

# Integration of contours: new insights

Robert Hess and David Field

**Psychophysical, neurophysiological and anatomical research of the last few years has converged on a new explanation of how the components of a contour become integrated. Borrowing from the Gestalt rules of good continuation, this research suggests that components of a curved contour become integrated when the alignment follows specific rules. Here, we review some of the behavioral, anatomical and physiological findings that support the notion of an 'association field' that integrates the outputs of neurons through the use of long-range lateral connections. These results provide an interesting insight into how the information from arrays of neurons distributed across the visual field might be integrated. What emerges is a new concept of a 'receptive field', in which the output of a neuron is a time-dependent, complex combination of feedforward, feedback and lateral connections that produce a rich description of the visual world at early stages of visual processing.**

Fueled by neurophysiological data showing that the visual system fundamentally consists of computing elements (neurons), the mainstream theories of sensory experience have, over the last 40 years, become increasingly structuralist. However, some researchers resisted this way of thinking, most notably the Gestalt psychologists. They proposed a series of rules (symmetry, proximity, good continuation, closure, etc.) that govern perceptual organization, and stated that our perceptual experience could not be decomposed into a simple set of features. The debate has recently been re-invigorated by new results from both the physiological and psychological literature. At the heart of the issue lies the question of what a cell in the visual pathway 'represents'. As a consequence of the early work of Hubel and Wiesel and others on the properties of cells in the visual cortex, many principle theories assume that individual cells code particular features of the environment. On this view, cells are considered to be 'filters', with higher levels of the visual system representing structure with greater complexity. Much of vision research over the past 20 years has been concerned with specifying the filtering properties of cortical cells and establishing how these neuronal 'feature detectors' are distributed within the visual cortex. What has emerged from this research is the notion that different cells are tuned to different stimulus attributes (e.g. spatial location, orientation, scale contrast, disparity and motion) as defined by the properties of their 'classical receptive field'.

Although even Hubel and Wiesel were well aware of important response properties beyond the classical receptive field (e.g. the end-stopping properties of some cortical receptive fields), their basic proposal that the visual system can be described as a hierarchy of filters is widely accepted. However, recent research across the fields of cortical anatomy, physiology, psychophysics and computational modeling is beginning to paint a new picture of the primary visual cortex

in which the classical notion of a 'receptive field' is fading. As important as this concept has been in the evolution of our thinking of cortical processing, the recent literature suggests that we must consider the cortical cell not as an isolated element but as a part of a functional network designed to accomplish specific visual tasks in a dynamic and flexible fashion<sup>1</sup>. One line of inquiry that is driving this thinking develops directly out of one of the Gestalt rules of organization: that of good continuation.

This article addresses a rather simple and fundamental question: if the visual system breaks up the visual image into arrays of neurons, each coding an individual component of the image, how is this information integrated into a perceptual whole? Although one can ask this question at many levels, we suggest that fruitful insights might be gained by looking at the integration of contours. We describe here research from psychophysical, anatomical and physiological approaches, that supports the notion that cells early in the visual pathway represent complex spatial relationships, in a manner not far from the proposals of the Gestalt psychologists. What emerges is the idea that cells respond to relatively complex relationships through lateral, feedback and feedforward connections. We outline what has been learnt about the network interactions underlying the integration of contours, and we describe a recent psychophysical approach that sheds light on this specific issue and we discuss some of the general rules that have emerged from a number of studies on contour integration. From these findings, we speculate on how the visual system represents object contours.

