

# Grouping mechanisms for object-based vision and attention

by

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A dissertation submitted to The Johns Hopkins University in conformity with the  
requirements for the degree of Doctor of Philosophy.

Baltimore, Maryland

May, 2017

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# Abstract

The visual brain faces the difficult task of reconstructing a three-dimensional (3D) world from two-dimensional (2D) retinal images. In doing so, visual information is organized in terms of objects in 3D space, and this organization is the basis for selective attention, object recognition, and action planning. In complex visual scenes, both the foreground and the background are rich in features of different types, scales, *etc.* The brain must find a way to group together the features that belong to objects on the foreground, and distinguish them from features in the background.

The goal of this thesis is to understand how the neural circuits in primate cortex accomplish this task using feedback grouping mechanisms for object-based vision and attention. In Chapter 1, we introduce the background information needed to understand the physiology and previous modeling experiments. In Chapter 2, we propose a quantitative neural model of contour grouping constrained by recent physiological data. We validate the model by reproducing several experimental results, including the measure of contour-response  $d'$ , as well as the magnitude and time course of neuronal responses to contours. In Chapter 3, we extend this model to natural images,

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and the results are quantitatively compared with human-generated segmentations and figure-ground labels (Berkeley Segmentation Dataset). Beginning with Chapter 4, we shift our focus to the representation of 3D information in the visual system. First, we show that 3D surfaces can be represented by a feedforward, linear combination of basis functions whose response properties are similar to those of disparity-selective neurons commonly found in early visual cortex. With our model, we are able to reproduce results from a set of psychophysical experiments where attention has to be directed to surfaces. In Chapter 5, we propose a model of 3D visual saliency and show that the added depth information improves saliency prediction. Overall, this work will investigate whether feedback grouping mechanisms are fundamental for linking early feature representations to perceptual objects. The models developed will address how visual features are grouped into 2D and 3D object representations.

Primary Reader: Ernst Niebur

Secondary Reader: Rüdiger von der Heydt

# Acknowledgments

As I was sitting on the boat, I was thinking about how the trip was really a metaphor for my PhD experience. I have had opportunities to steer the boat (sometimes in the wrong direction!), gone through both good and bad weather, and through it all, have had a good captain whom I can trust to guide me to the finish.

# Dedication

This thesis is dedicated to my younger sister Joy, whose perseverance in the face of adversity has been my inspiration.

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# Chapter 1

## Introduction

### 1.1 Segmentation and figure-ground organization

The task of partitioning an image into regions bounded by contours (segmentation) and the task of assigning border ownership of these contours to either the foreground or the background (figure-ground organization) are important first steps in achieving image understanding. Gestalt psychologists were the first to recognize the importance of the whole in influencing perception of the parts, and with this observation, laid out several principles for figure-ground organization (Koffka, 1935; Wertheimer, 1923). For example, the rule of good continuation states that well-aligned contour elements should be grouped together. This is closely related to the concept of a "local as-

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sociation field,” where collinear contour elements excite each other and noncollinear elements inhibit each other (Ullman et al., 1992; Field et al., 1993). Results from neuroanatomy lend support to these ideas, as the lateral connections within V1 predominantly link similar-orientation cortical columns. *However, our understanding of the neural mechanisms of these processes remains surprisingly limited.*

The brain must keep track of which regions and contours belong to which objects. This is known as the binding problem, as it is not clear how the features of an object are bound together (Treisman, 1996). One solution involves differential neural activity, where the neurons responding to the features of an object show increased firing compared with neurons responding to the background. This response enhancement is known as figure-ground modulation (FGM), and was first observed in primary visual cortex (V1) for texture-defined figures (Lamme, 1995). Similar results have been found using other tasks and techniques, including more recent voltage-sensitive dye imaging of populations of neurons during a contour grouping task (Gilad et al., 2013). However, this solution only works if there is a single object in the foreground, as multiple objects each labeled with higher neural activity could be interpreted as parts of a single object. Furthermore, each neuron’s firing rate is inherently ambiguous, as higher activity could be due to labeling with FGM or because the neuron’s preferred feature falls within its receptive field. As a result, the binding problem cannot be solved with models that only represent object information in terms of enhanced neural activity in early visual areas (Niebur, 2000). *I believe that this strongly points to*

