Contour integration: Psychophysical, neurophysiological and computational perspectives

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Abstract

One of the important roles of our visual system is to detect and segregate objects. Neurons in the early visual system extract local image features from the visual scene. To combine these features into separate, global objects, the visual system must perform some kind of grouping operation. One such operation is contour integration. Contours form the outlines of objects, and are the first step in shape perception. We discuss the mechanism of contour integration from psychophysical, neurophysiological and computational perspectives.

1. A psychophysical perspective

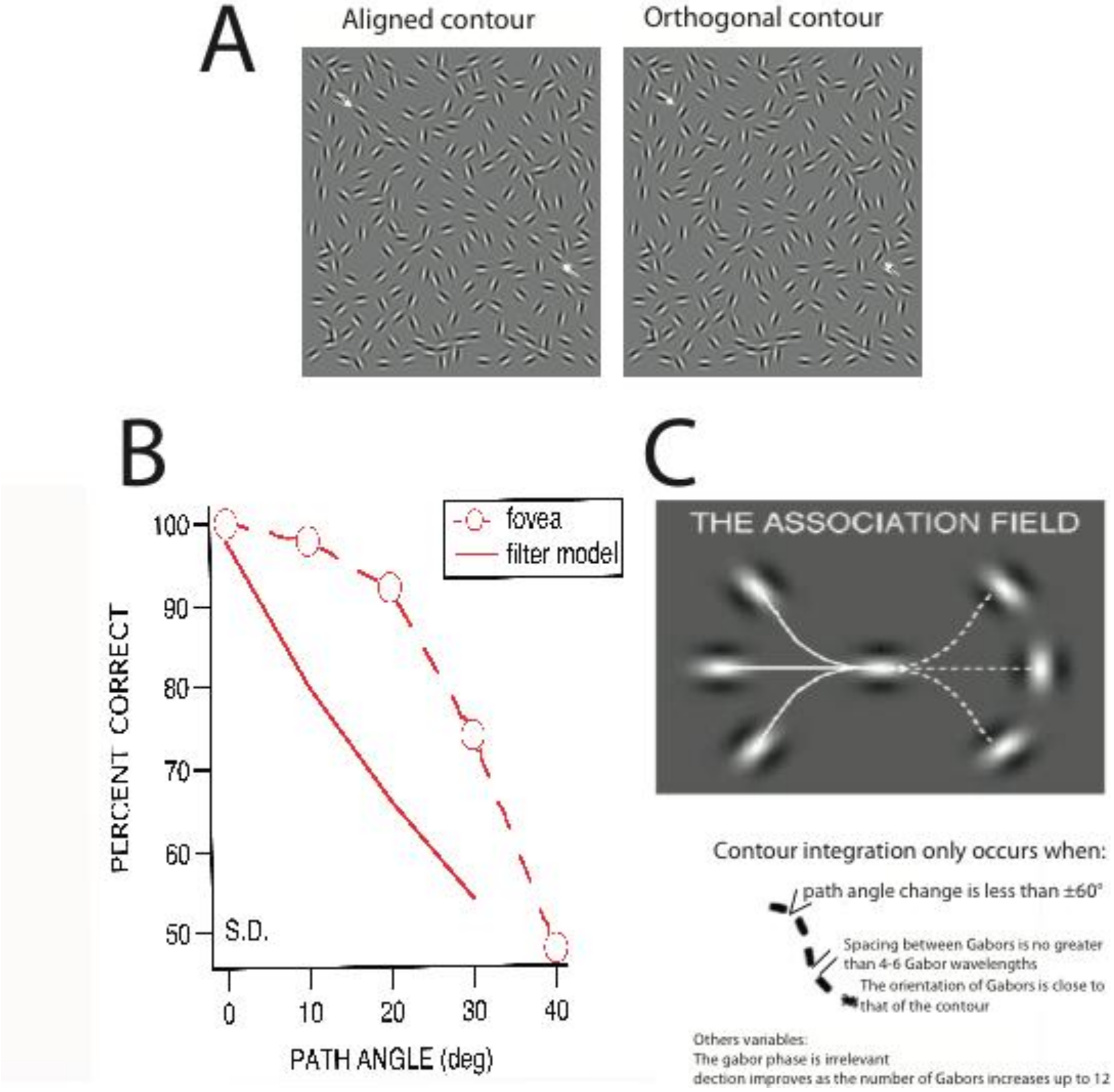
1.1. Natural scenes and the visual system

The mammalian visual system has evolved to extract relevant information from natural images that in turn have specific characteristics, one being edge alignments that define image features. Natural scenes exhibit consistent statistical properties that distinguish them from random luminance distributions over a large range of global and local image statistics. Edge co-occurrence statistics in natural images are dominated by aligned structure {Geisler, 2001 #3299;Sigman, 2001 #1440;Elder, 2002 #3254} and parallel structure (Geisler et al. 2001). The aligned edge structure follows from the fact that pairs of separated local edge segments are most likely to be aligned along a linear or co-circular path. This pattern occurs at different spatial scales (Sigman et al. 2001). The co-aligned information represents contour structure in natural images. The parallel information, on the other hand, is most frequently derived from regions of the same object and arises from surface texture. Edges are an important and highly informative part of our environment. Edges that trace out a smooth path show correspondence of position over a wide range of different spatial scales. As edges become more jagged, and indeed more like edges of the kind common in natural images (i.e. fractal), correspondence in position becomes limited to a smaller band of spatial scales. Although jagged edges have continuous representation over spatial scale, the exact position and orientation of the edge changes from scale to scale (Field, Hayes & Hess 1993). The contour information is therefore quite different at different spatial scales so, to capture the full richness of the available information, it is necessary to make use of a range of contour integration operations that are each selective for a narrow band of scales.