## The problem of integration

The notion that the outputs of neurons in the visual cortex must somehow be integrated is a longstanding problem. Much of the work on texture segregation addresses exactly

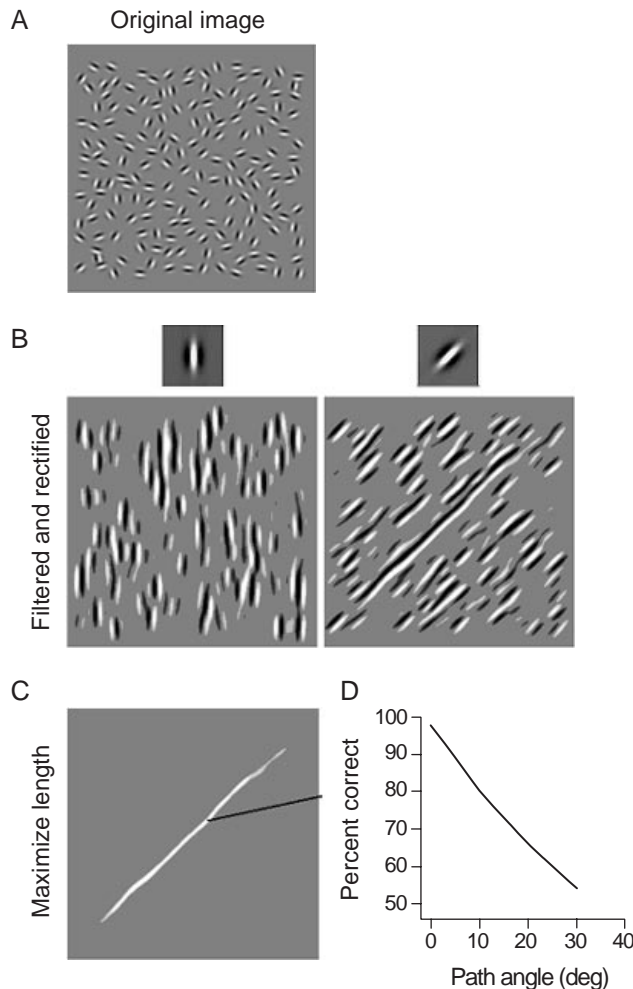
*R. Hess is at the  
Department of  
Ophthalmology,  
McGill University,  
Montreal, Quebec,  
Canada.*

tel: +1 514 843 1690  
fax: +1 514 843 1691  
e-mail: rhess@  
bradman.vision.  
mcgill.ca

*D. Field is at the  
Department of  
Psychology, Cornell  
Ithaca, NY, USA.*

tel: +1 607 255 6393  
fax: +1 607 255 8433  
e-mail: djf3@  
cornell.edu

### Box 1. The simple filter model; integration within orientation bands



**Fig. 1. The simple filter model for detection of a contour path embedded in a field of similar background elements. (A)** The original stimulus contained elements 12 operation of two filters from the full bank of 12 is shown. These filter outputs are 'thresholded' (all grey levels falling within  $\pm 1$  SD of the mean are replaced with the mean value), producing a new image containing both positive and negative polarity 'blobs', where blobs have been contrast-enhanced to further demarcate them **(B)**. Using these descriptions it is possible to identify the longest blob across all filter outputs **(C)**. It is this feature that is identified as the 'path'. **(D)** model predictions are shown in as a function of contour curvature. (Data from Ref. a).

Before asserting that the outputs of cortical cells with different orientation preferences are integrated to define contours, one must first show that the task of integration cannot be solved by summation within the orientation properties of single cells. To show this, Hess and Dakin constructed a model with minimal assumptions (Ref. a). They assumed that cortical cells are bandpass for both spatial frequency and orientation and that a range of different orientations are represented across the population (difference of Gaussian filters were used, based on the work of Phillips and Wilson, Ref. b). The same two-alternate forced-choice method of presentation was used as in the psychophysical study; namely, the model received two input images in random order – either the background elements alone or the contour embedded within the background elements. After convolution, the cells' responses were 'thresholded' (by removing grey levels that were less than 1 SD over all pixels, see Fig. 1B) and a symbolic, sentence-based description generated (using Watt's image scheme; Refs c,d) in terms of the centroid, mass, length and orientation. The form of this description is reminiscent of Marr's primal sketch (Refs e,f). The neural image with the longest 'blob' (Fig. 1C) was used to identify the image with the contour.

