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Contour integration and cortical processing

R.F. Hess [a,*], A. Hayes [b], D.J. Field [c]

[a] *McGill Vision Research, Department of Ophthalmology, McGill University, 687 Pine Ave W, Montreal, Que., Canada H34 1A1*
[b] *Department of Psychology, The University of Hong Kong, Pokfulam Road, Hong Kong, China*
[c] *Department of Psychology, Cornell University, Ithaca, NY, USA*

Abstract

Our understanding of visual processing in general, and contour integration in particular, has undergone great change over the last 10 years. There is now an accumulation of psychophysical and neurophysiological evidence that the outputs of cells with conjoint orientation preference and spatial position are integrated in the process of explication of rudimentary contours. Recent neuroanatomical and neurophysiological results suggest that this process takes place at the cortical level V1. The code for contour integration may be a temporal one in that it may only manifest itself in the latter part of the spike train as a result of feedback and lateral interactions. Here we review some of the properties of contour integration from a psychophysical perspective and we speculate on their underlying neurophysiological substrate.
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1. Introduction

Our understanding of visual processing has undergone considerable change in recent years. The picture we used to entertain of the visual pathway was of populations of cells with discrete functions that became more elaborated at more distal sites. The concept of the classical receptive field and its feedforward response lay at the heart of this interpretation. For some time it has been known that there is more to cortical processing than can be captured either from a knowledge of the classical receptive field or its feedforward response. A cortical cell's response can be influenced by stimuli falling outside the boundaries of its classical receptive field, and its response is also modified by feedback from higher centres.

It is only recently that the functional significance of what is now termed the non-classical receptive field has been revealed. Lamme and co-workers [1–3] have shown that cells in monkey V1 are capable of contextural discriminations because the surround regions outside the classical receptive field may be modulated by feedback from lateral interactions within V1, as well as from higher visual sites. This modulation endows the cell with the ability to conduct figure/ground discriminations involving texture, motion, and stereo. Cortical cells, once thought of as elementary feedforward filters, can now be thought of as having taken on another role as generic figure/ground operators. The code appears to be a temporal one in that the early, feedforward, response may reflect the filtering characteristics of the cell, with the intra- and inter-cortical feedback influence that is seen in the latter part of the spike train reflecting more global operations [2,4]. It appears that V1 takes a much larger role in form processing that had been previously thought.

One important cortical design feature of V1 is that of orientation columns; the orderly grouping of cells with similar orientation preference into columns stretching from the surface of the cortex to the white matter, with adjacent columns of contiguous orientation [5]. Indeed the cortex is composed of cells arranged in an orderly manner along a limited number of key dimensions (e.g., ocular dominance, direction, spatial frequency). Since these arrangements are likely to be more than mere anatomical curiosity, they presumably have important functional roles. The role of such an orderly orientation-preference representation may be to facilitate communication between cells that have similar orientation preferences but that are located in different visual field

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positions. Anatomical and neurophysiological studies in the cat [6], tree shrew [7], and monkey [8], have demonstrated that long range, lateral connections, occur between cells of similar orientation preference. Using an ingenious technique, both Malach et al. [9] and Bosking et al. [10] combined optical imaging, to determine the orientation columns across the cortex, and biochemical tracers, to track where the horizontal axons of a particular cell project, to show that V1-cell long-range connections primarily project to orientation columns with similar orientation preference. Furthermore, Bosking et al. [10] have shown that the labeled axons extend for a longer distance along the axis of the receptive field than orthogonal to it. This finding suggests that cells in V1 may be arranged to undertake orientation analysis across the visual field in addition to, or as part of, generic figure/ground discriminations discussed above. The question remains of what is the precise nature of this analysis. An answer may be provided by understanding the statistical properties of contours found in natural images.