1.2. Quantifying contour detection

The history of studies on contour integration stretches back to the Gestalt psychologists (Koffka 1935) who formulated rules for perceptually significant image structure, including contour continuity: the Gestalt "law" of good continuation. More recent attempts to examine these ideas psychophysically have used element arrays composed of dots or line segments (Beck, Rosenfeld & Ivry 1989, Moulden 1994, Smits & Vos 1987, Uttal 1983). Although these studies were informative, the broadband nature of the elements used and the lack of control for element density made it difficult to appreciate the relationship between the tuning properties of single cells and the network operations describing how their outputs might be combined. Contours composed of broadband elements or strings of more closely spaced elements could always be integrated using a single, broadband detector without the need for network interactions (relevant to this is fig 2).

Since local edge alignment in fractal images depends on scale, Field, Hayes and Hess (1993) addressed this question using spatial frequency narrowband elements (i.e. Gabors) and ensured that local density cues could not play a role. We thought there might be specific rules for how the responses of orientation-selective V1 cells are combined to encode contours in images. A typical stimulus is seen in figure 1A; it is an array of oriented Gabor micropatterns, a subset of which (frame on the left) are aligned to make a contour (indicated by arrow).



Contour integration only occurs when:

path angle change is less than ±60°

Spacing between Gabors is no greater than 4-6 Gabor wavelengths

The orientation of Gabors is close to that of the contour

Others variables:
The gabor phase is irrelevant
dection improves as the number of Gabors increases up to 12

Figure 1: Contours defined by orientation-linking. In A, a comparison of a straight contour defined by elements that are aligned with the contour (left) or orthogonal to it (right). In B, the visual system's performance on detecting orientationally-linked contours of different curvature, compared with that of a single elongated filter (solid line). In C, the proposed mechanism, a network interaction called an "Association Field" (adapted from Field et al 1993 & Hess and Dakin, 1997)

In the figure in the left frame of figure 1A, the contour in the middle of the field going from the bottom right to the top left is clearly visible, suggesting that either elements aligned or of the same orientation group together. The figure in the right frame of figure 1A on first inspection does not contain an obvious contour, yet there is a similar subset of the elements of the same orientation and in the same spatial arrangement as in the left frame of figure 1A. These elements are however not aligned with the contour path, but orthogonal to it, and one of our initial observations was that although this arrangement did produce visible contours, the contours were far less detectable than those with elements aligned with the path. This suggested rules imposed by the visual grouping analysis relating to the alignment of micropatterns, which may reflect the interactions of adjacent cells with similar orientation preference exploiting the occurrence of co-oriented structure in natural images.

1.2.1.Snakes, ladders, and ropes.

Most experiments on contour integration have used “snake” contours in which the contour elements are aligned, or nearly aligned, with the path (see figure 1 A-top left). Other forms of contours are “ladders” (Bex, Simmers & Dakin 2001, Field et al. 1993, Ledgeway, Hess & Geisler 2005, May & Hess 2007a,b; May and Hess, 2008) in which the elements are perpendicular to the path (see figure 1A-top right), and “ropes”(coined by S. Schwartzkopf) (Ledgeway et al. 2005), in which the elements are all obliquely oriented in the same direction relative to the contour. Snakes are the easiest to detect and ropes are the hardest (Ledgeway et al. 2005). Since the three types of contour are distinguished by a group rotation of each contour element, they are identical in their intrinsic detectability (an ideal observer would perform identically on all three); the difference in performance between the different contour types therefore reveals something about the mechanisms that the visual system uses to detect them, i.e. it constrains models of contour integration.

Since ropes are essentially undetectable, models tend to possess mechanisms that can link elements arranged in a snake or ladder configuration, but not in a rope configuration (May & Hess 2007b, May & Hess 2008, Yen & Finkel 1998). To explain the inferior detection of ladders, Field et al (1993) and May and Hess (2007b) proposed weaker binding between ladder elements than snake elements. Using a model based on Pelli et al.’s (2004) crowding model, May and Hess (2007b) showed that this single difference between snake and ladder binding was sufficient to explain their finding that detection of ladder contours was fairly good in the centre of the visual field, but declined much more rapidly than snakes with increasing eccentricity.