The resulting filter prediction as a function of the angle between individual elements comprising the contour (contour angle:  $0^\circ$  for straight contours and  $30^\circ$  for very curved contours) is shown in Fig. 1D. The results of the model show that straight contours are easily detected by such a mechanism but that performance falls off abruptly for curved contours. Contours having a path angle of greater than  $30^\circ$  would be invisible to such a mechanism.

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this issue<sup>2</sup>. The standard theories propose that the visual system groups (or 'attends to') cells with similar properties (e.g. orientation, scale) allowing one texture to segregate from another. The difficulty in applying this approach to contours is that a contour of any natural object is likely to twist and turn in various ways and it seems highly unlikely that the cortex represents every possible contour by a unique cell.

Earlier work on segregation of contours<sup>3–6</sup> involved detecting straight contours composed of dots or short line segments (referred to as test elements) embedded in a field of similar elements of random position and orientation. As valuable as these early approaches were, they were subject to one major criticism: the broadband nature of the elements (wide spatial and orientation-spectra) left open the possibility that a single, large receptive field could solve the task of integrating the test elements into a continuous contour. Instead of measuring how the outputs of different cells are integrated one might be measuring summation within a single cell or a population of cells with similar properties (this is often referred to as the linear filter model; see Box 1).

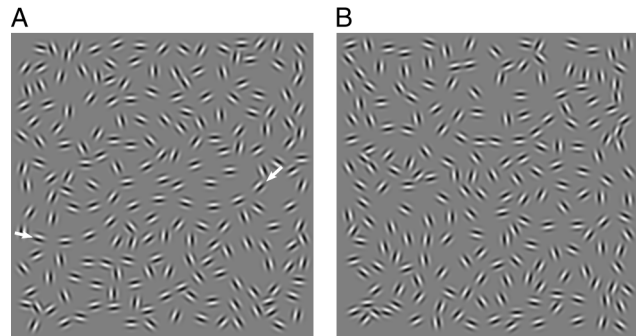
To address this issue, together with Tony Hayes, we developed a technique that we refer to as the 'path paradigm'<sup>7</sup> (outlined in Box 2; see also Ref. 8). Subjects were presented with arrays of oriented elements, a subset of which were aligned along a path (Fig. 1 A–C). The elements were chosen to match approximately the tuning properties of 'simple cells' in primary visual cortex (V1), and they were spaced at a distance that made it unlikely that a single neuron was responding to more than one element. Subjects demonstrated that they could not detect the contour reliably when the elements along the path differed in orientation by more than  $30^\circ$  (Fig. 1D,E). A relatively specific relationship must hold for the path to segregate from the background (Fig. 1F,G). The alignment required, which we called an 'association field', agrees with the 'reliability' of surfaces proposed by Kellman and Shipley<sup>9</sup>, and shows similarities to the integration models of Grossberg and Mingolla<sup>10</sup>, and Parent and Zucker<sup>11</sup>. We proposed that the underlying mechanism of this grouping might be the lateral connections between cortical V1 neurons that have been described by a number of researchers<sup>12,13</sup>.

## Box 2. The 'path' paradigm

Previous approaches to contour detection have involved the measurement of reaction time or noting phenomenal 'pop-out' of contours composed of lines of dots. We wanted to put the measurement of contour linking on a solid psychophysical footing by using criterion-free measures of detectability for stimuli that would, by their very nature, defeat any single-cell explanation (Ref. a). We used Gabor elements (a 1-D sinusoid multiplied by a 2-D Gaussian profile) whose spatial frequency and orientation properties mirrored that of visual cortical cells. Contours of various curvature were constructed by aligning the orientation of a subset of these elements within a field of identical but randomly oriented elements (Fig. 1A). The path was constructed of ten invisible line segments, which were joined at an angle uniformly distributed between  $+a$  to  $-a$ , where  $a$  is defined as the path angle. A null stimulus consisted of all the same elements but the elements comprising the path were also of random orientation. Subjects were asked in a standard two-alternate forced-choice paradigm to choose which of two presentations contained the contour. (See Fig. 1 in main text for some typical results of these experiments.)