2. Contour properties of natural images

2.1. Orientation/scale

Study of the statistical properties of natural images has provided insights into the filtering properties of cortical cells. Findings that natural images, whether they be of forests, beaches, fields or mountains, contain a similar spectral fall-off, one where the energy/octave band remains constant, led to predictions about the optimum tuning properties of cortical cells [11,12]. Edges are an important and highly informative part of our environment that themselves have this property of equal energy in octave bands. Edges that are smooth 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, correspondence in position becomes limited to a smaller band of spatial scales. This property of natural edges of local correspondence over a (limited) range of spatial scales has been utilized by a number of workers to develop edge detection algorithms that make important image structure explicit [13–15]. Although jagged edges have continuous representation over spatial scale, the exact position and orientation of the edge changes from scale to scale. Thus, the solution of an edge continuity problem may necessitate operating at only one scale at a time. Orientation information is vital for detecting contours in general, but if these contours are jagged, as many in natural images are, then it is important that edge-identification operations occur within, as well as across, different spatial scales [16]. Cells in V1 are ideally placed for this type of analysis

because they are bandpass in both spatial frequency and orientation.

2.2. Contour structure

An important property of natural images is the types of edge alignments that they contain. Natural scenes exhibit consistent statistical properties that distinguish them from random luminance distributions over a large range of global and local image statistics. Indeed, natural images form a class of images that is a tiny subset of all possible images. The distribution of oriented image segments is a particularly compelling example of a statistic that is highly consistent amongst most natural images. The edge co-occurrence statistics in natural images show two fundamental properties; one corresponding to aligned structure [17,18], and another to parallel structure [18]. These properties of natural images are depicted in Fig. 1 where the results of a conjoint occurrence analysis of edge structure is shown from recent work of Geisler et al. [18]. In A, locations of significant edge elements of a natural scene are marked. In B, the line segments show the most frequently encountered orientation difference for each given distance and
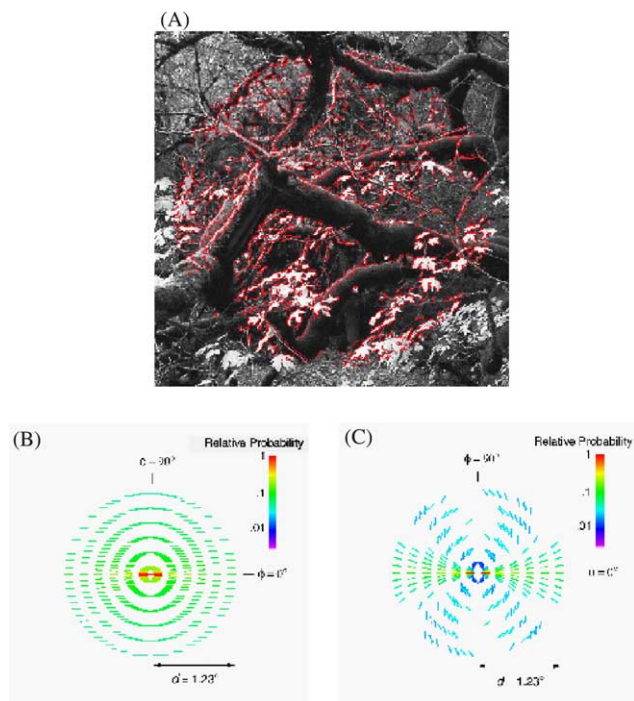

Fig. 1. Statistical analysis of edge co-occurrence in natural images. (A) Edge elements. Each red pixel indicates the location of the centre of a significant edge element. (B) First edge co-occurrence property, the line segments indicate the most frequently occurring orientation difference for each given distance and direction from the central reference element. (C) Second edge co-occurrence property. The line segments show the most frequently encountered direction for each given distance and orientation difference from the central reference element. Note the frequently encountered co-circular structure (from [18]).

direction from the central reference element. In C, the line segments show the most frequently encountered direction for each given distance and orientation difference from the central reference element. The predominance of parallel and aligned structure is evident. The alignment structure follows the co-circularity rule such that pairs of separated local edge segments are most likely to be aligned along a linear or curved path. This pattern occurs at different spatial scales [17]. The co-aligned information is due to the contour structure in natural images. The parallel information, on the other hand, is most frequently derived from regions of the same object or texture.