1.3. The Association Field concept

To determine how visual performance varies as a function of the curvature of the contour, the angular difference between adjacent 1-D Gabors along the contour path is varied. The effect of this manipulation (unfilled symbols) is shown in figure 1B where psychophysical performance (% correct) is plotted against path angle (degrees). Performance remains relatively good for paths of intermediate curvature but declines abruptly once the path becomes very curved. These paths were jagged in that the sign of the orientation change from element to element is random, in contrast to smooth curves where the angular change always has the same sign. Smooth curves are easier to detect by a small amount (Dakin & Hess 1998, Hess, Hayes & Field 2003, Pettet, McKee & Grzywacz 1996) but otherwise show the same dependence on curvature. While straight contours could in principle be detected by an elongated receptive field, avoiding the need for more complex inter-cellular interactions, this would not be the case for highly curved contours. The solid line in figure 1B gives the linear filtering prediction (Hess & Dakin 1997) for a single elongated receptive field: its dependence on curvature is much stronger than that measured psychophysically, adding support to the idea that contours of this kind are detected by interactions across a cellular array rather than by spatial summation within an individual cell. This conclusion was further strengthened by the finding that performance is only marginally affected if the contrast polarity of alternate contour elements (and half the background elements) is reversed (Field, Hayes & Hess 1997). This manipulation would defeat any elongated receptive field that linearly summated across space. This suggests that even the detection of straight contours may be via the linking of responses of a number of cells aligned across space but with similar orientation preferences.

On the basis of the above observations Field, Hayes and Hess (1993) suggested that these interactions could be described in terms of an Association Field, a network of cellular interactions specifically designed to capitalize on the edge-alignment properties of contours in natural images. Figure 1C illustrates the idea and summarizes the properties of the Association Field. The facilitatory interactions are shown by continuous lines and the inhibitory interactions by dashed lines. The closer the adjacent cell is in its position and preferred orientation, the stronger the facilitation. This psychophysically defined “Association Field” matches the joint-statistical relationship that edge-alignment structure has in natural images (Geisler, 2001; Sigman, 2001; Elder, 2002; Kruger, 1998; for more detail, see Elder, this volume).

So far we have assumed that the detection of contours defined by the alignment of spatial frequency bandpass elements embedded within an array of similar elements of random orientation is accomplished by a low-level mechanism operating within spatial scale (i.e. V1-V3 receptive fields) rather than by a high-level mechanism operating across scale. This latter idea would be more in line with what the Gestalt psychologists envisaged. The question then becomes, are contours integrated within or across spatial scale? Figure 2 shows results obtained when the spatial frequency of alternate micropatterns is varied (Dakin & Hess 1998). The top frames show examples of curved contours made up of elements of the same spatial scale (B) as opposed to elements from two spatial scales (A and C). The results in the bottom frames show how the psychophysical contour detection performance depends on the spatial frequency difference between alternate contour elements. Contour integration exhibits spatial frequency tuning, more so for curved than for straight contours, suggesting it is primarily a within-scale operation, providing support for orientation linking as described by the Association Field operating at a low level in the cortical hierarchy.

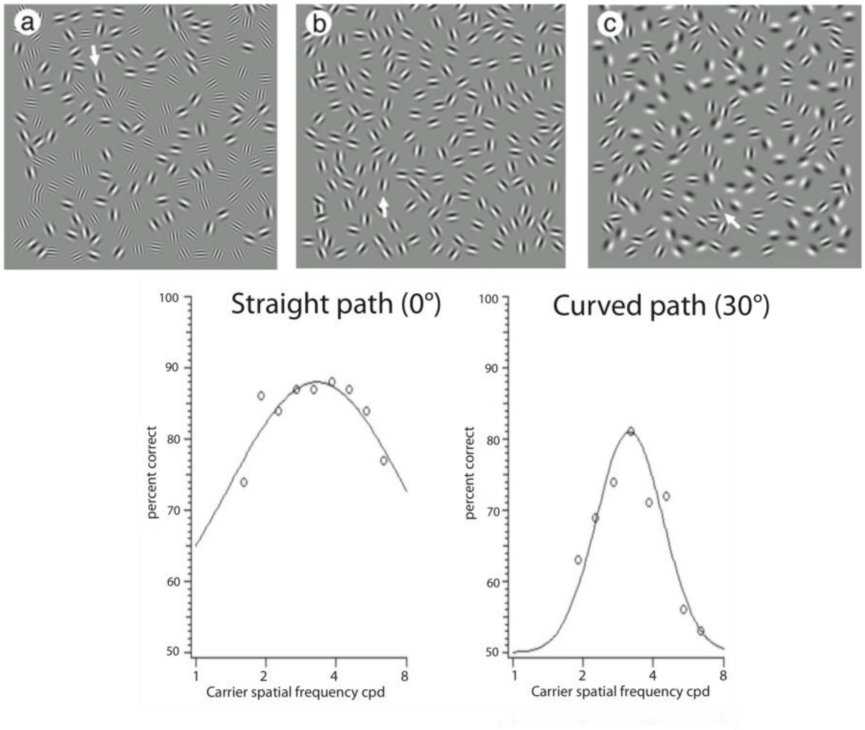


Figure 2: Orientational linking occurs within spatial scale. Frames at the top left and right (a&c) show examples of contours defined by the orientation of elements that alternate in spatial scale. The frame at the top centre illustrates a contour defined by the orientation of elements within the one scale. In the bottom frames, the detectability of contours, be they straight (bottom left) or curved (bottom right), shows spatial scale tuning (adapted from Dakin and Hess, 1998). In this experiment, one set of Gabors had a carrier spatial frequency of 3.2 cpd, and the other set had a spatial frequency indicated by the horizontal axis of the graphs.