Importantly, the detectability of such a stimulus when curved cannot be easily accounted for by the summation within a single linear detector. Neither is it particularly useful to consider that such a stimulus, in general, is detected by specialized 'curvature-detectors' (sometimes referred to as 'collator units'). While we do not rule out the possibility that there are specialized receptive fields for certain common visual forms such as circles, to have one for every possible contour shape would be computationally extravagant.

Furthermore, the stimuli here are constructed to ensure that there is no local density cue to which stimulus contains the contour. This differs from a number of other approaches (see Ref. b). The proof of the lack of a density cue is that a contour stimulus composed of isotropic elements is undetectable



**Fig. 1. Embedded contours.** (A) a contour path (marked by white arrows) is embedded in similar background elements (see text for details). (B) Only the background elements are shown, but the local density is the same as in A.

(Ref. c). A small degree of variability was added to each of the important parameters of path construction (positioning, element orientation, path angle, average inter-element distance) to ensure that detection was based on the perception of a global contour.

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Recent anatomical and neurophysiological studies in the cat<sup>14</sup>, tree shrew<sup>15</sup> and monkey<sup>16</sup> have demonstrated that our psychophysically defined association field maps well onto the kinds of lateral connections that have been found to occur between cells of similar orientation preference. In a novel approach, both Malach *et al.*<sup>16</sup> and Bosking *et al.*<sup>15</sup> used optical imaging to determine the pattern of orientation columns across the cortex, then injected biochemical tracers to track where the horizontal axons of a particular V1 cell project. The results showed that the long-range connections project primarily to orientation columns that have a similar orientation preference. Furthermore, Bosking *et al.*<sup>15</sup> showed that the labeled axons extend for a greater distance along the axis of the receptive field than orthogonal to it. This agrees well with psychophysical results that demonstrate much better grouping when the elements are aligned along the axis than when they are orthogonal to that axis (compare Fig. 1A with B). Some recent results have even suggested that the off-axis projections appear to connect with off-axis orientations like those shown in Fig. 1F (G. Blasdel, pers. commun.). A related line of research involving both psychophysics and neurophysiology has demonstrated that detection of an oriented line segment is enhanced by the detection of flanking line segments<sup>17–22</sup>. These studies have also argued that long-range lateral connections are involved. We will return to this point later, but we first consider a variety of psychophysical studies that explore the parameters of contour grouping.