The conclusion that one can draw from the above studies is that there may be a direct relationship between the contour statistics of natural images and the structure and function of the visual cortex. The strongest long-range connections occur between cells of similar orientation preference when those cells fall within an elliptical space oriented along the axis of the cell's orientation preference, matching the contour statistics of natural images (i.e., demonstrating a conjoint statistic of orientation and position) [6,9,10]. Indeed, the responses of V1 cells are facilitated when co-aligned structure occurs outside their classical receptive fields [19], and are inhibited when co-oriented structure flanks the receptive field [20], suggesting that these two types of image structure represent different image features and are processed differently by the visual system [16].

3. The contour integration approach

The history of studies on contour integration is a long one, stretching back to the Gestalt psychologists [21] who formulated rules for perceptually significant image structure, including contour continuity: the Gestalt "law" of good continuation [22]. More recent attempts to examine these ideas psychophysically have used element arrays composed of dots or line segments [23–26]. As interesting as these studies have been, it has been difficult, because of the broadband nature of the elements used, and the lack of control for element density, to understand what the relationship might be between the tuning properties of single cells and the network operations that describe how their outputs are combined. Contours composed of broadband elements are always open to an explanation that invokes the use of a single, broadband detector.

David Field, Tony Hayes and I [27] developed a new approach to psychophysically investigating how the visual system codes contour continuity by using contours of varying curvature made up of spatial frequency narrowband elements. The contour stimulus is shown in Fig. 2. Within a field of evenly spaced, randomly oriented, Gabor elements, a subset of the elements is aligned in orientation and position along a notional contour (Fig. 2A). In a 2AFC task, this stimulus is paired with an otherwise identical stimulus (Fig. 2B), where all of the elements are unaligned (called the background elements). This stimulus has the important advantage that we can limit the visual system to one scale of analysis—that of the individual Gabor—while asking questions about the visual system's contour-detection capacities. We believed that the continuity problem was likely, on the basis of the properties of natural images, to be solved separately at each scale. Observers were asked to discriminate between these two stimuli (Fig. 2) in a standard forced-choice paradigm. We ensured that there were no local or global density cues to aid discrimination. An indication that the ability of human observers to detect the contour displayed in Fig. 2A told us something interesting about visual processing was the finding that contours composed of

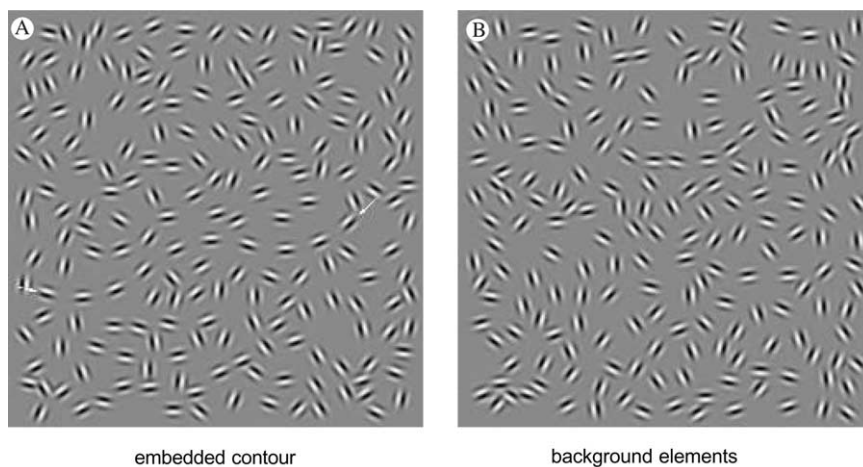embedded contour   background elements

Fig. 2. The Psychophysical task. Subjects are required to detect which of two intervals contain the embedded contour fragment. The embedded contour fragment is depicted in A where as it is absent in B. There is no local or global density difference between these two images so that contour detection is solely due to orientation alignment.

elements whose local orientation was orthogonal to the contour are far less detectable. This type of "contour" is illustrated in Fig. 3 (compared Fig. 3A and B). From a simple information point of view Fig. 3A and B are equivalent, so a difference in their detectability reflects constraints imposed by the visual system.