1.3.1. The nature and site of the linking process.

The linking code within the Association Field must be conveyed in the firing pattern of cells in early visual cortex. The typical form of this response as reflected in the post-stimulus time histogram involves an initial burst of firing within the first 50 milliseconds followed by a slow sustained response declining in amplitude over a 300 millisecond period. In principle, the extent of facilitative inter-cellular interaction reflecting contour integration could be carried by the amplitude of the initial burst of firing or the later sustained response or the pattern (including synchronicity) of spikes. The initial burst of spikes is thought to carry the contrast-dependent signal (Lamme 1995, Lamme, Super & Speckreijse 1998, Zipser, Lamme & Schiller 1996), and this is unlikely to carry the linking signal because it has been shown that randomizing the contrasts of the Gabor elements has little effect on contour integration performance (Hess, Dakin & Field 1998).

Contour integration (i.e. its curvature dependence) does not depend critically on the element temporal frequency so long as it is within the temporal window of visibility of individual elements (Hess, Beaudot & Mullen 2001), again suggesting a decoupling from contrast processing. However, when the local orientation of contour elements changes over time, three interesting finding emerge. First, the dynamics of contour integration are slow compared with contrast integration. Second, the dynamics are dependent on curvature; the highest temporal frequency of orientation change that would support linking varied from around 10Hz for straight contours to around 1-2 Hz for curved contours. Third, this does not depend on absolute contrast of elements (Hess et al. 2001). These dynamics are not what one would expect if either synchrony of cellular firing which is in the 1-2 millisec range (Singer & Gray 1995) (Beaudot 2002, Dakin & Bex 2002) or contrast (Polat 1999, Polat & Sagi 1993, Polat & Sagi 1994) were involved in the linking process. The sluggish temporal properties of the linking process may point to the code being carried by the later sustained part of the spike train (Lamme 1995, Lamme et al. 1998, Zipser et al. 1996).

Contour integration is not a cue-invariant process (Zhou & Baker 1993) in that not all oriented features result in perceptual contours: contours composed of elements alternately defined by chromaticity and luminance do not link into perceptual contours (McIlhagga & Mullen 1996) and elements defined by texture-orientation do not link together either (Hess, Ledgeway & Dakin 2000). The rules that define linkable contours provide a psychophysical cue as to the probable site of these elementary operations. McIlhagga and Mullen (1996) and Mullen, McIllhagga and Beaudot (2000) showed that contours defined purely by chromaticity obey the same linking rules but that elements alternately defined by luminance and chromatically do not link together. This suggests that, at the cortical stage at which this occurs, luminance and chromatic information are processed separately, suggesting a site later than V1since in V1 cells tuned for orientation processing both chromatic and achromatic information (Johnson, Hawken & Shapley 2001). Hess and Field (1995) showed that contour integration must occur at a level in the cortex where the cells process disparity. They devised a dichoptic stimulus in which the embedded contour could not be detected monocularly because it oscillated between two depth planes - it could be detected only if disparity had been computed first. These contours were easily detected and their detectability did not critically depend on the disparity range, suggesting the process operated at a cortical stage at or after where relative disparity was computed. This is believed to be V2 (Parker & Cumming 2001).

2. A neurophysiological perspective

2.1. Cellular physiology

Neurons in primary visual cortex (V1 or striate cortex) respond to a relatively narrow range of orientations within small (local) regions of the visual field (Hubel & Wiesel 1968). As such, V1 can be thought of as representing the outside world using a bank of oriented filters (De Valois & De Valois 1990). These filters form the first stage of contour integration. In line with this filter notion, the V1 response to visual stimulation is well predicted by the contrast-energy of the stimulus for synthetic (Boynton, Demb, Glover & Heeger 1999, Mante & Carandini 2005) and natural images (Dumoulin, Dakin & Hess 2008, Kay, Naselaris, Prenger & Gallant 2008, Olman, Ugurbil, Schrater & Kersten 2004).

Even though V1 responses are broadly consistent with the contrast-energy within the images, a significant contribution of neuronal interactions is present that modulate the neural responses independent of the overall contrast-energy (Allman, Miezin & McGuinness 1985, Fitzpatrick 2000). These neuronal interactions can enhance or suppress neural responses and may also support mechanisms such as contour integration. The Association Field might be implemented by facilitatory interactions between cells whose preferred stimuli lie close together on a smooth curve, and inhibitory interactions between cells whose preferred stimuli would be unlikely to coexist on the same physical edge. There is anatomical evidence for such a hard-wired arrangement within the long-range intrinsic cortical connections in V1 (Gilbert & Wiesel 1979, Gilbert & Wiesel 1989). Neurons in different orientation columns preferentially link with neurons with co-oriented, co-axially aligned receptive fields {Bosking, 1997 #1057;Kisvárday, 1997 #3943;Malach, 1993 #1060;Stettler, 2002 #3745;Weliky, 1995 #1802;Schmidt, 1997 #1056;Pooresmaeili, #3892}.

