

Contour integration and the Association Field

James R. Golden^a, David J. Field^a, and Anthony Hayes^b

^aDepartment of Psychology
Cornell University
Ithaca, NY 14850, USA

^bDivision of Psychology
Nanyang Technological University
Singapore

Field, D. J., Golden, J. R., & Hayes, A. (2013). Contour integration and the association field. MIT Press.

```
@incollection{field2013contour,  
  title={Contour integration and the association field},  
  author={Field, David J and Golden, James R and Hayes, Anthony},  
  year={2013},  
  publisher={MIT Press}  
}
```

Edges and extended contours are key components of any object or natural scene. Mechanisms that are sensitive to edges and lines were amongst the first to be described with the invention of techniques that permitted the recording of the responses of cells in visual cortex. However, the steps between the coding of edges and the recognition of objects have remained elusive. In this chapter, we focus on one of those steps: the integration of edge or line elements into a contour. The idea that continuity is important to visual perception was a central idea of the Gestalt psychologists who, in the first half of the 20th Century, described a set of perceptual grouping principles that included the “law of good continuation”. Over the past twenty years, there has been renewed interest in the representation of contours and continuity. Researchers in visual anatomy, neurophysiology, computer science, and visual psychophysics, have combined their approaches to develop models of how contours are perceived and integrated by the visual system. In the late 1950’s, Hubel and Weisel (see Hubel, 1988, for review) provided the first clear evidence that neurons in the primary visual cortex (V1) responded to local regions of space and were selective to properties such as orientation, position, spatial frequency, and direction of motion. However, there remained the question of how this information, encoded by different neurons, is used in the perception of whole objects and scenes.

In this chapter we review recent work that suggests that the response properties of neurons in the visual pathway depend on a complex relationship between the input, the activity of neighboring neurons, and feedback from higher levels of processing. In particular, neurons in primary visual cortex make use of long-range lateral connections that allow integration of information from far beyond the classical receptive field, and

the evidence suggests that these connections are involved in associating neurons that respond along the length of a contour.

The classical receptive field of a visual neuron is defined as the area of the visual field that has the capacity to modify the resting potential of the neuron. However, while this basic, feed-forward, linear model of the simple cell receptive field has been invoked to explain a wide variety of perceptual phenomena – and is at the heart of a wide range of modeling studies – it is essentially wrong. Some of the earliest studies that measured receptive-field properties of cortical neurons recognized that stimuli presented outside the classical receptive field can modify the activity of the neuron, even if those regions by themselves cannot effect a response (e.g., Maffei and Fiorentini, 1976). Neurons in primary visual cortex show a variety of interesting nonlinearities, with many occurring within the classical receptive field. However, the non-linearities that are of interest to us here are the responses to regions outside the classical receptive field. Stimulation of these areas typically does not produce a response, but it can modulate the activity of the neuron. This modulation in activity was commonly described as inhibitory, and a variety of theories have been proposed (e.g., Allman, Miezin, and McGuinness, 1985). One popular account has argued that modulation can serve to normalize the neuron’s response and make greater use of the neuron’s relatively limited dynamic range (Heeger, 1992).

In this chapter, we concentrate on one component of these non-linear effects. This approach proposes that the non-classical surrounds of receptive fields are intimately involved in a process called “contour integration.” We do not mean to imply that contour integration is their only role; however, the evidence suggests that it is one role. Indeed, some of the effects that have given rise to the notion of non-classical surrounds may be generated by the active grouping or “association” of cells in neighboring regions of the visual field. In accord with the term “receptive field,” we used the term “association field” to describe the region of associated activity (Field, Hayes, and Hess, 1993), and that has proven to be relatively popular (e.g., Li, Piëch and Gilbert, 2008; McManus, Li and Gilbert, 2011) Others have used the term “integration field” (e.g., Chavane, Monier, et al., 2000) or “contextual field” (e.g., Phillips and Singer, 1997) or “extension field” (Papari and Petkov, 2011).

We address four questions and explore some of the research that is providing new insights. The questions are as follows: (i) What is contour integration, and why is it important? (ii) What does anatomy and physiology suggest about the underlying mechanism? (iii) What does the behavior of individuals (i.e., psychophysics) suggest about the underlying mechanism? (iv) What insights are provided by computational models of the process?

We note that when putting this review together we discovered over a thousand papers published in the last 20 years that bear directly on these issues. A number of excellent reviews and discussions published on the topic or on associated topics. We recommend Fitzpatrick (2000), Gilbert (1998), and Callaway (1998), for discussions of the anatomy

and physiology; Polat (1999), Hess and Field (1999), and Graham (2011) for reviews of the psychophysics; and the papers by Li (2011), Yen and Finkel (1998), and Papari and Petkov (2011) for their comprehensive discussions of the computational issues.

What is Contour integration?

Because reflection and illumination vary across different surfaces, occlusions between surfaces commonly produce a luminance discontinuity (i.e., an edge). However, edges in scenes do not occur only at occlusions. They may also arise from textures within surfaces, as well as from luminance and shading discontinuities.

In the 1980s, a number of modeling studies were published that proposed computational strategies that would help to identify which of the edges in a scene made up the principal boundaries of an object. Under the assumption that boundary edges were likely to extend over large regions of the visual field, the computations were designed to extract only those edges that were continuous over an extended area. The algorithms that were developed were based on the assumption that the problem could be at least partially solved by integrating over neighboring regions that had similar orientations. Although some of these integration models included, or were derived from, known physiology (e.g., Grossberg and Mignolla, 1985; Parent and Zucker, 1989), the evidence that an integration algorithm of this kind was actually performed by the visual system was not widely accepted.

Two lines of research helped to support the plausibility of a scheme as described above. The first line comes from a series of anatomical and physiological studies that used both cat and primate and suggest that there exist long-range connections between neurons in primary visual cortex that link neurons with similar orientations. The second line consists of psychophysical studies that have provided evidence for the sorts of associations implied by the physiological and anatomical results (e.g., Field, Hayes, et al., 1993; Polat and Sagi, 1993; Dakin and Baruch, 2009). The results of these studies converge on an account that suggests that neurons in primary visual cortex integrate information from outside the classical receptive field in a way that helps with the integration of contours. Below we review some of these studies.