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*neural circuits that employ populations of neurons which explicitly represent (i.e. in their firing rate) the organization of the visual scene in terms of perceptual objects.*

### 1.2 The role of cortical feedback

The degree of collinear facilitation observed in V1 is strongly context-dependent, and can change with the behavioral task (Li et al., 2004, 2006) as well as perceptual learning (Li et al., 2008; Yan et al., 2014). As a result, feedback connections from higher areas may play an important role in shaping the responses of neurons in early visual areas. In fact, simultaneous neural recordings from areas V1 and V4 during two different figure-ground segregation tasks show that V4 is intimately involved in the FGM process (Poort et al., 2012; Chen et al., 2014). In these studies, the FGM signal appears first in V4 and is then fed back to V1, with a delay representing recurrent processing. Additional studies of curve-tracing (Roelfsema et al., 1998) and border ownership (Zhou et al., 2000; Qiu et al., 2007; Zhang and von der Heydt, 2010) further demonstrate that feedback mechanisms are necessary for explaining FGM in the presence of multiple objects. *However, essential questions still remain about the nature of the interactions between and within different cortical areas.* How is early-level feature information about an object combined with global context information about the object in a synergistic way in order to generate FGM?

## 1.3 The role of attention

Behavioral studies have shown that attention can be directed to objects (Egley et al., 1994) and electrophysiological results demonstrate that attention can act as a top-down signal which influences FGM (Qiu et al., 2007; Poort et al., 2012). In an ambiguous figure-ground display, attending to one region increases the probability that this region is perceived as figure (Driver and Baylis, 1996; Vecera et al., 2004). Spatial attention, which has been extensively studied, acts like a "spotlight" that enhances neural responses within the focus of attention and suppresses responses outside (Motter, 1993). Attention can also operate in a feature-based or object-based manner. Feature-based attention acts broadly across the visual scene and increases the responses of all components that share similar feature attributes (e.g. color, orientation, or direction of movement) with the attended component (Treue, 1999). Object-based attention highlights all the parts of an object, also encompassing all the features that belong to the object (Roelfsema et al., 1998; Schoenfeld et al., 2014). Attention has been found to modulate border ownership in an object-based manner (Qiu et al., 2007). Border ownership is a property of many neurons in V2 which encodes the side to which an object border belongs relative to their receptive field (Zhou et al., 2000). To explain these results, Craft et al. (2007) proposed a model in which populations of grouping neurons explicitly represent (in their firing rates) the perceptual organization of the visual scene. Grouping neurons are reciprocally connected to border ownership selective (BOS) neurons through feedforward

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and feedback connections. Attention broadly targets grouping neurons, which can then modulate the activity of BOS neurons through feedback (Mihalas et al., 2011). A feedforward version of this model has been applied to natural images, where it outperforms other models in predicting the location of eye fixations (Russell et al., 2014).

The proposed project explains perceptual organization by a combination of top-down and lateral interactions in visual cortex. The interest in the mechanisms of perceptual organization related to visual (not cognitive ) top-down information over the last years was sparked by the co-sponsor’s discovery of border ownership selectivity in extrastriate cortex (Zhou et al., 2000). A series of subsequent physiological findings (von der Heydt et al., 2000, 2003b; Qiu and von der Heydt, 2005; von der Heydt et al., 2005; von der Heydt and Pierson, 2006; Qiu and von der Heydt, 2007; Qiu et al., 2007; O’Herron and von der Heydt, 2009; Zhang and von der Heydt, 2010; Sugihara et al., 2011; O’Herron and von der Heydt, 2013) and computational results (Dong et al., 2008; Craft et al., 2007; Mihalas et al., 2011; Ardila et al., 2012; Russell et al., 2014) elaborated many details of these mechanisms. The sponsor has a long-standing interest in the role of intra-areal lateral (“horizontal”) connections in early visual cortex in the representation of contours. The resulting computational model developed by Stemmler et al. (1995b) has since been corroborated by a large number of independent studies (e.g. Simonotto et al., 1997; Polat et al., 1998; Chatterjee et al., 2011; Xie et al., 2014). However, in agreement with others at the time, the underlying