Neurophysiological recordings further support these anatomical observations (Gilbert, Das, Ito, Kapadia & Westheimer 1996, Kapadia, Ito, Gilbert & Westheimer 1995, Li, Piech & Gilbert 2006, Nelson & Frost 1985, Polat, Mizobe, Pettet, Kasamatsu & Norcia 1998). Neuronal responses to local oriented bars within the classical receptive field are modulated by the presence of flanking bars outside the classical receptive field, i.e. in the extra-classical receptive field. Importantly, the elements in the extra-classical receptive field are not able to stimulate the neuron alone, so the response modulation critically depends on an interaction between the elements placed within the classical receptive field and those placed outside it. Furthermore, the amount of response modulation is greatly affected by the relative positions and orientations of the stimulus elements. Co-axial alignment usually increases neural responses whereas orthogonal orientations usually decrease neural responses (Blakemore & Tobin 1972, Jones, Wang & Sillito 2002, Kastner, Nothdurft & Pigarev 1997, Knierim & Van Essen 1992, Nelson & Frost 1978, Nothdurft, Gallant & Van Essen 1999, Sillito, Grieve, Jones, Cudeiro & Davis 1995). These neural modulations may partly be explained by the hard-wired intrinsic connectivity in V1 but may also be supported by feedback or top-down influences from later visual cortex (Li, Piech & Gilbert 2008).

The evidence suggests that the extra-classical receptive field modulations resemble the proposed contour Association Field. For example, recording in V1, Kapadia and colleagues (Kapadia et al. 1995) presented flanking bars in many different configurations in the extra-classical receptive field while presenting a target bar in the classical receptive field at the neuron's preferred orientation. Kapadia and colleagues found that facilitation was generally highest for small separations and small or zero lateral offsets between the flanker and target bar. They also varied the orientation of the flanking bar while maintaining good continuation with the target bar. The distribution of preferred flanker orientations was strongly peaked at the cell's preferred orientation, indicating co-axial facilitation. Yet some cells did not have an obvious preferred flanker orientation or appeared to prefer non-co-axial flanker orientations. Kapadia and colleagues suggested that the latter neurons might play a part in integrating curved contours. Tuning to curvature is also highly prevalent in V2 and V4 (Anzai, Peng & Van Essen 2007, Hegde & Van Essen 2000, Ito & Komatsu 2004, Pasupathy & Connor 1999) suggesting a role for these sites in co-circular integration along curved contours. V4 neurons are also tuned to simple geometric shapes, further highlighting its role in intermediate shape perception (Gallant, Braun & Van Essen 1993, Gallant, Connor, Rakshit, Lewis & Van Essen 1996).

2.2. Functional imaging

Functional MRI studies further highlight the involvement of human extra-striate cortex in contour integration. For example, Dumoulin, Dakin and Hess (2008) contrasted the responses to several natural and synthetic image categories (Figure 3). They found distinct response profiles in V1 and extra-striate cortex. Contrast-energy captured most of the variance in V1, though some evidence for increased responses to contour information was found as well. In extra-striate cortex, on the other hand, the presence of sparse contours captured most of the response variance despite large variations in contrast-energy. These results provide evidence for an initial representation of natural images in V1 based on local oriented filters. Later visual cortex (and to a modest degree V1) incorporates a facilitation of contour-based structure and suppressive interactions that effectively amplify sparse-contour information within natural images.

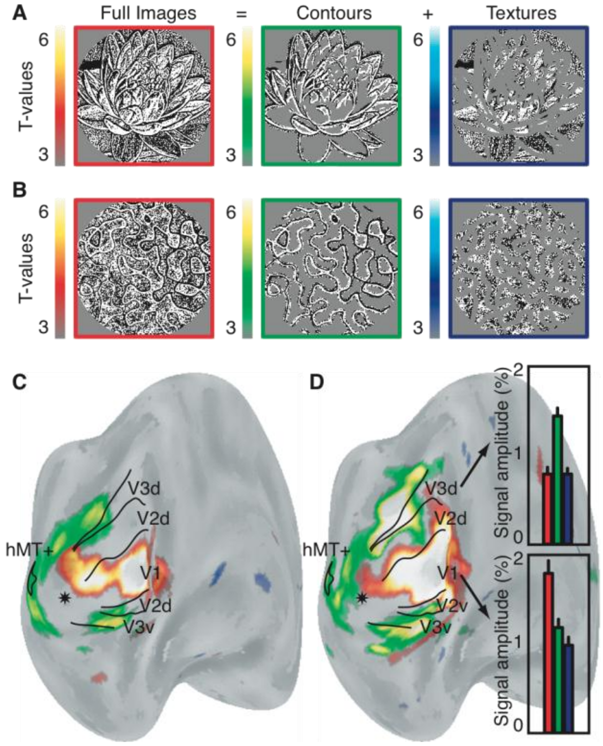


Figure 3: fMRI responses elicited by viewing pseudo-natural (A, C) and synthetic (B, D) images. The fMRI responses are shown on an inflated cortical surface of the left hemisphere (C, D). The responses are an average of five subjects and the average visual area borders are identified. Both pseudo-natural and synthetic images yield similar results. In V1 strongest responses are elicited by viewing of the "full images" (D, bottom inset). This supports the notion that V1 responses are dominated by the contrast-energy within images. In extra-striate cortex, on the

other hand, strongest responses are elicited by viewing "contour" images (D, top inset). These results suggest that facilitative and suppressive neural interactions within and beyond V1 highlight contour information in extra-striate visual cortex. Adapted from Dumoulin, Dakin and Hess (2008).