Another finding of this study was our ability to detect increasingly curved contours. The results displayed in Fig. 3D show performance for contour detection against the curvature of the contour expressed as the angular difference between segments of an invisible backbone on which are aligned the individual Gabors that comprise the contour [27]. Performance (unfilled symbols) is good even for quite curved contours, suggesting that the output of cells with similar, but by no means necessarily the same, orientation preference are being integrated (rather than linkage between of cells with the same orientation preference). The solid curve in Fig. 3D represents the performance of a multi-channel, linear filtering model [28] in which only the information from single orientation bands is used. As expected it shows a stronger dependence on contour curvature than is observed psychophysically. Fig. 3C shows another stimulus manipulation that reinforces the notion that the task of contour integration reflects the action of a network rather than that of single neurons. Here we flip the polarity of every other Gabor element. The contour (and background) is now composed of Gabor elements alternating in their contrast polarity. The visibility of the contour in Fig. 3A and C is similar. Psychophysical measurement shows that although there is a small decrement in performance in the alternating polarity condition (compare filled and unfilled symbols in Fig. 3E), curved contours are still readily detectable when composed of elements of alternating polarity. This finding would not be expected as a consequence of detection via a single linear detector with an elongated receptive field (e.g., "simple cells", but perhaps not "complex cells") since summing over more than one element would be detrimental. This is shown by the performance of the linear filtering model (solid line in Fig. 3E) being close to chance.

The results of these different manipulations suggest that detection of these extended contours, when density cues are removed, is due to selective integration of the outputs of cells at different spatial locations with different orientation preferences. This model of cellular function can be summarized in terms of a notional "association field" in much the same way as we have traditionally described a neurone's retinal response profile as a receptive field. The "association field" is depicted in Fig. 4. The linking strength between orientation-tuned cells depends on their joint relative orientation and spatial position so as to optimize their encoding of simple first-order curves. Weakest linking occurs between cells with inappropriate joint orientation and spatial location. This psychophysically defined
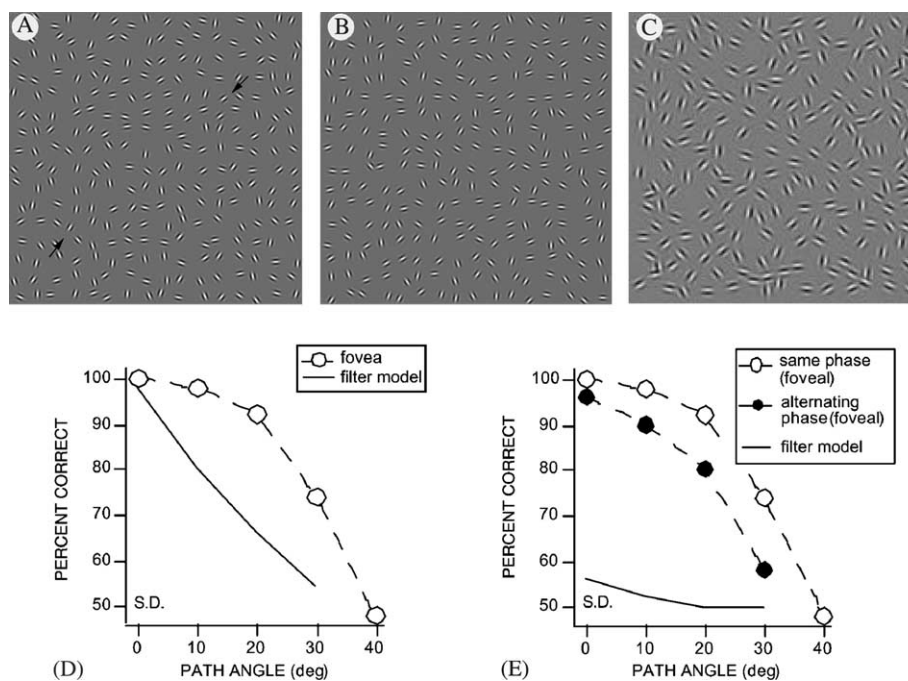

