influenced by stimuli outside their classical receptive field (RF). We propose a simplified model architecture of V1 that incorporates a sequence of preprocessing stages and a recurrent loop based on long-range interaction. The results demonstrate that noisy low contrast arrangements can be significantly enhanced to form elementary items of smooth contour segments which are precursory for subsequent integration and organization into salient structure. Beyond the formation of salient contour fragments this scheme of processing is able to enhance contour responses at corner and junction configurations. These higher order features have been identified to play a significant role in object recognition and depth segregation (e.g., [1]).

2 Empirical Findings

The computational models have the following key components:

- feedforward and feedback processing between two areas or layers
- localized receptive fields for oriented contrast processing
- lateral competitive interaction
- lateral horizontal integration

In order to motivate the model design, we summarize recent anatomical and physiological data on recurrent processing and horizontal long-range interaction in early visual areas. The summary is accompanied by a review of recent psychophysical data on visual grouping and context effects. A more detailed review is given in [29].

2.1 Anatomy and Physiology

Wiring schemes of projections. Feedback is a general principle of cortical architecture and arises at different levels. A coarse distinction can be made between cortico-cortical loops (e.g., V1–V2) and intracortical loops (e.g., V1 layer 4→2/3→5→6→4 [2,10]).

The pattern of *feedforward* projections preferably link patches of similar feature preference, as shown for orientation selective cells in V1 and V2 [12]. The pattern of *feedback* projections show a retinotopic correspondence [3], as suggested for the linking of cells in cytochrome oxidase blobs and bands [27]. However, the feedback connections diverge from V2 to multiple clusters in V1, which may reflect the convergence of information flow within V2 [34]. In V1, the intracortical feedback loop connects cells within the same column. Cells within one column have common receptive field properties, e.g., ocular dominance and orientation preference [2].—We conclude that the wiring scheme is specific for contrast orientation and curved shape outline.

Modulatory feedback. Several physiological studies indicate that feedback projections have a gating or modulating rather than generating effect on cell activities [19,35,20]. Feedback alone is not sufficient to drive cell responses [36, 19].

Context influences. The response of a target cell to an individual stimulus element is also modulated by the visual context. V1 cell responses to isolated optimally oriented bars are reduced if the bar is placed within a field of randomly oriented bars, but enhanced if the bar is accompanied by several coaligned bars [23]. A texture of bars of the same type has a suppressive effect, which is maximal for bars of the same orientation and weakest for orthogonal orientation [24].

Wiring of horizontal long-range connections. The grouping of aligned contours require a mechanism that links cells of proper orientation over larger distances. Horizontal long-range connections found in the superficial layers of V1 and V2 may provide such a mechanism: They span large distances [11] and selectively link cells with similar feature preference [12,37]. Receptive field sizes in V2 are substantially larger than in V1 [41].

Response to illusory contours. Contour cells in V2 respond both to oriented contrasts and to illusory contours [43]. Response is maximal for physical contrast [42], but there is also a response to coherent arrangements of two inducers of an illusory contour. If one inducer is missing, response drops to spontaneous activity [30]. Unlike V2, cells in macaque V1 do not respond to illusory contours induced by two flanking bars placed outside their classical receptive field, but show a response increase to the same configuration if the classical receptive field is also stimulated [23].

2.2 Psychophysics

Perceptual grouping is a key mechanism to bind coherent items and to form chunks of surface and object outline. Several studies investigated the dependence of target detection on visual context. Spatial arrangements of Gabor patches within a field of distractors are facilitated by other patches coaligned with the target patch [6,32]. In another study the context effect of flanking bars on contrast threshold for a target bar is investigated [23]. The distance along the axis of colinearity, orthogonal displacement and deviation in orientation are critical parameters for the optimal placement of flanking bars.

Grouping mechanisms help to form object boundaries which are precursory for surface segmentation and figure-ground segregation. Such processes necessitate contour completion over gaps where luminance differences are missing [31]. This completion can be initiated by inducers which are oriented in the direction of the interpolated contour. Completion occurs in the same direction as the inducing contrasts as well as orthogonal to line ends [22,33,38].