Similarly, Kourtzi and colleagues implicated both early and late visual cortex in the process of contour integration (Altmann, Bulthoff & Kourtzi 2003, Altmann, Deubelius & Kourtzi 2004, Kourtzi & Huberle 2005, Kourtzi, Tolias, Altmann, Augath & Logothetis 2003). Using a variety of fMRI paradigms they demonstrated involvement of both V1 and later visual areas. However, the stimuli in all these fMRI studies contain closed contours. Contour closure creates simple concentric shapes that may be easier to detect (Kovacs & Julesz 1993) and may involve specialized mechanisms in extra-striate cortex (Altmann et al. 2004, Dumoulin & Hess 2007, Tanskanen, Saarinen, Parkkonen & Hari 2008). Furthermore, contour closure may introduce symmetry for which specialized detection mechanisms exist (Wagemans 1995). Therefore these fMRI results may reflect a combination of contour integration and shape processing, and may not uniquely identify the site of the contour integration.

Beyond V2 and V4 lies ventral cortex, which processes shapes. In humans, the cortical region where intact objects elicit stronger responses than their scrambled counterparts is known as the lateral occipital complex (LOC) (Malach, Reppas, Benson, Kwong, Jiang, Kennedy, Ledden, Brady, Rosen & Tootell 1995). It extends from lateral to ventral occipital cortex. The term 'complex' acknowledges that this region consists of several visual areas. Early visual cortex (V1) is often also modulated by the contrast between intact and scrambled objects but in an opposite fashion, i.e. fMRI signal amplitudes are higher for scrambled images (Dumoulin & Hess 2006, Fang, Kersten & Murray 2008, Grill-Spector, Kushnir, Hendler, Edelman, Itzchak & Malach 1998, Lerner, Hendler, Ben-Bashat, Harel & Malach 2001, Murray, Kersten, Olshausen, Schrater & Woods 2002, Rainer, Augath, Trinath & Logothetis 2002). Stronger responses to scrambled objects have been interpreted as feedback from predictive coding mechanisms (Fang et al. 2008, Murray et al. 2002) or incomplete match of low-level image statistics including the breakup of contours (Dumoulin & Hess 2006, Rainer et al. 2002). These results highlight the interaction between early and late visual areas in the processing of contour and shape.

3. A computational perspective

3.1. Two main classes of contour integration model

Models of contour integration generally fall into one of two categories: *Association Field* models or *filter overlap* models [although see Watt, Ledgeway & Dakin (2008) for consideration of other models]. In contrast to the Association Field, in filter overlap models, grouping occurs purely because the filter responses to adjacent elements overlap.

Association Field models. Field et al (1993) did not explicitly implement an Association Field model, but several researchers have done so since. Yen and Finkel (1998) set up a model that had two sets of facilitatory connections: co-axial excitatory connections between units whose preferred stimulus elements lay on co-circular paths (for detecting snakes, as in figure 1A left), and trans-axial excitatory connections between units whose preferred stimulus elements were parallel (for detecting ladders, as in figure 1A right). The two sets of connections competed with each other, so the set of connections carrying the weaker facilitatory signals was suppressed. Their model did a fairly good job of quantitatively accounting for a range of data from Field et al. (1993) and Kovács and Julesz (1993).

Another Association Field model was set up by Li (1998), who took the view that contour integration is part of the wider task of computing visual saliency. Li's saliency model was based firmly on the properties of V1 cells. The same model was able to account for contour integration phenomena, as well as many other phenomena related to visual search and segmentation in multi-element arrays (Li 1999, Li 2000, Li 2002, Zhaoping & May 2007). However, Li provided only qualitative demonstrations of the model's outputs, rather than quantitative simulations of psychophysical performance like those of Yen and Finkel.

The models of Li and of Yen and Finkel were recurrent neural networks, which exhibit temporal oscillations. Both models showed synchrony in oscillations between units responding to elements within the same contour, but a lack of synchrony between units responding to elements in different contours. Both sets of authors suggested that this might form the basis of segmentation of one contour from others or from the background. In addition, the units responding to contour elements responded more strongly than those responding to distractor elements.

The Association Field models described so far used ad hoc weightings on the facilitatory connections. A different approach is to assume that the connection weights reflect the image statistics that the observer is using to do the task. In this view, the Association Field is a statistical distribution that allows the observer to make a principled decision about whether two edge elements should be grouped into the same contour. Geisler et al (2001) used this approach and found that Association Fields derived from edge co-occurrence statistics in natural images accurately accounted for human data on a contour detection task. Elder and Goldberg (2002) followed with a similar approach.