Physiology and anatomy of lateral connections

It is now well understood that stimuli outside of the classical receptive field of a neuron in visual cortex can modulate that neuron's activity. The sources of modulation potentially originate from feed-forward connections, feedback connections from neurons further along the visual pathway, as well as lateral projections from neighboring neurons. Although we concentrate here on lateral connections, the modulation activity is almost certainly dependent on a more complex circuit involving all three. What has been remarkable, however, has been the close ties found between the anatomy and physiology of the lateral connections and visual behavior of humans and macaques when completing appropriate psychophysical tasks. However, we will also note some exceptions to this general rule (May and Hess, 2007; Dakin and Baruch, 2009)

Early studies exploring the horizontal connections in visual cortex discovered that pyramidal neurons have connections that extend laterally for 2mm to 5mm parallel to the surface and have terminations that are patchy and selective (Gilbert and Wiesel, 1979; Rockland and Lund, 1982). Studies on the extent and specificity of lateral projections have been completed on tree shrew (e.g., Rockland and Lund, 1982; Bosking, Zhang, Schofield, and Fitzpatrick, 1997), primate (e.g., Malach, Amir, Harel, and Grinvald, 1993; Sincich and Blasdel, 2001), ferret (e.g., Ruthazer and Stryker, 1996), and cat (e.g., Gilbert and Wiesel, 1989) with largely good agreement between species, but also some important differences.

Figure 1a illustrates an impressive combination of optical imaging and anatomical techniques that reveal the specificity of V1 projections. These results from Bosking, Zhang, et al. (1997) show an overlay of the orientation columns revealed from optical imaging with the lateral projections of pyramidal neurons near the injection site synapsing onto the surrounding regions. The lateral projections are revealed through extracellular injections of biocytin which label a small number of neurons near the injection site, along with their projections. The orientation tuning of a particular neuron is estimated by its location within an orientation column.

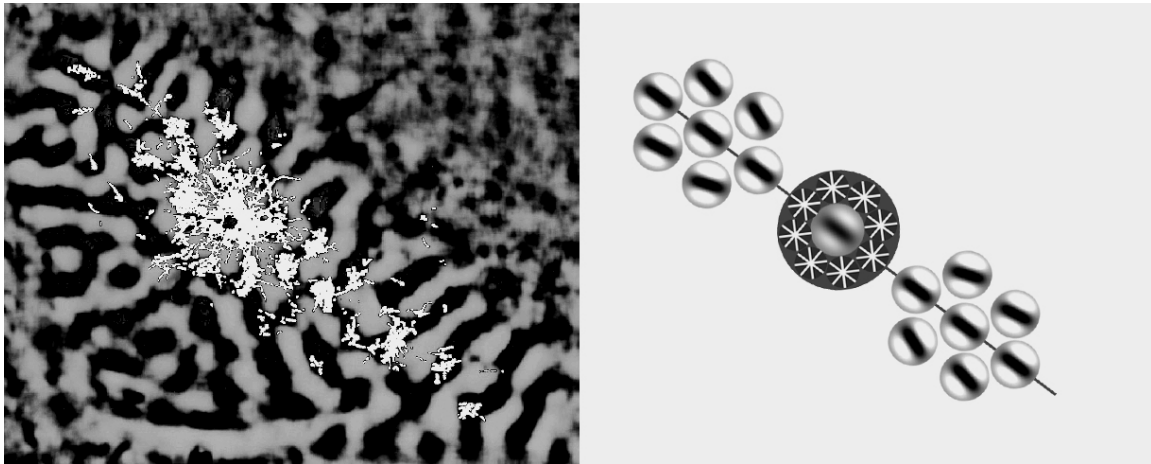


Figure 1. The image on the left (A) shows results modified from Bosking, Zhang, et al., (1997) demonstrating the orientation-specific projections of a set of V1 neurons in the tree shrew. Optical imaging is used to reveal the orientation columns while injections of biocytin are used to map the projections of a set of neurons taking up the biocytin (shown in white). As can be seen, the location of the orientation column of the injection is the same in most cases as the orientation column of the projection. The figure on the right is an experimentally and theoretically derived “association field” (Field, Hayes, et al., 1993) summarizing our beliefs regarding the underlying projections. Short-range connections are theorized to be largely inhibitory and independent of orientation, while long range connections are orientation specific and largely excitatory.

As Figure 1a shows, the orientation column of the injection (shown by the dark areas) is the same orientation column as the majority of the long-range projections (i.e., they synapse onto neurons that are also in the dark regions). The short-range projections do not show such specificity. Bosking, Zhang, et al. also found that in tree shrew the extent of the long-range projections was significantly greater along the axis corresponding to the orientation of the central neuron.

Other work has demonstrated that the lateral projections of these pyramidal neurons are quite specific, projecting to regions of the cortex with iso-orientation columns, as well as similar ocular dominance columns and cytochrome oxidase blobs (e.g., Malach, Amir, et al., 1993; Yoshioka, Blasdel, Levitt and Lund, 1996). Pyramidal cells that are tuned to an orientation aligned with the axes of the projections are shown to project primarily to iso-orientation columns. That is, neurons project primarily to neurons of similar orientation preference.

In some species, as exemplified in Figure 2a, the projections are considerably longer along the primary axis than orthogonal to the primary axis. For tree shrew (Bosking, Zhang, et al., 1997), owl monkey and squirrel monkey (Sincich and Blasdel, 2001) the axis of projections is a factor of 2 to 4 longer along the primary axis than the orthogonal axis. Much of the anatomical work has been conducted in layers III and V of primary visual cortex. We should note here that layer IV neurons do not show the high degree of connectivity to neurons with similar orientations that has been found in layers III and V (Chisum, Mooser and Fitzpatrick, 2003). Karube and Kisvarday (2011) have found that a large fraction of neurons in layer IV of cat primary visual cortex synapse with neurons in orientation columns with a preferred orientation shifted 60° - 90° from the parent cell, providing connections between orientation columns, which they speculate could aid in coding image features such as discontinuities and junctions.

In addition to anatomical studies, neurophysiological studies have explored the effects of co-oriented stimuli presented outside of the classical receptive field (Ito and Gilbert, 1999; Kapadia, Ito, Gilbert, and Westheimer, 1995; Kapadia, Westheimer, and Gilbert, 2000; Polat, Mizobe, Pettet, Kasamatsu, and Norcia 1998; Li, Piëch and Gilbert, 2006; McManus, Li et al 2011;). These studies demonstrate that when a neuron is presented with an oriented stimulus within its receptive field, a second collinear stimulus can increase the response rate of the neuron while the same oriented stimulus presented orthogonal to the main axis (displaced laterally) will produce inhibition, or at least, less facilitation. Kapadia, Westheimer, et al. (2000) attempt to map out these inhibitory and facilitatory effects in awake behaving macaques with the results showing good agreement with the anatomy and with human behavior.