3 Computational Models

In this section we present the two models of recurrent processing, a model of cortico-cortical V1–V2 interaction [29] and a model of intracortical V1 interaction [17]. The two models are intended to selectively study different properties of intracortical and cortico-cortical processing. Both models have distinct and partly complementary features, and are designed to be integrated eventually within a single more complex model.

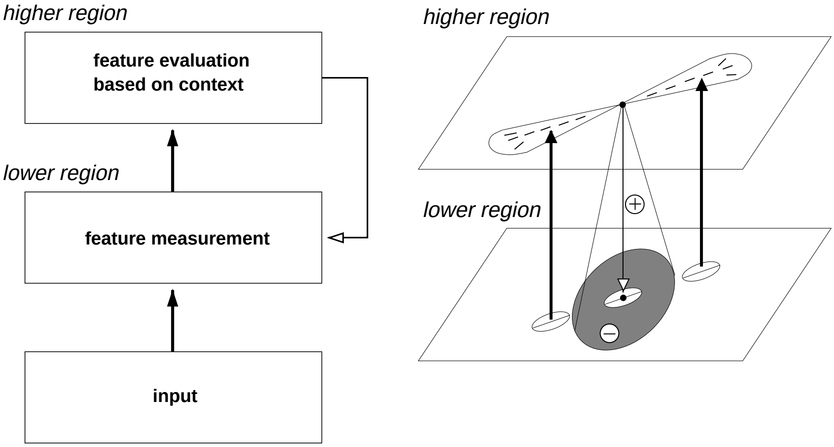

Fig. 1. Sketch of the general scheme of recurrent interaction (left) and of long-range interaction (right). Filled arrowheads indicate driving feedforward connections, unfilled arrowheads indicate modulating feedback connections. In the right sketch, input from the lower region provided by two cells with similar orientation preference is integrated by the long-range filter at the higher region. Integrated activity is fed back to modulate the response of the target cell. Inhibitory influence is generated on neighboring cells (gray circle). Together with the excitatory mechanism this defines a scheme of recurrent on-center/off-surround interaction

Common to both models is the response to oriented contrast and the basic interaction scheme of two bidirectionally linked regions. The term "region" refers to cortical areas (cortico-cortical V1–V2 model) or layers (intracortical V1 model). We propose that for a pair of bidirectionally connected cortical regions the "lower" region serves as a stage of feature measurement and signal detection. The "higher" region represents expectations about visual structural entities and context information to be matched against the incoming data carried by the feedforward pathway (see Fig. q1, left). The matching process generates a pattern of activation which is propagated backwards via the feedback pathway. This activation pattern serves as a signature for the degree of match between the data and possible boundary outlines. The activation is used to selectively enhance those signal patterns that are consistent with the model expectations. A gain control mechanism, that is accompanied by competitive interactions in an on-center/off-surround scheme, realizes a "soft gating" mechanism that selectively filters salient input activations while suppressing spurious and inconsistent signals. As a result the primary functional role of the feedback pathway realizes a gain control mechanism driven by top-down model information, or expectation [14,28,40]. The gain control mechanism enhances only cells which are already active [20]. In other words, feedback is *modulatory*, i.e., feedback alone is not sufficient to drive cell responses. The proposed scheme of driving feedforward and modulating feedback connections is consistent with the no-strong-loops hypothesis by Crick and Koch [4], which only forbids loops of *driving* connections.

The differences between both models are summarized in Table 1. These differences are motivated by the different properties of V1 and V2 as reviewed above. In the remainder of this section we briefly describe the two models, focusing on the basic computational principles employed. A detailed mathematical description, including parameter settings, can be found in the respective references.