Watt et al. (2008) have pointed out that many of the patterns of performance found in contour integration experiments may reflect the difficulty of the task, rather than the properties of the visual mechanism that the observer is using. Traditionally, task difficulty is factored out by expressing the participant's performance relative to the performance of the ideal observer for the task (Banks, Geisler & Bennett 1987, Geisler 1984, Geisler 1989). For many simple visual tasks, it is straightforward to derive the ideal algorithm, but this is not the case for most contour integration tasks because of the complexity of the algorithms used for generating the contours. Recently, Ernst et al. (2012) tackled this problem in an elegant way: they turned the idea of the Association Field on its head and used it to *generate* the contours in the first place. The Association Field used to generate the contours is then the correct, i.e. optimal, statistical distribution for calculating the likelihood that the stimulus contains the contour. Using this approach, the properties of the contour, such as curvature, element separation, etc., are determined by the parameters of the Association Field; the ideal observer, who always uses the Association Field that generated the contour in the first place, would therefore have an advantage over the human observer in knowing which sort of contour was being presented on each trial. Not surprisingly, Ernst et al. found that, although the ideal observer's pattern of performance, as a function of contour properties, was qualitatively similar to human performance, the ideal observer performed much better. They investigated the possibility that the human observer was using the same Association Field on each trial. This strategy would be optimal for contours generated using that Association Field, but suboptimal in all other cases. They generated the single Association Field that fitted best to all the data, but even this suboptimal model outperformed the human observers. Ernst et al. ruled out the effect of noise because the model's correlation with the human data was the same as the correlations between individual subjects, so it would seem that their model was simply using a better Association Field for the task than the human observers.

Although the ideal observer's performance can provide a useful benchmark against which to compare human performance, it may be over-optimistic to assume that human observers will be able to implement a strategy that is optimal for whichever psychophysical task they are set: it is more likely that the human observer possesses mechanisms that are optimal for solving real-world tasks, and recruits them to carry out the artificial psychophysical task at hand (McIlhagga & May 2012). The natural-image-based approach to deriving the association Field taken by Geisler et al. and Elder and Goldberg may therefore be more fruitful than a pure ideal-observer approach.

Filter-overlap models. As an alternative to Association Field models, Hess and Dakin (1997) implemented a model in which the contour linking occurred due to spatial overlap of filter responses to different elements. Applying a V1-style filter to the image has the effect of blurring the elements so that they join up. Thresholding the filter output to black and white generates a set of blobs, or zero-bounded response distributions (ZBRs), and a straight contour will generate a long ZBR in the orientation channel aligned with the contour. In Hess and Dakin's model, the formation of ZBRs took place only within orientation channels, and this severely limited its ability to integrate curved contours. The model's performance, as a function of contour curvature, is plotted in Figure 1B, which shows that, while the model could successfully detect straight contours, its performance deteriorated rapidly as the contour became more curved. Hess and Dakin suggested that this kind of model may reflect contour integration in the periphery, while the Association Field may reflect processing in the fovea.

The poor performance of Hess and Dakin's filter-overlap model on detection of highly curved contours was not a result of the filter-overlap process itself, but a result of the fact that formation of ZBRs took place within a single orientation channel. May and Hess (2008) lifted this restriction, and implemented a model that could extend ZBRs across orientation channel as well as space. Unlike Hess and Dakin's model, May and Hess's model can easily integrate curved contours, and we have recently found that it provides an excellent fit to a large psychophysical data set (Hansen, May & Hess, in preparation). May and Hess's model forms ZBRs within a 3-

dimensional space, (x, y, θ), consisting of the two dimensions of the image (x, y), and a third dimension representing filter orientation (θ). A straight contour would lie within a plane of constant orientation in this space, whereas a curved contour would move gradually along the orientation dimension as well as across the spatial dimensions. This 3-dimensional space is formally known as the *tangent bundle*, and subsequently other researchers have confirmed its usefulness in contour-completion tasks (Ben-Yosef & Ben-Shahar 2012).

Around the same time that May and Hess (2008) were developing their model of contour integration, Rosenholtz and colleagues independently had the same idea, but applied it to a much broader set of grouping tasks (Rosenholtz, Twarog, Schinkel-Bielefeld & Wattenberg 2009). To perform grouping on the basis of some feature dimension, f, you can create a multidimensional space (x, y, f), and then plot the image in this space. Then image elements with similar feature values and spatial positions will be nearby and, if you blur the representation, they join up.

3.1.1. Spatial extent of contour linking

Contour integration performance generally declines with increasing distance between the elements in a contour stimulus (Field et al. 1993, May & Hess 2008). As with the comparison between different contour types (snake, ladder and rope), increasing the separation does not make the task intrinsically harder, so the effect of increasing the separation tells us about the spatial extent of the linking mechanism.

May and Hess (2008) varied both the element separation and Gabor carrier frequency in a factorial design and found that the results strongly constrained the architecture of filter-overlap models of contour integration. They found that performance was largely unaffected by the carrier wavelength of the elements; high-frequency elements could be integrated over almost as long distances as low-frequency ones. This rules out filter-overlap models that use a linear filter to integrate the elements because, to integrate over a large distance, you need a large-scale filter, and large-scale filters tend not to respond well to high-frequency elements. To explain this result, May and Hess proposed a 2nd-order mechanism in which a squaring operation lies between two linear filters. If we adjust the scale of the 1st-stage filter (before the nonlinearity) to match the contour elements, and adjust the scale of the 2nd-stage filter (after the nonlinearity) to be large enough to bridge the gap between the elements, then we can accommodate pretty much any combination of element spacing and carrier wavelength. If the 1st and 2nd stage filters are parallel, the model detects snakes; if they are orthogonal, the model detects ladders. The very poor performance on ropes suggests that there is no corresponding mechanism in which the 1st and 2nd stages are oriented at 45° to each other.