Figure 1b shows our theoretical depiction of these lateral projections which we have called an “association field” (Field, Hayes, et al., 1993). This depiction incorporates results from our psychophysical measurements with the particular example from Figure

1a.. However, first we summarize what we see as some of the principal anatomical and neurophysiological findings that are important to our discussion of contour integration.

1. Long-range projections of pyramidal cells are ‘patchy,’ projecting primarily to neurons in iso-orientation columns (i.e., with similar orientation tuning) (Gilbert and Wiesel, 1989; Malach, Amir, et al., 1993).
2. Long-range projections commonly extend to distances two to four times the size of classical receptive fields, and extend primarily in a direction collinear with orientation tuning of the cell (Bosking, Zhang, et al., 1997; Sincich and Blasdel, 2001; McManus, Li, et al., 2011).
3. Long-range projections to collinear neurons appear to be largely facilitatory (Kapadia, Ito, et al., 1995; Nelson and Frost, 1985; Polat, Mizobe, et al., 1998); however, the neurophysiology results also suggest that facilitation is largely dependent on contrast with excitation predominant at low contrasts (or with high contrast, cluttered, backgrounds) and inhibition predominant at high contrasts (Kapadia, Westheimer and Gilbert, 1999).
4. Long-range connections appear to be reciprocal (Kisvardy and Eysel, 1992).
5. Short-range projections appear to be largely independent of orientation and have been argued to be predominantly inhibitory (Das and Gilbert, 1999).

These conclusions are not unequivocal. For example, as noted above, not all species show elongation of projections along the primary axis. Furthermore, there is some debate as to whether these long range connections are the source of facilitatory effects. Kapadia, et al.’s (2000) results imply that regions orthogonal to the main axis will produce inhibitory modulation. However, Walker, Ohzawa, and Freeman (1999), using patches of gratings at positions adjacent to the classical receptive field, found little evidence for facilitation. Although they did find inhibition, that inhibition was rarely symmetric, and was typically distributed unevenly. Kapadia, Ito, et al. (1995) and Polat, Mizobe, et al. (1998) have also shown that when a second line segment is presented collinearly outside of the classical receptive field and is aligned with the preferred orientation, a small majority of neurons produce a stronger response when the line segments are separated by a small gap. Their response is stronger to a discontinuous line than to a continuous line. These results might be expected if we assume that short range inhibition could, in some neurons, cancel out facilitatory collinear effects.

The diagram in Figure 1b is a simplified representation of what we believe is the underlying mechanism of contour integration. We have made certain assumptions that lack clear support in the anatomy and neurophysiology. For example, in our model we imply that projections to regions offset from the primary axis will project to orientations that are offset in a regular manner. Figure 1a provides a weak suggestion that the off-axis projections are not as centered in the orientation column as those along the main axis, but this suggestion lacks quantitative physiological or anatomical data (the hypothesis has not been adequately tested). The motivation for the arrangement shown

in the figure comes not from the anatomy and physiology, but from behavioral data discussed below.

McManus, Li, et al. (2011) may provide the most thorough physiological evidence yet demonstrating the role of an association field in contour integration. They show that V1 neurons in macaque are selective to contours that extend over the cells' non-classical receptive fields. They believe this is achieved through the top-down gating of the lateral connections. In their study, neurons in V1 were recorded with an awake, behaving macaque. The macaque was cued with a contour composed of three line elements. It then performed a match-to-sample task by observing two fields of random line segments and saccading to the one containing a contour identical to the cue. To identify a cell's preferred contour, a number of contours composed of three segments were presented in the receptive field and the cell's response was recorded. An optimization algorithm was used to find the preferred contour, which then become a starting point for finding the optimal contour with five segments. This procedure was then carried out for extended contours made up of seven segments - several times the width of the classical receptive field.

McManus et al. argue that the association field provides a good account of their V1 responses to these multi-bar stimuli. For smooth contours, the association fields match closely with theory in that they are collinear or co-circular. However, they not only observed selectivity in response to line segments, but found selectivity to sinusoidal and closed circular contours as well. They observed a number of individual neurons that could shift between linear and circular selectivity depending on the cue given in the matching task. By aggregating the single-unit recordings, they determined that the contour selectivity of populations is also context-dependent. The contour selectivity of V1 neurons is therefore a dynamic property that McManus et al. speculate is wholly dependent on top-down, task-specific control signals from higher processing levels that may functionally turn on or off sets of lateral connections between V1 neurons. They note this is distinct from the conventional view of top-down control of V1 through minor amplitude modulation of neuronal responses (e.g., contrast gain control).]

Li, Piech, et al. (2008) addressed the role of top-down influences on contour integration in a different manner. They examined the time course of contour integration in macaque, and found results that strongly suggested a form of perceptual learning. There was gradual improvement up to an asymptote, and the improved accuracy was restricted to the trained location in visual field. To directly investigate the role of attention, before training, monkeys were given a distracter task and were simultaneously shown contour stimuli in the trained areas of the visual field. Before training, recordings of V1 neurons revealed that responses were no different from the responses to noise patterns. However, after training, responses of V1 neurons were directly related to the length of the contours during the contour task and were weakly related in the distracter task. Contour-related responses wholly disappeared when the monkeys were anesthetized.

Psychophysics

Psychophysical research using different methodologies has demonstrated effects that correspond to the anatomical and physiological data discussed above..

An example of a stimulus used in psychophysical research is demonstrated in Figure 2. Human observers are presented with arrays of high contrast, oriented, elements in which a subset has been aligned according to one of several alignment rules. Human observers attempt to identify the presence of this subset of elements as a function of the alignment. Figures 2a and 2b provide examples of two different rules. As is readily observed from the figure, observers are more sensitive to collinear alignment than to orthogonal alignment, even though the stimuli are equated for their information content (Field, Hayes, et al., 1993).