Fig. 3. At the top, straight paths (path angle = 0°) composed of aligned (A), orthogonal (B) and phase-alternating (C) elements are embedded in a background field of identical, randomly-oriented elements. In D and E, performance is plotted as a function of path angle. In each frame, human performance is compared with the performance of a model (solid line) in which there is no integration across filters tuned to different orientations, here referred to as a simple filter model (see [28] for details). In D, foveal performance (symbols) is compared with that of the simple filter model (solid line). In E, foveal performance (filled symbols) is compared for elements having alternating spatial phase (see C) with that of the filtering model (solid line). For comparison human performance for elements having the same spatial phase is shown by open symbols (from [54]).
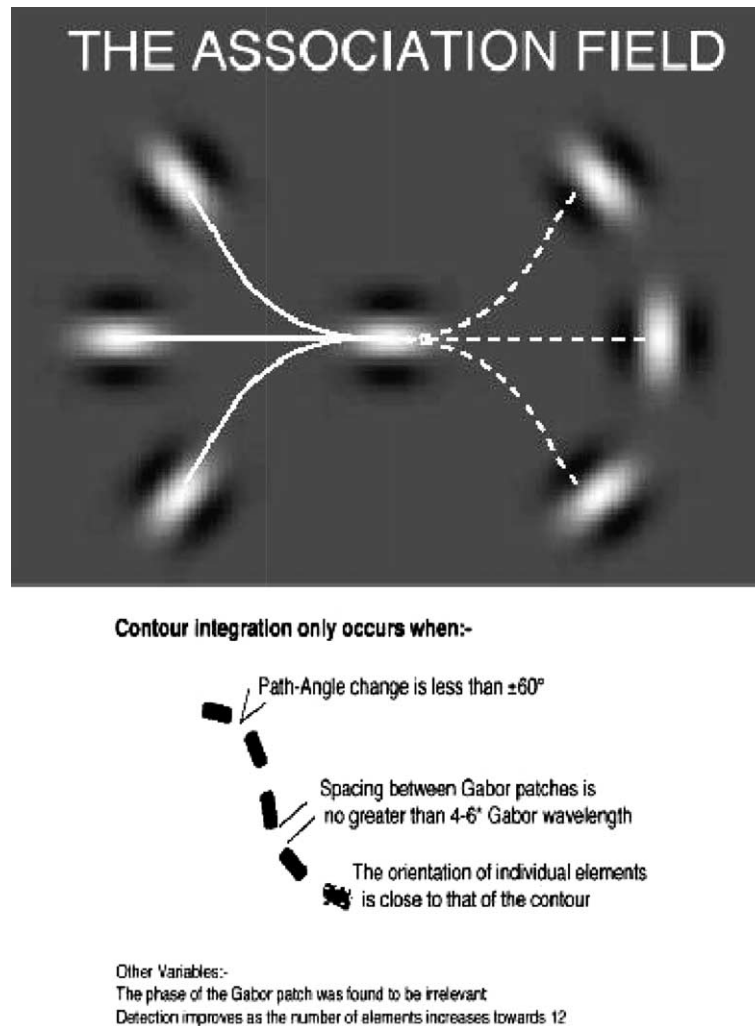
THE ASSOCIATION FIELD

Contour integration only occurs when:-

Path-Angle change is less than ±60°

Spacing between Gabor patches is no greater than 4-6* Gabor wavelength

The orientation of individual elements is close to that of the contour

Other Variables:-
The phase of the Gabor patch was found to be irrelevant
Detection improves as the number of elements increases towards 12

Fig. 4. At the top, the "association field" illustrates the strength of linking depends on orientation and distance. At the bottom, a summary of the important factors for contour integration.

"association field" bears a close joint-statistical relationship to the edge-alignment structure found in natural images [17,18] as seen in Fig. 1C (i.e., the co-circularity rule). It also has a similarity to the arrangement of lateral connections between cortical V1 neurons, described by a number of laboratories. Some recent results have even suggested that off-axis projections appear to project to off-axis orientations as shown in Fig. 4 (Blasdel, personal communication).