3.1.2. Does the same mechanism mediate both contour integration and psychophysical flanker facilitation?

It has often been suggested that the mechanism that mediates contour integration is also responsible for the psychophysical flanker facilitation effect, whereby a low-contrast target is made more detectable by the presence of spatially separate flanking elements positioned a moderate distance from the target. This is an attractively parsimonious idea that has been suggested by many researchers

(Gilbert et al. 1996, Kapadia et al. 1995, Li 1996, Li 1998, Pettet, McKee & Grzywacz 1998, Polat 1999, Polat & Bonneh 2000, Stemmler, Usher & Niebur 1995, Yen & Finkel 1998). If the same mechanisms underlie psychophysical flanker facilitation and contour integration, one would expect both phenomena to be observed in the same range of conditions. This prediction was tested by Williams & Hess (1998). Firstly, they found that, unlike foveal contour integration, flanker facilitation requires the elements to have the same phase. Secondly, flanker facilitation was abolished when co-circular target and flankers differed in orientation by 20°, whereas contours are easily detectable with larger orientation differences between neighbouring elements. Thirdly, flanker facilitation was abolished or greatly reduced when the stimulus was placed only 3° into the periphery, whereas contour integration can be performed easily at much larger eccentricities. More recently, Huang, Hess, & Dakin (2006) showed that flanker facilitation was disrupted by dichoptic presentation to a much greater extent than contour integration, suggesting that contour integration has a more central cortical site than flanker facilitation. The results from Williams & Hess (1998) and Huang et al. (2006) showed that flanker facilitation occurs in a much more limited range of conditions than contour integration, so it seems unlikely that contour integration could be achieved by the mechanisms responsible for psychophysical flanker facilitation. Williams and Hess argued that the latter effect might arise through a reduction in positional uncertainty due to the flanking elements, a view subsequently supported by Petrov, Verghese and McKee (2006).

3.1.3. Does the same mechanism mediate both contour integration and crowding?

Crowding is the phenomenon whereby a stimulus (usually presented in the periphery) that is easily identifiable becomes difficult to identify when flanked by distracting stimuli. One view is that crowding is caused by excessive integration across space. Pelli, Palomares, and Majaj (2004) proposed that, at each point in the visual field, there is a range of integration field sizes, and the observer uses the size of field that is best for the task at hand; integration fields are used for any task that involves integration of information from more than one elementary feature detector. Pelli et al. argued that, at each location in the visual field, the minimum available integration field size scales with eccentricity. This means that, particularly in the periphery, the observer may be forced to use an integration field that is inappropriately large for the task, and that is when crowding occurs.

Pelli et al.'s integration field sounds much like Field et al.'s Association Field, and May and Hess (2007b) argued that the Association Field is in fact an example of the kind of integration field that Pelli et al. suggested mediates the crowding effect. May and Hess implemented a simple version of Pelli et al.'s crowding model and showed that this model could explain data on contour detection in fovea and periphery, as well as showing Pelli et al.'s three key diagnostic features of crowding: The critical target-flanker spacing for crowding to occur is independent of the size of the target, scales with eccentricity, and is greater on the peripheral side of the target. Subsequently, van den Berg, Roerdink and Cornelissen (2010) reported a population code model of feature integration that, like May and Hess's (2007b) model, explained both contour integration and crowding.

May and Hess (2007b) provided only circumstantial evidence for their proposed link between contour integration and crowding. Pelli and Chakravarthy (2011) later directly tested this proposal by using the same stimuli for both a contour integration task and a crowding task. As the “wiggle” in the contours increased, the contour integration performance got worse (indicating less integration), and performance on the crowding task got better (again indicating less integration). The “wiggle threshold” was the same on both tasks, indicating that the same mechanism mediated both contour integration and crowding (see also Rosenholtz, this volume).

4. Conclusion

The visual system groups local edge information into contours that are segmented from the background clutter in a visual scene. We have outlined two ways that this might be achieved. One is an Association Field, which explicitly links neurons with different preferred locations and orientations in a way that closely matches edge co-occurrence statistics in natural images. The other is a simple filter-rectify-filter mechanism that, in the first stage, obtains a response to the contour elements and, in the second stage, blurs this filter response along the contour; contours are then defined by thresholding the filter output and identifying regions of contiguous response across filter orientation and 2D image space. Both proposed mechanisms are consistent with much of the available evidence, and it may be that either or both of these mechanisms play a role in implementing contour integration in biological vision. Evidence from electrophysiology and functional imaging suggests that contour integration is implemented in early visual cortices, perhaps V1, V2, and V4, but the exact biological implementation needs further elucidation. The grouping phenomena discussed here involve local edge information, but similar grouping processes might also be manifested in other domains. Indeed, Rosenholtz and colleagues (2009) have shown how May and Hess’s (2008) filter-overlap algorithm for contour integration can be extended to accommodate a wide variety of grouping tasks. Contour integration may also be related to other pooling phenomena such as crowding. If this is the case, then the Association Field that has been proposed as a mechanism for contour integration may be a specific example of the integration field that is thought to be responsible for crowding.

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