### The rules of grouping

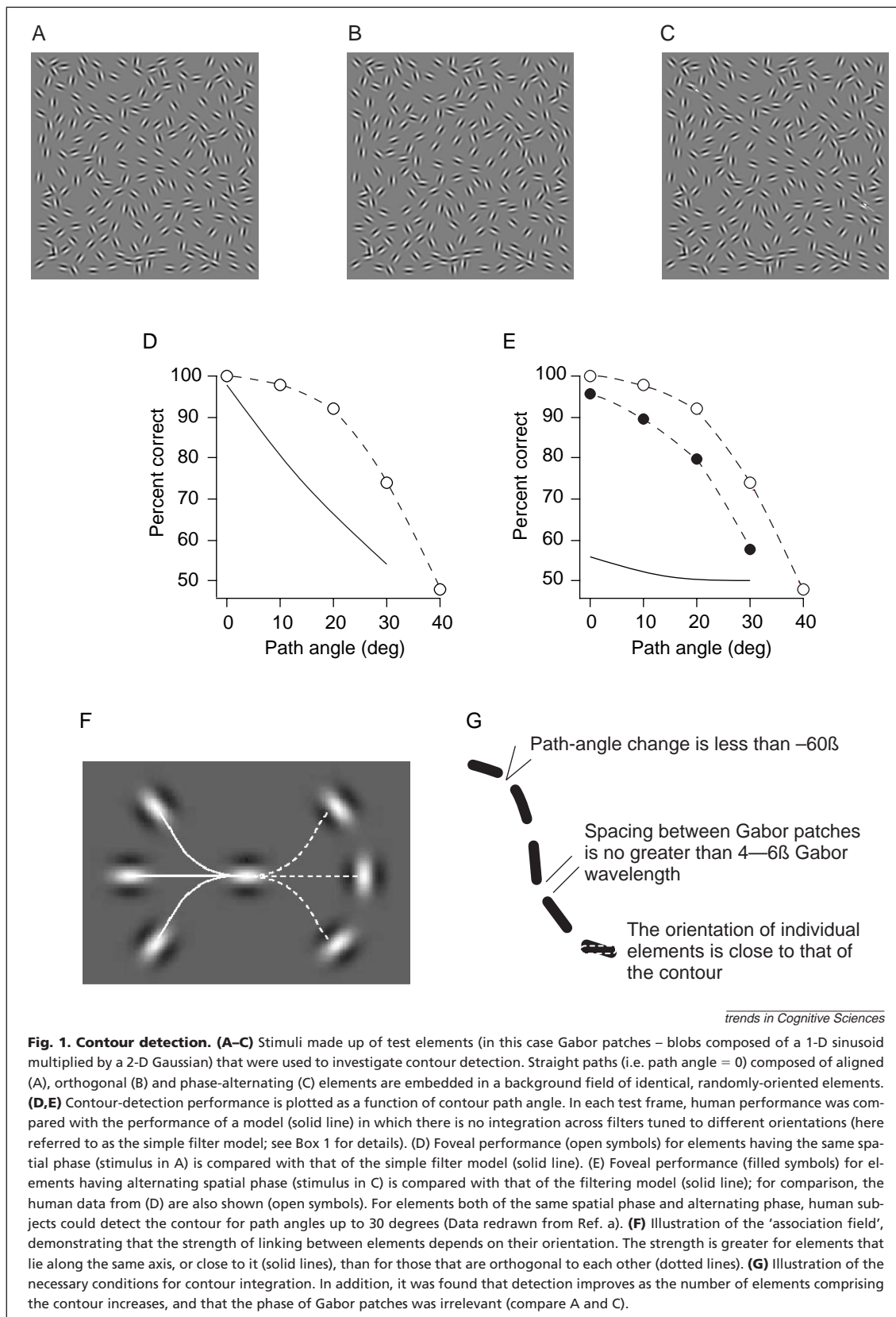
The investigation of the rules of grouping has three lines of motivation. First, one may identify the sorts of contours

that occur in our environment and ask whether the visual system has developed rules that provide efficient means of extracting natural contours. This was part of the motivation of our original work<sup>7</sup>. Second, one can investigate whether, by way of computational necessity, filling-in processes are contained<sup>1</sup>. Third, one can look at the tuning properties of cells in V1 and ask whether the grouping appears to respect these established properties; that is, are V1 cells principally grouped according to similar tuning properties? In addition, there are important differences concerning how contours are integrated in central as opposed to peripheral vision (see Box 3).

Cells in the cortex are selective along a number of dimensions including orientation, position, spatial scale (i.e. spatial frequency, which is reflected in receptive field size), hue, spatial bandwidth, contrast sensitivity and disparity. Initial work looked at the relationship between orientation and position (as described above). Since that time, a number of recent studies have developed further insights into the rules that determine whether a contour is segregated.

### Spatial scale

Evidence suggests that grouping operates independently within different spatial scales<sup>23,24</sup>. However, there appears to be some selectivity to bandwidth. Grouping does not appear to operate between phase-aligned (where components are added coherently) broadband and narrowband elements<sup>24</sup> although the spatial phase is not very important when the linking is between exclusively narrowband elements (Ref. 25 and Field, Hayes and Hess, unpublished; but for an opposing view, see also Ref. 26)



### Hue

There does not appear to be any deficit in contour integration for red/green or blue/yellow post-receptoral mechanisms (Mullen, Beaudot and McIlhagga, pers. commun.). However when contour elements alternate between either red/green and blue/yellow, or luminance and colour, there is a significant loss in performance<sup>26</sup>.