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concept of horizontal connections in that model was that they are essentially static, or varying over time scales given by ontogenetic development or neuronal plasticity. Such structures could thus implement overall statistics of natural scenes (like circular structures, e.g. Sigman et al., 2001) but they could not flexibly represent the myriad of instantaneously present and constantly changing visual shapes observed during perception of dynamic scenes. This view has been considerably enlarged over the last decade or so, with the Chen et al. (2014) article, on which Brian bases a large part of his model, being the latest in a series of psychophysical and physiological studies. What is emerging is a view in which the lateral connections are in place but can be actively and rapidly modulated by top-down connectivity from higher areas. It may thus be that two “classical” approaches to explain perceptual organization, one using the horizontal connections as a substrate (e.g. Zhaoping, 2005; Piëch et al., 2013), the other using white-matter projections from higher areas (e.g. Craft et al., 2007; Mihalas et al., 2011), can be converged into an integrated model.

**Contributions of this project.** *This project has the potential to deepen and extend our understanding of the neural mechanisms of FGM.* Most existing models (Grossberg, 1994, 1997; Zhaoping, 2005; Piëch et al., 2013) group object features by a diffusion-like process that propagates neural activity along lateral connections within early visual areas. Another class of models relies on the fast temporal coding structures of spike trains (Singer, 1999), but experimental evidence is controversial (Thiele and Stoner, 2003; Roelfsema et al., 2004; Dong et al., 2008). In my proposed



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model, FGM involves grouping mechanisms that make use of feedforward, feedback, and lateral connections between and within multiple cortical areas. Previous models on the neural coding of border ownership have identified a plausible network architecture for perceptual organization and object-based attention. I will extend these models to explain how feedback grouping mechanisms could be used to perform segmentation of both artificial and natural images. My model will also offer several falsifiable predictions which can be used to test it and compare it with competing computational models. *This study also has implications for patients with object-based neglect.* Patients who exhibit this type of neglect are unable to process certain parts of an object due to lesions in higher areas of the brain (Marshall and Halligan, 1993). Clarifying how top-down attention interacts with the neural circuits responsible for grouping together the features of an object could guide therapies for individuals with object-based neglect.

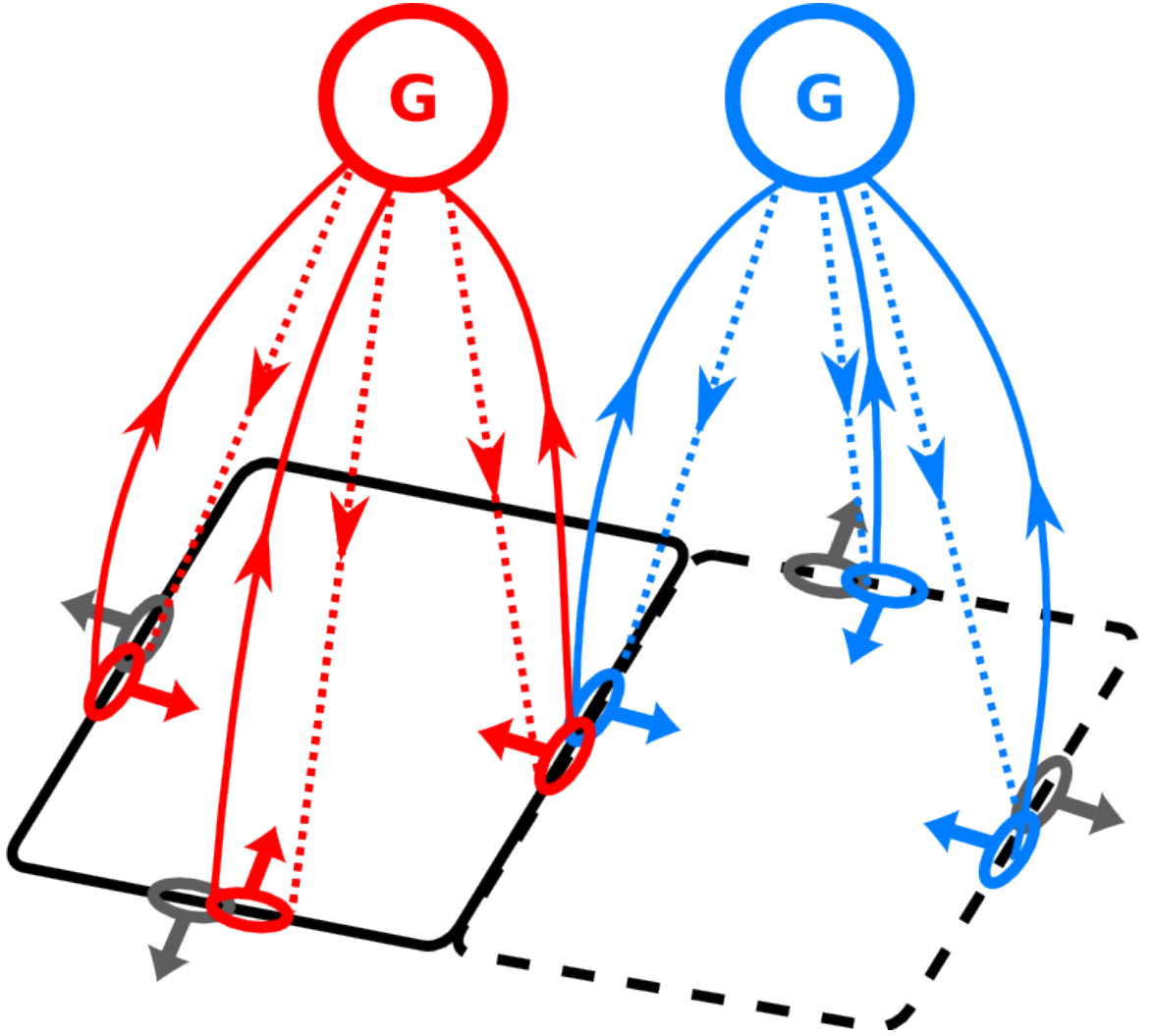
Grouping mechanisms are important not only for piecing together object contours, but also for providing a structure for selectively attending to groups of objects (Treisman and Gelade, 1980). Supported by extensive psychophysical data, Nakayama, He, and Shimojo (1995) proposed that surface representations play a key role in intermediate-level vision. For example, by selectively attending to a surface in 3D space, subjects can perform efficient search for a conjunction target (Nakayama and Silverman, 1986). In a separate cueing experiment, attention was shown to spread automatically across surfaces (He and Nakayama, 1995). These abilities indicate