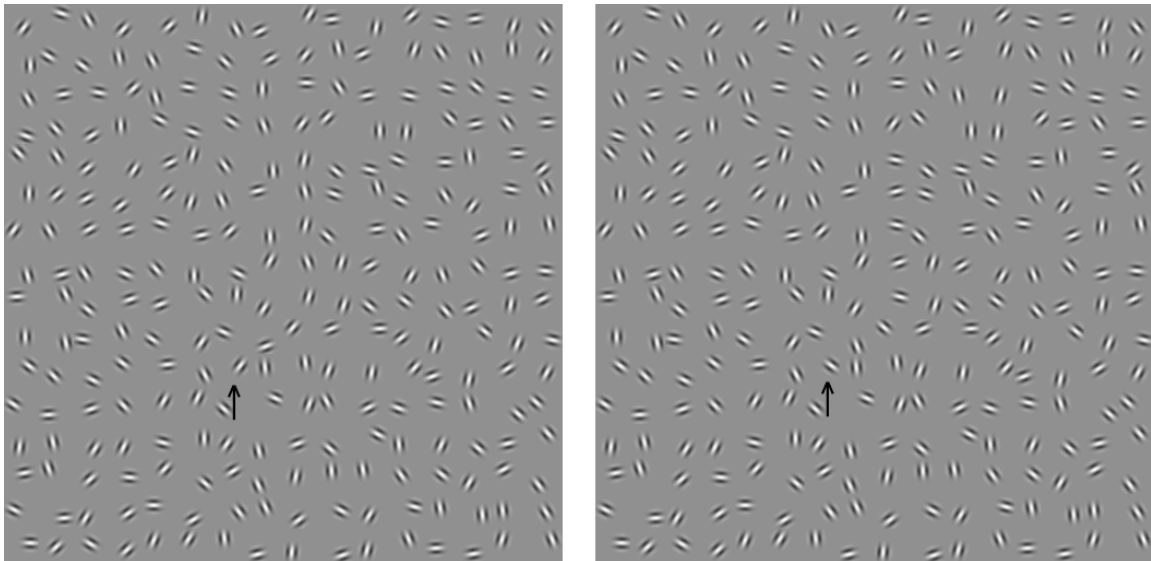


Figure 2. An example of two stimuli used to measure human sensitivity to contours. The two images contain a path at the same location in each image (as marked by arrows) but created according to two different rules (after Field, Hayes, et al., 1993). The reader should be able to see that the contour or “path” contained in the image on the left (A) is more visible than that on the right (B). This figure is one example that demonstrates the human visual system’s increased sensitivity to collinear arrangements.

A raft of studies that use the contour integration task have been published over the last 20 years to investigate the conditions under which integration occurs. For example, studies have demonstrated that integration is possible with elements that have multiple depth planes (Hess and Field, 1995; Hess, Hayes, and Kingdom, 1997), with elements that have different phase or polarity (Field, Hayes, and Hess, 2000), with elements that have different bandwidths, and rather weakly with elements at multiple scales (Dakin and Hess, 1998; 1999). Hayes (2000) has demonstrated that when a local-motion signal induces an apparent displacement of each whole element, integration is stronger when

the alignment corresponds to the elements' perceptual location as opposed to their physical location. Mullen, Beaudot, and McIlhagga (2000) demonstrate that although integration across multiple hues is possible, integration is more effective between similar hues. Lee and Blake (2001) show a similar effect for movement. Hess and Dakin (1997) have suggested that there is a precipitous decline in contour integration in the periphery, although others have found that contour integration declines in the periphery at a similar rate to other visual functions, such as acuity (Nugent, Keswani, Woods, and Peli, 2002).

Other psychophysical techniques have demonstrated intriguing results. Chavane, Monier, et al., (2000) have demonstrated that the speed of an oriented element appears higher when it moves in a direction collinear to its axis than when it moves in a direction orthogonal to its axis. They argue that long-range connections may be responsible. Kapadia, Westheimer, et al., (2000) have demonstrated that elements placed along the ends of a central element can induce a perceived change in the orientation of the central element towards the orientation of the central element. However, when the flanking elements are placed along the opposite axis (adjacent to the central element), the central element can be shifted away from the orientation of the flanking elements. They also demonstrated the spatial distribution of this effect showed good agreement to the neurophysiology of cortical facilitation produced by the flanking lines. Mareschal, Sceniak, and Shapley (2001) have also demonstrated that, with a collinear arrangement, flanking grating patches can significantly increase the orientation discrimination thresholds of the central patch. Furthermore, the threshold increase is significantly higher in the collinear arrangement than when the orientation of the elements is perpendicular to the positions of the three patches.

Fulvio, Singh, and Maloney (2008) tested the ability of subjects to interpolate contours between two line segments. In their experiment, the two contours were spatially separated by several degrees of visual angle by an occlusion, with a short fragment visible between them. The subjects were required to align this fragment to match a continuous contour between the two segments. This is used to test the "relatability hypothesis" of Kelleman and Shipley (1991), which claims that for contour elements to be linked, they must have an intersection and that the angle which one must turn is less than 90° . This view is slightly less strict than the collinearity/co-circularity linkages of the association field. Kelleman and Shipley (1991) predict a sharp dropoff in the ability for subjects to link contours with a turning angle greater than 90° . Fulvio et al. tested subjects for a continuous range of turning angles below and above 90° , and found a smooth dropoff instead in their abilities to interpolate contours.

Kovacs and Julesz (1993) have demonstrated that when measuring the visibility of a path of elements as a function of the density of the surrounding elements, the path is significantly more visible if the contour forms a closed figure. Pettet, McKee, and Grzywacz (1998) argue that this effect may be related to the directional smoothness of the contours (i.e., a circular figure has all the elements changing orientation in a

consistent direction). In either case, both results demonstrate that sensitivity depends on elements further away than the immediate neighbors. The simple model, based on excitatory effects between neighbors, will not produce this effect. Of course, there is no reason to assume that these psychophysical effects necessarily occur in V1, and these psychophysical results may be an indication of the direction of attention towards features that undergo predictable change. Nonetheless, the results suggest that thresholds for perceiving contours depend on complex relationships.

Dakin and Baruch (2009) investigated the interplay between these psychophysical areas: how contextual modulation affects contour integration directly. They sought to test this phenomenon under the flanking conditions described by Polat and Sagi (1993). They created Gabor-element contours in noise backgrounds where the orientation of distracter elements to contour elements was systematically varied. A strong effect was observed for “snakes” (see figure 2a), such that parallel distracter elements significantly inhibited integration of the actual contours compared with randomly aligned flankers, while distracter elements aligned perpendicularly with the path facilitated integration. Interestingly, all alignments of flankers facilitated the integration of “ladders” (see figure 2b) equally over randomly aligned flankers, but not nearly as much as that found with snakes. Dakin and Baruch note this result is not predicted by the original association field model, nor has the physiological support for this been investigated (although see Meirovithz, Ayzenshtat, Bonnef, Itzhack, Werner-Reiss and Slovin, 2010). Dakin and Baruch also propose a detailed computational model that will be discussed below.