### Disparity

Contour integration can occur across elements that differ in disparity in a binocular presentation even when the contour is not visible in the monocular images<sup>27,28</sup>. Kovacs, Papathomas and Feher<sup>29</sup> have demonstrated that even a contour that is ‘scrambled’ by dichoptic presentation can be unscrambled in a binocular presentation. Thus, even when the elements

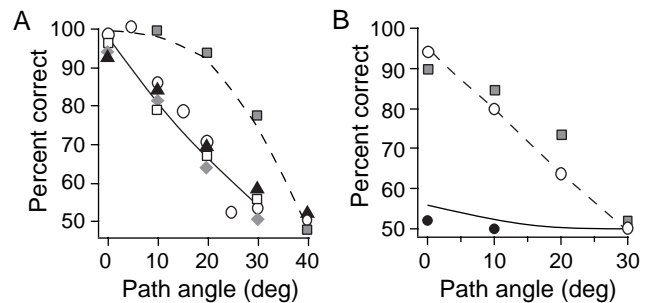


### Box 3. Foveal specialization

Peripheral contour integration appears to operate in a very different way from that of its foveal counterpart. First, contour detectability is poorer in the periphery, although there seems to be very little dependence beyond 10° of eccentricity. The usual factors that one considers to explain reduced peripheral visual performance – namely spatial scaling, contrast sensitivity, positional uncertainty or orientational uncertainty – do not offer a suitable explanation for this loss of contour performance (Refs a,b). An important clue comes from how these peripheral contours appear to subjects; they are described as somewhat continuous ‘creases’, as if smeared along the length of the contour and only straight segments of very curved contours are perceived. This suggests that, instead of the outputs of cells with different preferred orientations being integrated, as in the fovea, there might be integration within cells of the same preferred orientation. In other words, a simple filtering model (see Box 1) for a population of orientationally selective cells, but without linking between cells, might provide a satisfactory explanation. Hess and Dakin (Refs a,b) showed that such a simple filtering model can capture the main features of the results concerning the detectability of peripheral contours (Fig. 1A). The definitive test of this model is to use contours composed of Gabor elements, alternating in their spatial phase by 180° (see main text Fig. 1C for example of this stimulus). Such contours are in fact invisible in the periphery indicating that integration within fixed orientation bands rather than across orientation is being used to detect peripheral contours (Fig. 1B).

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**Fig. 1. Detection of paths embedded in a background field of randomly oriented elements.** In each test frame, human performance was compared with the performance of a model in which there is no integration across filters tuned to different orientations, here referred to as a simple filter model (see Box 1). **(A)** Human performance, plotted as a function of path angle, is shown for a range of eccentric loci in the visual field (10° eccentricity, open circles, 20°, filled diamonds; 25°, filled triangles; 30°, open squares). The predictions of the filtering model are shown by the solid line. For comparison, foveal performance is shown at two widely different scales (3 cycle/deg. stimulus, dotted line; 24 cycle/deg. stimulus, filled squares). This task exhibits scale invariance and so decreased performance in periphery cannot be due to its coarser neural grain. **(B)** Peripheral performance for eccentricity of 20°, for elements having alternating spatial phase (filled circles), is compared with that of the filtering model (solid line). For comparison, human performance at the 20° locus for elements having the same spatial phase is shown (open symbols and dotted line). Foveal performance with an alternating phase path that has been scaled (to 24 cycle/deg.) to reflect the decrease in neural sampling at 20° eccentricity is also shown (filled squares). Poor performance with alternating-phase paths in the periphery (filled circles) is clearly not attributable to a scaling difference between fovea and periphery.

alternate between the two eyes, a contour can be integrated into a unified whole.