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powerful mechanisms for grouping objects into surfaces in 3D space, and suggest that structuring the world in terms of surfaces might be an ecologically important function (*e.g.* for locomotion along the ground plane, reaching for objects along a table top *etc.*). I hope to show that basis functions provide a suitable theoretical framework for studying how top-down signals, including those used by grouping and attentional mechanisms, may interact with feedforward and lateral connections to dynamically modify the responses of feature-selective neurons in a surface-based manner. *I believe that my models will provide insight into the neural circuits that represent surfaces, filling a critical gap in our understanding of intermediate-level vision.*

### 1.4 Overview of the grouping model

Several models have been proposed (Zhaoping, 2005; Sakai and Nishimura, 2006; Craft et al., 2007; Layton et al., 2012) to describe how a neuron’s border ownership selectivity can be modulated by visual input far away from its classical receptive field (RF). In the grouping model (Craft et al., 2007), BOS neurons participate in neural circuits that define perceptual objects early-on in processing (Figure 1.1). An object border activates a pair of orientation-selective BOS neurons whose RFs are shown as ellipses. The arrows on the RFs point towards the preferred direction of the neuron, indicating where the object is relative to the neuron’s RF. BOS neurons activated by the solid-line square (red ellipses) excite the appropriate grouping neuron (red G



**Figure 1.1:** Grouping model

in circle) through feedforward connections (red solid lines). The grouping neuron in turn enhances the activity of the same BOS neurons through feedback connections (red dotted lines). This type of facilitatory feedback may be mediated by NMDAR channels, which allow gating of sensory input by top-down signals (Palmer et al., 2014). Neurons consistent with other objects (e.g. the dashed-line square) project to other grouping neurons (blue G in circle in this case). Presence of the solid-line square

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increases the firing rate of the red grouping neuron over that of the blue (and other) grouping neurons since the latter receive less feedforward input. As a consequence, the red grouping neuron provides more feedback to the red BOS neurons than the blue and gray BOS neurons would receive from their respective grouping neurons. Likewise, presence of the dashed-line square increases the firing rates of all blue neurons over those of gray and red neurons. Thus, an object border is represented by two BOS neurons whose relative activity codes for the side of ownership. The relative difference in firing rate is also known as the BOS signal (Zhou et al., 2000).