Table 1. Different properties of V1–V2 and V1 model

	V1–V2 model	V1 model
location of model long-range connections	V2	V1
response to		
• illusory contours	yes	no
• corners	no	yes
bipole properties		
• RF size	≈ 8	≈ 3
	(multiple of resp. feedforward RF size)	
• combination of lobes	nonlinear "AND"-gate	linear
• feature compatibility	circular boundary segments	boundary segments of same orientation only
• subfields	on- and off-subfield	on-subfield only

3.1 Cortico-Cortical V1–V2 Interaction

We suggest that a variety of empirical findings about the physiology of cell responses in different contextual situations and about the psychophysics of contour grouping and illusory contour perception can be explained within a framework of basic computational mechanisms. We have realized an instantiation of this general interaction scheme described above to model the interaction between primary visual cortical areas V1 and V2. The model information is stored in "curvature templates" which represent shape segments of varying curvature. These templates are matched against the measurements of local oriented contrast. The matching is realized in a correlation process that utilizes oriented weighting functions which sample a particular segment of the spatial neighborhood. In order to combine significantly matching input from spatial locations from either side along the preferred orientation, a subsequent nonlinear accumulation stage integrates the activities from a colinear pair of lobes (compare [15]). An arrangement of consistent local contrast measurements activates a corresponding shape model which is represented in the spatial weights of double-lobed kernels and stands for model curve segments. This activation in turn enhances the activities of initial measurements by way of sending excitatory activation via the descending pathway. The net effect of bidirectional interaction generates a stabilized representation of shape in both model areas. A more detailed description of the mathematical definition of the model can be found in [29].

3.2 Intracortical V1 Interaction

In the model described above we have utilized center-surround feedback interaction for localized cells at the stage of model V1. We kept the model as simple as possible in order to study context effects that are exclusively generated at the higher cortical stages of model V2 to modulate the localized initial measurements. The effect of lateral oriented long-range interaction even at the stage of V1 is investigated in a second model described below.

In cortical area V1 layer 2/3, complex cells of like orientation are coupled via horizontal long-range connections which span two up to three hypercolumns on each side. We propose a model of V1 processing that incorporates both lateral horizontal interactions and recurrent intracortical processing. Oriented long-range interactions are utilized to enhance the significance of responses of coherent structure. We suggest that at a target cell location contrast activities from similar oriented cells are integrated via long-range excitatory connections. Unlike previous approaches, the integrated activation acts as a gain enhancer of activity that is already present by localized measurement of oriented contrast. In comparison to the long-range mechanism of the recurrent V1–V2 model, the bipole filter of long-range interaction is i) linear, adding the inputs of its two lobes, ii) connects cells of same orientation preference only and iii) is smaller in size compared to the size of the complex cell RFs in the feedforward stream (see Tab. 1).

The recurrent interaction at V1 enhances local coherent arrangements while incoherent noisy measurements is suppressed. In view of the cortico-cortical processing scheme described above, we claim that the localized interaction in V1 alleviates the detection of more global shape outline pattern in V2. By selectively enhancing coherent activity, this process maximizes the orientation significance at edges, compared to noisy arrangements of initial complex cell responses. At corner and junction configurations, significant responses for more than one single orientation emerge from the recurrent interaction, forming salient responses in independent orientation channels. In other words, contours and junctions are signaled by high orientation variance and high magnitude in individual orientation channels. This is consistent with recent studies [5], showing that correlated activities of V1 cells can signal the presence of smooth outline patterns as well as patterns of orientation discontinuity as they occur at corners and junctions. Our scheme generates such representations even without the requirement of specialized connectivity schemes between cells of different orientation preference. A more detailed description of the mathematical definition of the model can be found in [17].

4 Results

Simulation results demonstrate that the model predictions are consistent with a broad range of experimental data. The results further suggest that the different mechanisms of these models realize several key principles of feature extraction that are useful in surface segmentation and depth segregation.

The first two figures show results generated by the model of recurrent V1–V2 interaction. Figure 2 demonstrates the capability of grouping individual bar items of a fragmented shape into a representation of coherent activity in model V2. This activation is fed back to further enhance and stabilize those V1 activities that match the global structure. Figure 3 shows the correct prediction of illusory contour strength as a function of the ratio between inducer length and total contour length (Kanizsa figures) and as a function of line density (Varin figures).