#### Higher level grouping rules?

As noted above, results with stimuli in which the contour elements are in a straight line might be explicable in terms of one large receptive field. However, this becomes more difficult to explain when the contour elements are bandpass (allowing a band of spatial frequencies, which means that the contour is not a sharp edge), the spacing is large, and the orientation changes unpredictably along the contour. Furthermore, curved contours can still be detected when they are composed of Gabor elements (i.e. micropatterns comprising a 1-D sinusoid multiplied by a 2-D Gaussian) and when alternate elements differ in spatial phase by 180° (Ref. 30). However, contour integration is only one of a number of steps leading to perception: segregation and object analysis must also be involved. It is not unexpected therefore to find feedback contributions to figure-ground perception in V1 originating from extra-striate areas, as these areas have been associated with higher-level visual analysis<sup>31</sup>.

In terms of psychophysics, it has been shown that smooth contours are more detectable than jagged ones<sup>32–34</sup>. This difference occurs even for very curved contours (path angles exceeding 30°; see Box 2). It implies that the association field as depicted in Fig. 1 is not a complete description of the integrating process. The strength of association between the outputs of any two cells depends on the existence of a similar association between more distant cells. This cannot be captured in our original notion and goes beyond the long-range facilitatory and inhibitory connections between cortical orientation detectors.

Originally, Kovacs and Julesz argued that when the local stimulus properties were held constant, the global structure of the contour determined its salience<sup>8</sup>. In particular, they argued that closed contours produce a ‘synergistic process’ that increases the detectability of a closed contour to beyond that of an unclosed one (see also Ref. 35). The special status of closed contours has been questioned by recent experimental results and simulations<sup>25,32</sup>. Braun showed that the effect was smaller than previously reported<sup>25</sup>, and Pettet *et al.* showed that smoothness rather than closure may be the important determinate of contour visibility, be it closed or unclosed<sup>32</sup>. Preliminary evidence also suggests that when local stimulus properties are held constant, arc length determines contour detectability (Lovell and Wilson, pers. commun.). Furthermore, component arcs might be treated independently by pre-attentive vision.

#### Relationship to threshold facilitation effects

Lateral spatial interactions have been inferred from contrast-threshold experiments in which sensitivity to a test stimulus is facilitated by the presence of flanking stimuli. This facilitation has been shown for Gabor patches flanked by Gabor patches<sup>17–19</sup>, spots flanked by lines and edges<sup>20,21</sup>, lines flanked by small spots<sup>36</sup> and lines flanked by lines<sup>22</sup>. It has been assumed by many that this threshold facilitation results from lateral, spatial neural interactions, and as such forms the building blocks for the integration of extended contours<sup>37</sup>. Though this issue is not resolved<sup>38</sup>, three points argue against such a connection. First, these lateral spatial effects occur only at contrast threshold<sup>39</sup>. Second, they are greatly attenuated for flanking stimuli whose spatial phase differs from the central test stimulus by 180° (Refs 39,40). Third, simulations show

that there is no need to evoke lateral neural interactions to explain threshold facilitation; a single linear filter will suffice<sup>40</sup> (but see also Refs 38,41). From the little we know of contour integration neither contrast nor spatial phase seems to be a particularly crucial parameter. Single-cell recordings suggest that the basis for this facilitation at threshold may be a reduction in the noise of the cell responding to the test stimulus<sup>42</sup>; this would offer a simple explanation for why such effects might be limited to contrast threshold.