The BOS signal appears  $\sim 25$  ms after the visual response to an oriented edge, and the delay is essentially independent of object size (Zhou et al., 2000). This constant delay is consistent with a model in which grouping neurons of different sizes integrate local edge signals, and by feedback enhance the same edge signals (Craft et al., 2007). Attention enhances a BOS neuron’s response when an object is on the neuron’s preferred side, but has a suppressive effect if the object is on the non-preferred side (Qiu et al., 2007). This asymmetry is consistent with a model in which top-down attention targets grouping neurons, which then modulate the activity of BOS neurons through feedback (Mihalas et al., 2011). Additional support for the grouping model comes from observations of short-term memory of BOS signals (O’Herron and von der Heydt, 2009) and remapping of BOS signals across saccades and object movements (O’Herron and von der Heydt, 2013). These findings are difficult to explain with models that only represent object information in terms of neural activity in early

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visual areas. I believe that this strongly points to neural circuits that employ populations of neurons which explicitly represent (*i.e.* in their firing rate) the organization of the visual scene.

# Chapter 2

## Contour Integration

### 2.1 Introduction

Gestalt psychologists recognized the importance of the whole in influencing perception of the parts when they laid out several principles (“Gestalt laws”) for perceptual organization (Wertheimer, 1923; Koffka, 1935). Contour integration, the linking of line segments into contours, and figure-ground segregation, the segmenting of objects from background, are fundamental components of perceptual organization. Both processes require combining local, low-level and global, high-level information across different visual areas in order to segment the visual scene. The interaction between feedforward and feedback streams carrying this information, as well as the contribution of top-down influences such as attention, are not well understood.

The contour integration process seems to begin in primary visual cortex (V1),

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where the responses of orientation selective neurons can be enhanced by placing collinear stimuli outside the receptive fields (RFs) of these neurons (Stemmler et al., 1995a; Polat et al., 1998). Contextual interactions between V1 neurons have often been summarized using a “local association field,” where collinear contour elements excite each other and noncollinear elements inhibit each other (Ullman et al., 1992; Field et al., 1993). Results from neuroanatomy lend support to these ideas, as the lateral connections within V1 predominantly link together similar-orientation cortical columns (Gilbert and Wiesel, 1989; Bosking et al., 1997; Stettler et al., 2002). Computational models based on these types of local interactions have successfully simulated the ability of V1 neurons to extract contours from complex backgrounds (Li, 1998; Yen and Finkel, 1998; Piëch et al., 2013).

Segmenting an image into regions corresponding to objects not only requires knowledge about object contours, but also whether these contours belong to the foreground or the background. Border ownership cells that have been found in early visual areas, predominantly in secondary visual cortex (V2), appear to be dedicated to this task. Border ownership cells encode where an object is located relative to their RFs (Zhou et al., 2000). When an edge of the preferred orientation is presented in its RF, a border ownership cell will respond differently depending on the side of the figure to which the edge belongs. For example, a vertical edge can belong either to an object on the left or on the right. Even though the stimuli within its RF is kept constant, a border ownership cell will respond more strongly if the edge belongs

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to a figure on its preferred side than its nonpreferred side. Border ownership coding has been studied using a wide variety of artificial stimuli, including those defined by luminance (Zhou et al., 2000), motion (von der Heydt et al., 2003a), disparity (Qiu and von der Heydt, 2005), transparency (Qiu and von der Heydt, 2007), and more recently, natural stimuli (Williford and von der Heydt, 2014).

To explain this phenomenon, some computational models propose to group object features by a diffusion-like process that propagates neural activity along long-range horizontal connections within early visual areas (Grossberg, 1994; Sajda and Finkel, 1995; Zhaoping, 2005). However, these models have difficulties explaining the fast establishment of border ownership which appears about 25ms after the first stimulus response (Zhou et al., 2000). Propagation along horizontal fibers over the distances used in the experiments would imply a delay of at least  $\approx 70$ ms (Girard et al., 2001, calculations based on the conduction velocity of horizontal fibers in primate V1 cortex, we are not aware of corresponding data for V2). Furthermore, such models are difficult to reconcile with the observation that the time course of border ownership coding is largely independent of figure size (Sugihara et al., 2011).