The prevailing idea behind why the visual system integrates contours in the way it does is that it is optimized to the types of contours that occur most frequently in natural scenes. Snake-like elements usually indicate contours, ladder-like elements sometimes do so, and arrays of elements aligned somewhere between snakes and ladders usually do not. Extensions of the Field, Hayes, et al. (1993) design have been applied to task-dependent learning scenarios to show this optimization might not be immutable. Schwarzkopf and Kourtzi (2008) trained naïve observers on the contour integration task with ladders and demonstrated significant improvements in their performance. They found this improved performance persisted in a follow-up test 3-5 months following training. Additionally, they were able to train subjects to a high degree of accuracy (75%) with stimuli having Gabor elements offset at 30°-45°. This high level of performance required a longer training period than for ladder stimuli, but it is surprising considering that image elements with this offset usually signal discontinuities, not contours; additionally, it contradicts the conventional belief that contour integration abilities have evolved to match the contour statistics present in natural images. This study shows that the cortical connections that allow for contour integration can be thoroughly modified by short-term training and lend support to the idea of dynamic association fields of McManus et al. (2011).

Computational Modeling

Many computational models are simple reflections of the data found experimentally. They can be considered as “existence proofs” that demonstrate that it is at least possible to perform the desired task with the proposed architecture. They cannot demonstrate that the visual system necessarily uses the architecture of the model, but they can demonstrate that such a model would work if that architecture did underlie the task. However, at times, these models are most useful when they fail, and that may well be the case in some of the following studies we discuss.

While the physiology and anatomy that underlies contour integration is becoming clearer, the range of potentially plausible models is narrowing. In this section, we briefly review natural scene work, but for the most part we concentrate on recent computational strategies that focus on behavioral phenomena of contour integration whose underlying mechanisms have not been elucidated. Most of these computational explanations attempt to describe observed psychophysical phenomena, such as crowding, the effect of flankers, or short-term remapping of cortical connections.

To integrate contours, a variety of algorithms have been proposed that use the technique of integrating similar orientations along collinear directions. Part of the argument for using a co-linearity algorithm appears to be that the task demands it. However, these early studies also went to some lengths to explain how such an algorithm might fit with the known physiology and anatomy (e.g., Sha’ashua and Ullman, 1988; Grossberg and Mignolla, 1985; Parent and Zucker, 1989). In recent years, as our understanding of the underlying physiology has increased, so has the sophistication of computational models (e.g., Li, 2011; McManus, Ullman and Gilbert, 2008; Yen and Finkel, 1998). These models have demonstrated that the architecture revealed by the physiology and anatomy can be used to provide an efficient means of extracting contours in natural scenes, and can be used to account for a significant amount of the psychophysical data.

As noted above, early computational algorithms for contour detection operated on the principle that nearby image patches with the same orientation were likely elements of the same contour. A model that embodies this assumption has intuitive appeal as the way of performing contour integration. Some early models attempted to incorporate the known physiology (e.g., Grossberg and Mignolla, 1985; Sha’ashua and Ullman, 1988; Parent and Zucker, 1989); many more recent models hew closely to the physiology as it is now understood, though some forego this approach to simplify the exercise. We proposed the original association field model (Field, Hayes, et al. 1993) in part because it clearly was an efficient method to encode the practically infinite space of possible contours that could occur in natural scenes. An alternative model may propose neurons that each encode a particular contour, but this scheme would require a vast number of “contour feature detectors”.

Geisler, Perry, Super, and Gallogly (2001) and Sigman, Guillermo, Gilbert, and Magnasco (2001) took the ecological approach further and asked whether the contour integration model is an efficient means of coding natural scene contours. They measured

the co-occurrence statistics of edge elements in natural scenes and found that the relative orientations of neighboring contour segments match well with those predicted physiologically, and with psychophysically defined association fields. Geisler, Perry, et al.'s results are particularly interesting because of the requirements needed to measure these co-occurrence statistics. As they argue, these statistics are multi-dimensional in nature. Given an edge at a particular location with a particular orientation, the region around that location is a three dimensional probability map of x-position by y-position by orientation. Only by mapping out this full probability map does one see full set of statistical dependencies. And it is in these conditional probabilities that one finds the orientation dependencies that map onto the "association field" properties. The probability map is much higher in dimension if we include the additional dependencies across scale, chromaticity, motion, and disparity.

One approach proposes that continuity is represented by a temporal code, presumably tied to the synchronous activity of neighboring neurons. This approach to "binding" has received considerable recent attention and has some experimental support (e.g., Gray, Konig, Engel, and Singer, 1989). The difficulty with this model is that it requires a mechanism to detect the synchrony. Hess, Dakin and Field, (1998) suggest a rather different and more basic version of a temporal code. They suggest that contrast information is represented by the initial response generated by the feed-forward activity, with the later response determined by the lateral connections and the context of the surrounding regions. The contrast signal could then be extracted from the collinearity signal by simply tracking the timing of the response. This hypothesis was derived from the neurophysiological work of Zipser, Lamme, and Schiller (1996) that found for textures results consistent with this theory. However, Kapadia, Westheimer et al. (1999) provide data that are supportive in some ways, but also make the story more complex. As noted in the previous section, Kapadia, Westheimer et al. found that collinear facilitation for neurons in V1 occurs only at low contrasts or in complex backgrounds. They also noted that this facilitation occurs after the initial transient response of the neuron during the "sustained" component of the response. This aspect of the response fits the model proposed by Hess, Dakin, et al. (1998). At high contrasts, though, the neurons do not show this sustained response, but only the sharp transient response. What sort of model predicts this high contrast behavior? It may involve some degree of contrast normalization (e.g., Heeger, 1992) but at present we are not aware of any model that predicts both the timing of responses and the lack of facilitation at high contrasts.

One area of recent research where lateral connections play an important role is in the phenomenon of "crowding". Crowding describes a perceptual experience where the flanking stimuli (often letters) reduce the ability to recognize a central stimulus (e.g., a letter). Although crowding research has a large literature (see Levi, 2008 for a review), much of the recent work has focused on the importance of lateral interactions in visual cortex (e.g., Greenwood, Becks and Dakin, 2009; Dakin, Greenwood, Carlson and Becks, 2011).

May and Hess (2007) observed a crowding effect interfered with detection of “ladder” stimuli in the periphery. They describe a computational model that replicates the contour integration performance of their human subjects, and that is also susceptible to crowding in the periphery. They note that they are not explicitly modeling the physiological mechanisms underlying contour integration, but merely the computations that are carried out in physiology. The model receives as input only the coordinates and orientations of the Gabor elements in the input images; May and Hess claim that this is an accurate representation of the association field in physiology, as contour integration ability does not increase with contrast of Gabor elements (Hess, Dakin, et al., 1998). Association fields were created using methods similar to those of Pelli, Palomares and Majaj (2004), growing larger in the periphery. The association of each element with every other element is calculated based on whether the element is within an association field, how similar their orientations are and whether the pair is more snake- or ladder-like. A rule-based approach was used to sort these association strengths and form the longest possible snake and ladder contours. The model was applied to the same 2AFC experiment the subjects performed, and results were very similar, with ceiling accuracy for snakes at all eccentricities but a sharp drop-off as a function of eccentricity for ladders. The model was also applied to letter stimuli, and the linking of contours across different letters, as would be expected when crowding occurs, was also observed.