Fig. 2. V1–V2 model: Grouping by cortico-cortical feedback processing: Input pattern of fragmented shape (left), model V1 cell responses after center-surround feedback processing (middle), model V2 contour cell responses (right). Reprinted with permission from [29]

Figure 4 and 5 show results generated by the model of recurrent V1 long-range interaction. Figure 4 demonstrates the functionality of lateral long-range interaction for the enhancement of coherent structure. Outline contrasts are detected and subsequently enhanced such that the activities of salient contrast as well as orientation significance is optimized. Figure 5 shows the results of processing an image of a laboratory scene. Initial complex cell activations generated for localized high contrast contours are further stabilized. Initially weak activations in coherent spatial arrangements are enhanced. Spatial locations where high amplitude contrast responses exist in multiple orientation channels are marked by circles. They indicate the presence of higher order structure such as corners and junctions.

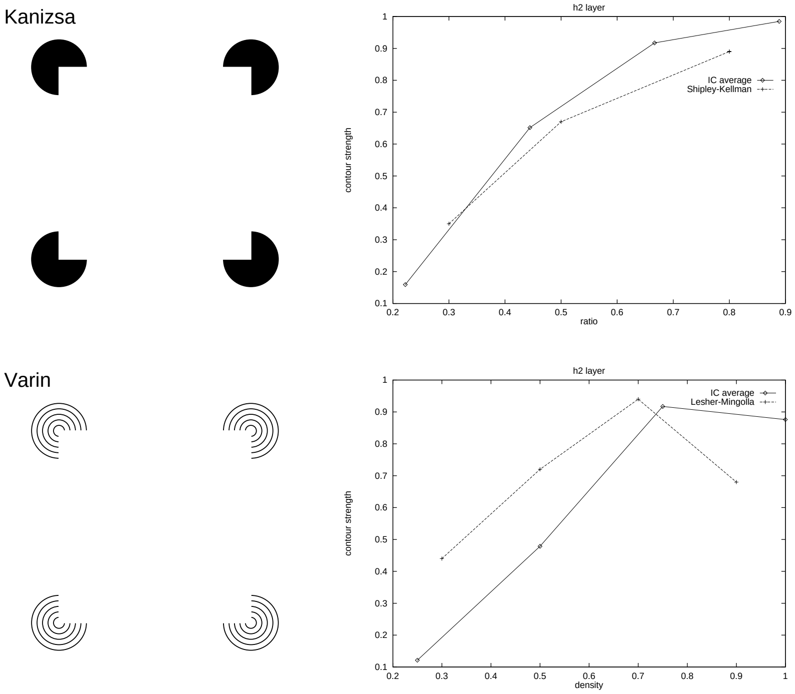

Fig. 3. V1–V2 model: Predictions for illusory contour strength after grouping (model V2 cell responses) for Kanizsa figure (top row) and Varin figure (bottom row). In the Kanizsa figure contour strength is displayed as a function of the ratio between increasing inducer radius and total length of the illusory contour for four different inducers sizes (top right). In the Varin figure contour strength is displayed as a function of line density. For a given radius the number of evenly spaced circular arcs determines the density of the inducers. Model predictions are shown for four different ratios (bottom right). Both graphs show model predictions (continuous lines) and psychophysical results (dashed lines) [39,25]

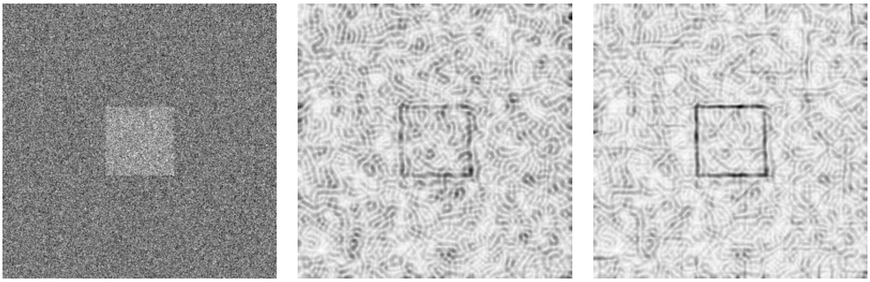

Fig. 4. V1 model: Processing of a square pattern with additive high amplitude noise: Input image (left), initial complex cell responses (middle), result of recurrent processing utilizing long-range interaction (right)