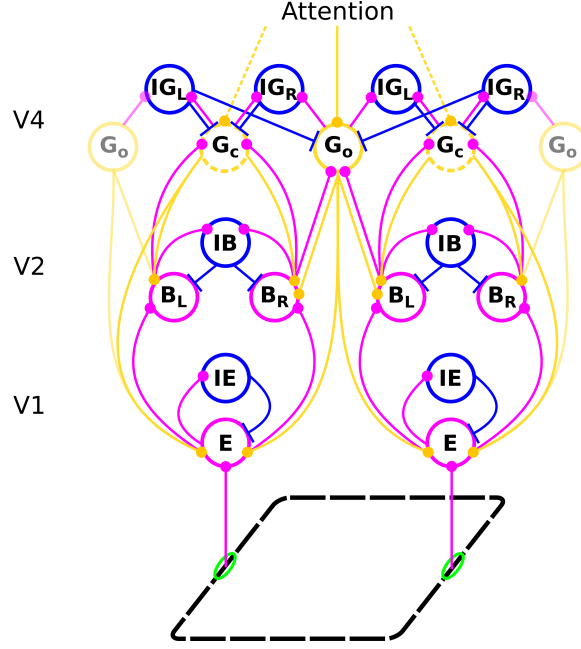
An alternative computational model involves populations of “grouping cells” which explicitly represent (in their firing rates) the perceptual organization of the visual scene (Craft et al., 2007). These cells are reciprocally connected to border ownership (B) neurons through feedforward and feedback connections. In an attention-to-objects task, attention targets grouping neurons, rather than low-level features within



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a spatially-defined area. Therefore attention is directed to objects, resulting in the modulation of B cell activity through feedback from grouping cells (Mihalas et al., 2011). This object-based approach is consistent with psychophysical and neurophysiological studies (*e.g.* Duncan, 1984; Egly et al., 1994; Scholl, 2001; Kimchi et al., 2007; Qiu et al., 2007; Ho and Yeh, 2009; Poort et al., 2012).

Previous experimental studies have suggested the involvement of different visual areas in contour integration and figure-ground segregation (Poort et al., 2012; Chen et al., 2014). However, many computational models do not address how top-down influences arising from the complex interplay between different visual areas are needed to accomplish these two tasks. Here we extend previous models of perceptual organization (Craft et al., 2007; Mihalas et al., 2011) to explain how feedback grouping circuitry can implement the mechanisms necessary to accomplish these tasks. Our model also allows us to explain effects of object-based attention and the role of feedback in parsing visual scenes.



**Figure 2.1:** Structure of the model network. Each circle stands for a population of neurons with similar receptive fields and response properties. Magenta, blue, and orange lines represent feedforward excitatory, lateral inhibitory, and feedback excitatory projections, respectively. Edges and other local features of a figure (black dashed parallelogram) activate edge cells (E), whose receptive fields are shown by green ellipses. Edge cells project to border ownership cells (B) that have the same preferred orientation and retinotopic position as the E cells they receive input from. However, for each location and preferred orientation there are two B cell populations with opposite side-of-figure preferences, in the example shown  $B_L$  whose neurons respond preferentially when the foreground object is to the left of their receptive fields and  $B_R$  whose members prefer the foreground to the right side of their receptive fields. E cells also excite other E cells with the same preferred orientation (connections not shown), as well as a class of inhibitory cells (IE) which, in turn, inhibit E cells of all preferred orientations at a given location (only E cells of one preferred orientation are shown). B cells have reciprocal, forward excitatory and feedback modulatory connections with two types of grouping cells,  $G_c$  and  $G_o$ , which integrate global context information about contours and objects, respectively. E cells also receive positive modulatory feedback from these same grouping cells. Opposing border ownership cells compete directly *via* IB cells and indirectly *via* grouping cells, which bias their activity and thus generate the response differences of opposing border ownership selective neurons. G cell populations also directly excite inhibitory grouping cells (IG; again with the indices L and R), which inhibit  $G_c$  cells nonspecifically and  $G_o$  cells in all orientations except the preferred one. Top-down attention is modeled as input to the grouping cells and can therefore either be directed towards objects (solid lines) or contours (dashed lines) in the visual field (top).

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