Pelli (2008) investigated the effects of the relative scale and distance of the flankers on crowding as a function of eccentricity. His work suggests that the critical spacing at all eccentricities corresponds to approximately 6 mm on the surface of the cortex. This roughly corresponds to the spatial extent of the lateral connections which he calls the “integration field”. Dakin and Baruch (2009) found that human subjects’ contour integration abilities were facilitated or impaired by surrounding Gabor elements, and they attempted to replicate the results of their experiment with a computational model. Their approach used a technique they call “opponent-orientation filtering”. Images were filtered with oriented Gabors, and then the difference of the outputs of orthogonal filters was calculated. At this stage, the response of the model for contours of any length was strongly positive and was inhibited by the surrounding orthogonal elements. They found that this inhibitory model provided a better model the contextual effects found when searching for contours in noisy backgrounds.

McManus, Ullman, et al. (2008) used an association field model to investigate the phenomenon of perceptual fill-in, which occurs when a subset of photoreceptors in both retinas are destroyed by a disease such as macular degeneration. After some time, patients are able to see features within the patches of their visual field that had been blind spots. This recovery is due to a reorganization of the horizontal connections of the association field in V1 (see Gilbert 1998 for review), where axons from V1 cells with normal input grow into the lesion-projection zone. The association field is used as the basis for a computational model of how perceptual fill-in occurs. McManus et al. developed a model that recurrently feeds V1 complex cells within the lesion projection zone input from co-circular horizontal connections. The model, shown in figure 3, outputs images that simulate what patients with fill-in actually perceive.

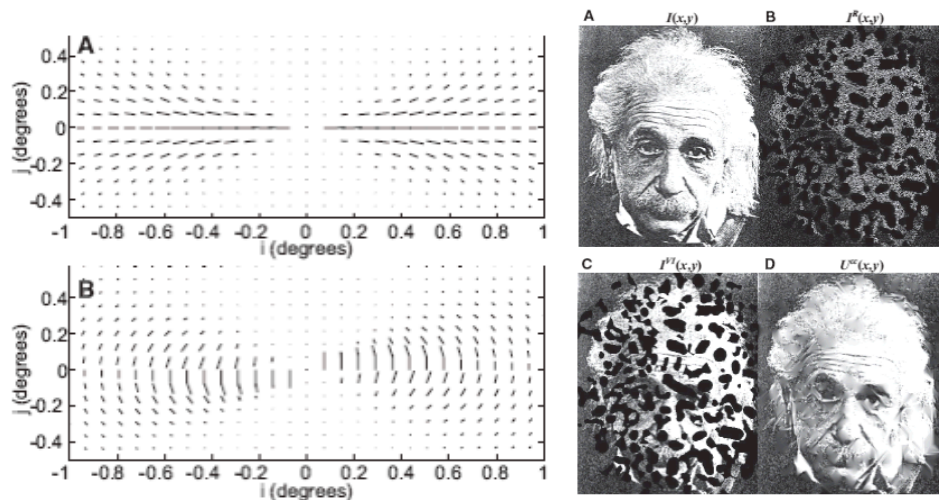


Figure 3. McManus et al. modeled the association field in a recurrent neural network. When the model was applied to images with patches missing to simulate retinal damage, the association field was able to “fill in” the missing information to a striking degree of accuracy.

Kovacs, Papathomas, Yang, and Feher (1996) demonstrated a binocular version of the above finding, by presenting to each eye two completely different natural scenes, such that each eye received patches from both images: the left eye received the complement of the right (e.g., right eye gets 1,2,1,2,2,1 with the left eye receiving 2,1,2,1,1,2). Kovacs, Papathomas, et al. found that observers commonly see complete images (1,1,1,1,1,1 or 2,2,2,2,2,2). The contours and other visual information were successfully integrated between the two eyes into a single perceptual whole. This result implies that the association field less sensitive to ocular origin than it is sensitive to continuity.

Summary and Conclusions

In the last two decades, a large number of studies in visual anatomy, neurophysiology, psychophysics, and computational modeling have provided significant new insights into how the information from different V1 neurons is integrated. Our original proposal in 1993 was that lateral-connections between V1 neurons played a key role in the process of contour integration. Evidence for this proposal has been supported by a wide range of studies. However, the simple “association field” model is incomplete and it cannot account for many aspects of contour perception: as described above, higher level processing is certainly involved. We know that feedback from higher levels can alter the activity of V1 neurons. The work of McManus et al. (2011) suggests that feedback may have a greater effect on the non-classical receptive field than it does on the classical receptive field. When the animal is involved in a search for a particular class of stimulus (e.g., curved lines or straight lines), lateral connections help tune the neuron to the particular stimulus. This work suggests that even at the level of V1, the visual system is much more dynamic and flexible than most of us have thought.

We also do not wish to argue that the only role of lateral connections in V1 is to

integrate contours. The crosstalk between neighboring neurons certainly plays a number of roles in pattern perception that range from spatial selectivity to contrast normalization, to texture segregation. Contour integration represents just one component of early visual processing. Furthermore, the visual system performs various forms of integration (e.g., motion, stereo, color). The general concept of an association field should perhaps include all aspects of the stimulus that are “associated”.

We should also note that it is likely that few “computational problems” are solved in V1. Lateral connections certainly play a significant role. However, we expect to see that a full account will include more complex dynamical interaction between neurons and regions of the brain.

In this chapter, we can address a fraction of the studies that bear on contour integration. This body of research is the result of remarkable feedback between a broad range of disciplines, where the advances in one discipline have very rapidly influenced the research in a second, and which have led to new advances in a third. There remain a number of fundamental questions that have yet to be answered. Exactly how does lateral input mediate the firing of V1 cells in response to contours? What is the physiological explanation for why some flanking stimuli facilitate and others inhibit? The phenomenon of crowding has had a number of different explanations over the past few decades, and now the association field seems to provide an explanation for some pieces of that puzzle. The exciting new finding pointing toward the dynamic, task-dependent gating of the association field (McManus et al., 2011) brings attention into the picture, which is itself a high-level mechanism of great complexity. Characterizing the physiology behind this interaction will be a daunting task.