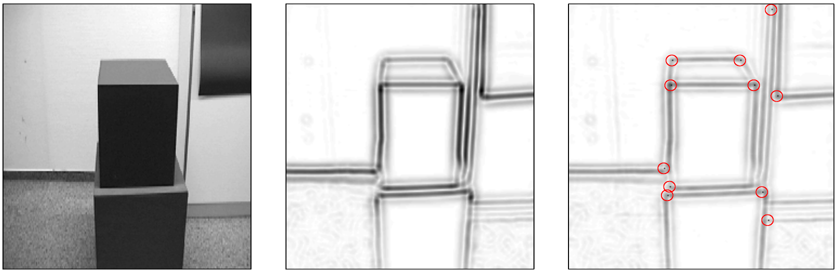

Fig. 5. V1 model: Enhancement of activity distribution in model V1 and detection of corner and junction features in a laboratory scene: Luminance distribution of input image (left), initial complex cell responses (middle), V1 cell responses generated by long-range interaction and recurrent processing (right). Locations of corners and junctions are marked and indicate positions with significant responses in more that one orientation channel

5 Summary and Discussion

5.1 Results

We propose a computational scheme for the recurrent interaction between two cortical regions. In this basic scheme of two interacting regions, the “lower region” serves as a stage of signal measurement and feature detection, while the “higher region” evaluates the local features within a broader context and selectively enhances those features of the “lower region” which are consistent within the context arrangement.

V1–V2 cortico-cortical interaction. The model of V1–V2 cortico-cortical interaction links physiological and psychophysical findings. The model predicts the generation of illusory contours both along (Kanizsa figures) and perpendicular to line ends (Varin figures) in accordance with psychophysical results [25] (see Fig. 3). Further successful predictions (see [29]) include responses to bar texture patterns [24,23], to abuting gratings, and to the suppression of figure contour when placed in a dense texture of similar lines [21].

For the processing of noisy and fragmented shape outline, the model groups coherent activity and completes contour gaps at the V2 stage (see Fig. 2, right) and shapes both spatial and orientational tuning of initial responses at the V1 stage.

V1 intracortical interaction. The model of V1 intracortical interaction, like the V1–V2 model, enhances consistent contours while suppressing noisy, inconsistent activity, both in space and orientation domain. Further, at locations of inherent orientation variability, such as corners or junctions, the relevant orientations remain. Such points of high orientational variance which "survive" the recurrent consistency evaluation reliably mark corners or junctions. This mechanism for junction detection emerges from the recurrent processing of distributed contrast representations, thus questioning the need for explicit corner detectors.

5.2 Related Work

Among the first approaches that utilize recurrent processing for contour extraction is the Boundary Contour System, e.g., [15,13]. A slightly revised version of the original BCS serves as the basic building block for a model of recurrent *intracortical* contour processing at V1 and V2 [16]. A main difference to our model is that V1 and V2 circuits are homologous and differ only in the size of the receptive fields, proposing that V2 is basically V1 at larger scale. In contrast, we propose that V1 and V2 have different and functional roles, such that, e.g., cells responding to illusory contours occur in V2 and corner selective cells occur in V1.

Other models selectively integrate activity from end-stop responses [42,18,7, 8], while we use activity from initial contrast measurement which is sharpened by feedback modulation.

A model architecture similar as our intracortical V1 model has been proposed by Li [26] that focuses on the detection of texture boundaries. The models differ in the feature compatibility used for contour integration: while we integrate activity between edges of same orientation only, Li uses a contour template of many orientations forming a smooth contour. Unlike in our model, feedback is not modulatory in Li's model.

5.3 Conclusion

We propose a computational framework, suggesting how feedback pathways are used to modulate responses of earlier stages. We particularly focus on the recurrent contour processing in V1 and V2. The models are not intended to generate biologically realistic responses, rather to elucidate the underlying computational principles. For the future, we are planning to integrate the two models within one framework. We claim that the proposed principles are not restricted to V1 and V2 but may be extended to recurrent interactions between other cortical areas, like V4 or MT.

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