### Models and their prediction for neurophysiology

As noted in the introduction, one of the exciting aspects of this line of research is that the psychophysical, anatomical and physiological results appear to have converged. A number of models have been devised to detect contours of the type described above<sup>10,33,35,43</sup> or more generally to extract curves<sup>11,44,45</sup>. While some of these models are not meant to provide insights into the possible neurophysiology<sup>33</sup>, others are<sup>10,35,43,45,46</sup>. Although one could argue about some of the finer points of these models, in particular the choice of the early units having complex-cell<sup>10,43</sup> or steerable<sup>10,35,43</sup> properties, a more fundamental general objection can be raised. All of these models rely on the cellular responsiveness of early filters comprising the contour being facilitated while those responding to background elements are attenuated. Because, in principle, contrast is also determined by the average responsiveness of cells, unless the model separates contrast and contour processing using different neural codes<sup>47</sup>, one would expect contrast enhancement of more detectable contours. Kovacs and Julesz reported an effect similar to this<sup>8,48</sup>, although our recent work with supra-threshold contrast estimation at longer exposure durations found no evidence for such an effect<sup>49</sup>. The perceived supra-threshold contrast of elements comprising a contour was no different from those comprising the background. Furthermore, element contrast can be randomized over a wide range even for short exposure durations without affecting detectability of a contour. It would appear, then, that at some level, the neural code for contrast and contour is separate.

We have proposed a ‘temporal sequencing’ model as a possible account for these results<sup>49</sup>. We assume that the information from feedforward inputs arrives slightly sooner than that from lateral and feedback connections. This temporal delay could, in theory, be used by the system to determine the separate relative effects of stimulus contrast (feedforward) from context (lateral and feedback connections). Recent neurophysiological results have indeed suggested that context (in this case figure-ground effects), does appear to show its effect on a relatively late part of a cell’s response curve<sup>50,51</sup>. Whether this effect also occurs for contour integration has yet to be determined. However, the model does allow a cell to code more than just ‘response magnitude’. It should also be noted that others have suggested a very different type of temporal code whereby the context is determined by the presence of oscillatory and/or synchronous activity of those neurons comprising the contour<sup>52</sup>. Although there appears to be clear evidence for this synchrony, it is not clear how later processing stages take advantage of it, or whether they in fact do. It may also be that synchrony is an epiphenomenon of the presence of lateral and feedback connections rather than a functional component, but this remains unresolved at present.

### Outstanding questions

- Are the anatomical and physiological results on lateral connections sufficient to account for integration of contours? For example, do the off-axis projections synapse on neurons with off-axis orientation (like those shown in Fig1F)?
- Do lateral connections represent the most efficient means of representing natural contours? Can neural networks searching for efficient representations ‘discover’ this efficient coding via learning?
- What role does response timing play in the integration process? Is the presence of a contour coded separately from contrast?
- What role is played by feedback, as opposed to lateral connections?
- What is the next stage of processing once these contours are integrated?
- Do specialized detectors exist for the detection of some common contours (for example, arcs and circles)?

### Conclusions

The classical concept of a ‘receptive field’ has been gradually eroded over the last decade. A neuron’s activity is not determined from only its feedforward input, but also its lateral and feedback connections. Neurophysiological data suggest that the surrounding context plays a crucial role in determining neural activity. In this review, we have considered one particular type of context: the continuity of edges, and the role they play in integrating contours. We have extended the concept of a receptive field to include an ‘association field’ to describe the rules that the visual system uses to integrate contours. The psychophysical experiments discussed here portray the sorts of connections we expect to see between neurons. It has been particularly exciting to see how well the psychophysical, physiological and anatomical results have converged on a single explanation. However, we have little doubt that further psychophysical and physiological experiments will expand this account and help provide an understanding of the sources of information that determine the ‘context’ of a neuron.

The integration of contours represents just one early step towards the goal of providing an object-level representation of the environment. Contours and textures must be integrated at some neural level to allow an object to be represented as a unified whole; however, we do not wish to argue that this integration of the visual input occurs as early as V1. It may well be that what we learn about integration at the level of V1 will provide important insights into how later stages of the visual system integrate information. Does the temporal-sequencing approach described above apply to higher levels of integration? Are there other means of integrating information not yet considered in the current models? We must look to further research to answer these questions.

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