Acknowledgements

This work was partially supported by research grant SUG XXXX to A. Hayes, and a Department of Psychology grant to David J. Field

References

- Allman J., Miezin F., and McGuinness E. (1985) “Stimulus specific responses from beyond the classical receptive field: neurophysiological mechanisms for local-global comparisons in visual neurons” *Annual Review of Neuroscience* **8** 407-30.
- Bosking W. H., Zhang Y., Schofield B., and Fitzpatrick D. (1997) “Orientation selectivity and the arrangement of horizontal connections in Tree Shrew striate cortex” *The Journal of Neuroscience* **17** 2112–2127.
- Callaway EM. (1998) “Local circuits in primary visual cortex of the macaque monkey” *Annual Review of Neuroscience* **21** 47-74.

- Chavane F., Monier C., Bringuier V., Baudot P., Borg-Graham L., Lorenceau J., and Fregnac Y., (2000) "The visual cortical association field: A Gestalt concept or a psychological entity?" *Journal of Physiology (Paris)* **94** 333-342.
- Chisum H.J., Mooser F., and Fitzpatrick D. (2003) "Emergent properties of layer 2/3 neurons reflect the collinear arrangement of horizontal connections in tree shrew visual cortex" *Journal of Neuroscience* **23** 2947–2960.
- Dakin, S. C., and Baruch, N. J. (2009) "Context influences contour integration" *Journal of Vision* **9(2):13** 1-13
- Dakin, S., Greenwood, J., Carlson, T. and Bex, P. (2011), "Crowding is tuned for perceived (not physical) location" *Journal of Vision* **11(9)**.
- Dakin S. C. and Hess R. F. (1998) "Spatial-frequency tuning of visual contour integration" *Journal of the Optical Society of America, Series A* **15** 1486-1499.
- Dakin S. C. and Hess R. F. (1999) "Contour integration and scale combination processes in visual edge detection" *Spatial Vision* **12** 309-327.
- Das A. and Gilbert C. D. (1999) "Topography of contextual modulations mediated by short-range interactions in primary visual cortex" *Nature* **399** 655-661.
- Field D. J., Hayes A., and Hess R. F. (1993) "Contour integration by the human visual system: evidence for a local 'association field'" *Vision Research* **33** 173-193.
- Field D. J., Hayes A., and Hess R. F. (2000) "The roles of polarity and symmetry in contour integration" *Spatial Vision* **13** 51–66.
- Fitzpatrick D. (2000) "Seeing beyond the receptive field in primary visual cortex" *Current Opinion in Neurobiology* **10** 438-43.
- Fulvio, J., Singh, M. and Maloney, L. (2008) "Precision and consistency of contour interpolation" *Vision Research* **48** 831-849.
- Geisler W. S., Perry J. S., Super B. J., Gallogly D. P. (2001) "Edge co-occurrence in natural images predicts contour grouping performance" *Vision Research* **41** 711-724.
- Gilbert C. D. "Adult cortical dynamics" (1998) *Physiological Reviews* **78** 467-485.
- Gilbert C. D. and Wiesel T. N. (1979) "Morphology and intracortical projections of functionally characterised neurones in the cat visual cortex" *Nature* **280** 120 –125.
- Gilbert C. D. and Wiesel T. N. (1989) "Columnar specificity of intrinsic horizontal and corticocortical connections in cat visual cortex." *Journal of Neuroscience* **9** 2432-2442.
- Graham, N. (2011) "Beyond multiple pattern analyzers modeled as linear filters (as classical V1 simple cells): Useful additions of the last 25 years" *Vision Research* **51** 1397-1430.
- Gray C. M., Konig P., Engel A. K., and Singer W. (1989) "Oscillatory responses in cat visual cortex exhibit inter-columnar synchronization which reflects global stimulus properties" *Nature* **338** 334-37.
- Greenwood, J., Bex, P. and Dakin, S. (2009) "Positional averaging explains crowding with letter-like stimuli" *Proceedings of the National Academy of Sciences* **106** 13130-13135.
- Grossberg S. and Mingolla E. (1985) "Neural dynamics of perceptual grouping: textures, boundaries, and emergent segmentations" *Perception and Psychophysics* **38** 141-171.
- Hayes A. (2000) "Apparent position governs contour-element binding by the visual system" *Proceedings of the Royal Society, Series B* **267** 1341–1345.

- Hess R. F. and Dakin S. C. (1997) "Absence of contour linking in peripheral vision" *Nature* **390** 602-604.
- Hess R. F., Dakin S. C., and Field D. J. (1998) "The role of 'contrast enhancement' in the detection and appearance of visual contours" *Vision Research* **38** 783-787.
- Hess R. and Field D. (1999) "Integration of contours: new insights" *Trends in Cognitive Sciences* **12** 480-486.
- Hess R. F. and Field D. J. (1995) "Contour integration across depth" *Vision Research* **35** 1699-1711.
- Hess R. F., Hayes A., and Kingdom F. A. A. (1997) "Integrating contours within and through depth" *Vision Research* **37** 691-696.
- Heeger D. J. (1992) "Normalization of cell responses in cat striate cortex" *Visual Neuroscience* **9** 181-197.
- Hubel D. H. (1988) *Eye, Brain, and Vision* Scientific American Library: New York.
- Ito M. and Gilbert C. D. (1999) "Attention modulates contextual influences in the primary visual cortex of alert monkeys" *Neuron* **22** 593-604.
- Kapadia M. K., Ito M., Gilbert C.D. and Westheimer G. (1995) "Improvement in visual sensitivity by changes in local context: parallel studies in human observers and in V1 of alert monkeys" *Neuron* **15** 843-856.
- Kapadia M. K., Westheimer G., Gilbert C. D. (1999) "Dynamics of spatial summation in primary visual cortex of alert monkeys" *Proceedings of the National Academy of Sciences, USA* **96** 12073-12078.
- Kapadia M. K., Westheimer G., and Gilbert C. D. (2000) "Spatial distribution of contextual interactions in primary visual cortex and in visual perception" *Journal of Neurophysiology* **84** 2048-2062.
- Karube, F. & Kisvárday, Z. (2011) "Axon topography of layer IV spiny cells to orientation map in the cat primary visual cortex (area 18)" *Cerebral Cortex* **21** 1443.
- Kellman P. J. and Shipley T. F. (1991) "A theory of visual interpolation in object perception" *Cognitive Psychology* **23** 141-221.
- Kisvárday Z. F. and Eysel U. T. (1992) "Cellular organization of reciprocal patchy networks in layer III of cat visual cortex (area 17)" *Neuroscience* **46** 275-286.
- Kovacs I. and Julesz B. (1993) "A closed curve is much more than an incomplete one: effect of closure in figure-ground segmentation" *Proceedings of the National Academy of Sciences, USA* **90** 7495-7497.
- Kovacs I., Pápathomas T. V., Yang M., and Feher A, (1996) "When the brain changes its mind: Interocular grouping during binocular rivalry" *Proceedings of the National Academy of Sciences, USA* **93** 15508-15511.
- Lee S. H., Blake R. (2001) "Neural synergy in visual grouping: when good continuation meets common fate" *Vision Research* **41** 2057-64.
- Levi, D. (2008) "Crowding—an essential bottleneck for object recognition: a mini-review" *Vision Research* **48** 635-654.
- Li W., Piëch V., and Gilbert C.D. (2006) Contour saliency in primary visual cortex. *Neuron* **50** 951-962.
- Li, W., Piëch, V. & Gilbert, C. D. (2008) "Learning to link visual contours" *Neuron* **57** 442-451.