4. Properties of the association field

4.1. Orientation tuning

Contour integration performance is best for straight contours and worst for very curved contours. This finding suggests that the component orientations are important. However, it is not just the range of orientations comprising the contour (its absolute orientation variance) that determines performance, but rather the variance relative to the contour (i.e., relative orientation variance) that is the important factor. The critical comparison here is between how performance falls off with contour curvature when the contour elements are perfectly aligned (in this case as contour curvature increases, absolute orientation variance increases but relative variance remains at zero) compared with that of a straight contour where the orientation about the contour is varied (increasing both relative and absolute variance). This comparison is shown in Fig. 5. Notice that path angle in the former case is equivalent to half the orientation jitter in the latter case. Performance here is quite different, yet the absolute orientation variance for the contour is identical in these two cases.

This finding demonstrates that what is important is the relative variance, in other words the extent to which the elements are aligned along a notional contour [28]. Even a small misalignment can reduce performance.
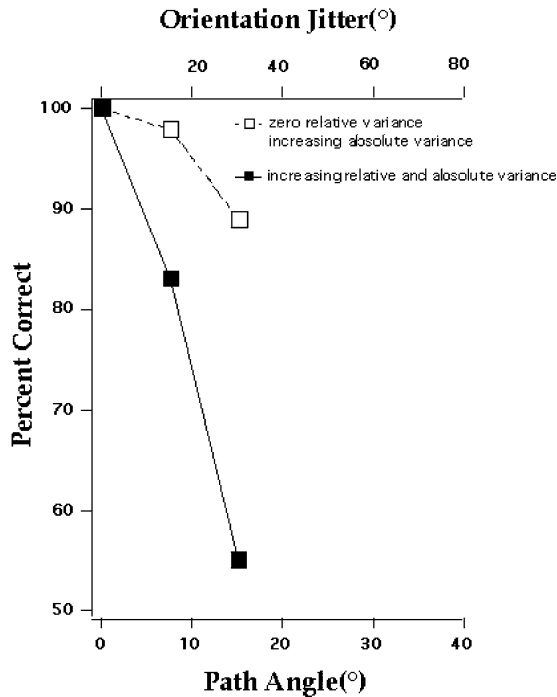
Orientation Jitter(°)

Fig. 5. Comparison of the absolute and relative orientation variance associated with detection of contour fragments. Results from two different experimental manipulations are replotted in terms of these two variance measures. The data shown by unfilled symbols are derived from the detection of contours of different curvature where all the elements comprising the contour are perfectly aligned along the curvature. The data shown by the filled symbols come from an experiment where the orientations of the elements comprising a straight contour are systematically misaligned or jittered with respect to the contour that they represent. Alignment (i.e. low relative orientational variance) is more important than the overall absolute orientation variance for contour integration.

Less is known about how tuned the individual contour elements need to be to produce optimal performance. It is tempting to answer this by simply changing the elongation of the elements themselves but this would not be the ideal manipulation. This manipulation will not only covary the coverage factor, but also will provide another source of orientation information; that from the elongated envelope. A better manipulation would be to orientationally filter symmetrical patches of 2-D fractal noise. This would allow the orientation bandwidth of individual elements to be manipulated without introducing unwanted second-order orientation components.

4.2. Distance tuning

4.2.1. Absolute distance

The results of early studies lead one to believe that there may be a tightly-tuned distance dependence for contour integration [30]; one that in turn depended on the spatial period of the contour elements. This was one of the key reasons why contour integration as described