- Li Z. (2011) "Neural circuit models for computations in early visual cortex" *Current Opinion in Neurobiology* **21** 808-815.
- McManus, J., Li, W. & Gilbert, C. (2011) "Adaptive shape processing in primary visual cortex" *Proceedings of the National Academy of Sciences* **108** 9739.
- McManus, J., Ullman, S. & Gilbert, C. (2008) "A computational model of perceptual fill-in following retinal degeneration" *Journal of Neurophysiology* **99** 2086-2100.
- Maffei L. and Fiorentini A. (1976) "The unresponsive regions of visual cortical receptive fields" *Vision Research* **16** 1131-1139.
- Malach R., Amir Y., Harel M., and Grinvald A. (1993) "Relationship between intrinsic connections and functional architecture revealed by optical imaging and in vivo targeted biocytin injections in primate striate cortex." *Proceedings of the National Academy of Science USA* **90** 10469-10473.
- Mareschal I., Sceniak M. P. and Shapley R. M. (2001) "Contextual influences on orientation discrimination: binding local and global cues" *Vision Research* **41** 1915-1930.
- May, K. & Hess, R. (2007) "Ladder contours are undetectable in the periphery: A crowding effect?" *Journal of Vision* **7**(13).
- Meirowitz, E., Ayzenshtat, I., Bonne, Y., Itzhack, R., Werner-Reiss, U. & Slovin, H. (2010) "Population response to contextual influences in the primary visual cortex" *Cerebral Cortex* **20** 1293-1304.
- Mullen K. T., Beaudot W. H., McIlhagga W. H. (2000) "Contour integration in color vision: a common process for the blue-yellow, red-green and luminance mechanisms?" *Vision Research* **40** 639-55.
- Nelson J. I. And Frost B. J. (1985) "Intracortical facilitation among co-oriented, co-axially aligned simple cells in cat striate cortex" *Experimental Brain Research* **61** 54-61.
- Nugent A. K., Keswani R. N., Woods R. L., and Peli E. (2002) "Contour integration in peripheral vision reduces gradually with eccentricity" forthcoming.
- Papari, G. and Petkow, N. (2011) "Edge and line oriented contour detection: State of the art" *Image and Vision Computing* **29** 79-103.
- Parent P., and Zucker, S. (1989) "Trace inference, curvature consistency and curve detection" *IEEE Transactions on Pattern Analysis and Machine Intelligence* **11** 823-839.
- Pelli, D. (2008) "Crowding: A cortical constraint on object recognition" *Current Opinion in Neurobiology* **18** 445-451.
- Pelli, D. G., Palomares, M., and Majaj, N. J. (2004) "Crowding is unlike ordinary masking: Distinguishing feature integration from detection" *Journal of Vision* **4**(12) 1136-1169
- Pettet M. W., McKee S. P., Grzywacz N. M. (1998) "Constraints on long range interactions mediating contour detection" *Vision Research* **38** 865-879.
- Phillips W. A. and Singer W. (1997) "In search of common foundations for cortical computation" *Behavioural and Brain Sciences* **20** 657-722
- Polat U. (1999) Functional architecture of long-range perceptual interactions *Spatial Vision* **12** 143-62.

- Polat U., Mizobe K., Pettet M. W., Kasamatsu T., and Norcia A. M. (1998) "Collinear stimuli regulate visual responses depending on cell's contrast threshold" *Nature* **391** 580–584.
- Polat U. and Sagi D. (1993) "Lateral interactions between spatial channels: suppression and facilitation revealed by lateral masking experiments" *Vision Research* **33** 993–999.
- Rockland K. S. and Lund J. S. (1982) "Widespread periodic intrinsic connections in the tree shrew visual cortex" *Science* **215** 1532–1534.
- Ruthazer E. S. and Stryker M. P. (1996) "The role of activity in the development of long-range horizontal connections in area 17 of the ferret" *Journal of Neuroscience* **16** 7253-7269.
- Schwarzkopf, D. & Kourtzi, Z. (2008) "Experience shapes the utility of natural statistics for perceptual contour integration" *Current Biology* **18** 1162-1167.
- Sha'ashua A. and Ullman S. (1988) "Structural saliency" *Proceedings of the International Conference on Computer Vision, Tampa, Florida* 482-488.
- Sigman M., Guillermo G. A., Gilbert C. D., and Magneasco M. O. (2001) "On a common circle: Natural scenes and Gestalt rules" *Proceedings of the National Academy of Sciences, USA* **98** 1935-1940.
- Sincich L. C. and Blasdel G. G. (2001) "Oriented axon projections in primary visual cortex of the monkey" *Journal of Neuroscience* **21** 4416-4426.
- Walker G. A., Ohzawa I., and Freeman R. D. (1999) "Asymmetric Suppression Outside the Classical Receptive Field of the Visual Cortex" *The Journal of Neuroscience* **19** 10536–10553.
- Yen S. C., Finkel L. H. (1998) "Extraction of perceptually salient contours by striate cortical networks" *Vision Research* **38** 719-741.
- Yoshioka T., Blasdel G. G., Levitt J. B., and Lund J. S. (1996) "Relation between patterns of intrinsic lateral connectivity, ocular dominance, and cytochrome oxidase-reactive regions in macaque monkey striate cortex" *Cerebral Cortex* **6** 297-310.
- Zipser K., Lamme V. A. F., and Schiller, P. H. (1996) "Contextual modulation in primary visual cortex" *Journal of Neurophysiology* **16** 7376-7389.