above and another paradigm, contrast facilitation [31–34], were thought to be closely associated [30,35]. However, in this previous study it was not the absolute inter-element distance that was varied, but the relative inter-element distance for contour and background elements. It is only recently that measurements of absolute inter-element spacing have been made, and these suggest only a weak distance dependence. This is shown in Fig. 6, where the absolute distance between contour elements has been varied. In A, the field size is kept constant so, as the inter-element distance increases, more peripheral elements are eliminated. In B, the number of elements is kept constant, but now the field size is allowed to vary. The result is that contours extend to more peripheral loci where contour integration is not as good [28]. Both ways of doing the task have drawbacks that inevitably contribute to reduced performance, along with reduced performance that can be ascribed to any purely inter-element distance effects. What is surprising is how resistant performance is to increasing the inter-element separation. There is a monotonic decrease in perfor-
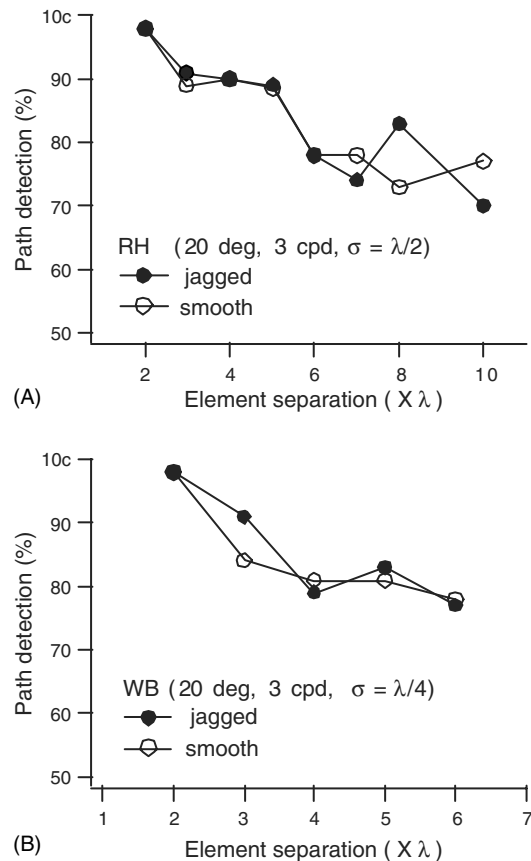

Fig. 6. Detectability of a 20° path as a function of inter-element separation of both contour and background elements. In A, the field size is kept constant whereas in B the number of elements is kept constant. Results are shown for jaggered and smooth contours and separation is plotted in multiples of the spatial wavelength of the Gabor elements (results from Hess and Beaudot, unpublished).

mance with increasing inter-element distance without any obvious tuning.

4.2.2. Relative distance

Early studies [23,24] showed that density and regularity were important determinants of performance on contour tasks when non-oriented elements were used. This finding, of course, is only applicable to the detection of straight contours. More recently, a number of studies have varied the relative distance between oriented contour and background elements as a means of quantifying performance for curved contours as a signal/noise ratio or salience [30,36–38].

4.3. Spatial tuning

4.3.1. Element level

Contour integration is not critically dependent on the absolute spatial frequency of the elements. We showed this in our 1993 study by demonstrating that the task exhibited scale invariance over a range of 3.5:1 [27]. Similar results were shown by Hess and Dakin [28] over a range of 8:1. In these cases, element spatial frequency and inter-element distance and overall field size were co-varied. The question arises as to what happens if all these factors are held constant and just the spatial frequency of the elements is varied? This manipulation was done by Dakin and Hess [39], and their results showed reasonably constant performance over a spatial frequency range of 7:1. Another way of answering this question would be to spatially filter symmetrical patches containing 1-D fractal noise.

4.3.2. Contour level

Orientation linking exhibits spatial frequency tuning at the level of the contour; this was demonstrated by Dakin and Hess [39] who spatially filtered alternate contour and background elements. Their results are displayed in Fig. 7 where it can be seen that the degree of spatial tuning itself depends on the overall curvature of the contour. For straight contours, the bandwidth (full width at half height) was around 1.15–1.43 octaves, whereas for more curved contours the bandwidth decreases to around 0.69–0.73 octaves. The fact that tuning for spatial frequency is found at all suggests that contour integration is solved by operations working within, rather than across, scales. This finding accords with the properties of natural images, displayed in Fig. 1. Dakin and Hess [39] present further evidence in support of this notion. They showed that contours composed of alternate narrowband (Gabor) and broadband (fractal noise) elements were able to be integrated. The above-mentioned finding that spatial tuning varies with contour curvature may also be a consequence of visual system developing strategies that are in tune with the particular statistics of natural images, in that it

suggests that straight contours require greater spatial support than curved ones. Fig. 8, from Dakin and Hess [39], is illustrative by way of a simple model. At the top are four contours, each increasing in curvature. Below each contour is a histogram of the responses of a bank of Gabor filters covering a three octave scale range, corresponding to the point marked by the arrow. As the contour curvature increases, high spatial frequency filters are preferentially activated; a simple consequence of oriented filters signaling the degree of local co-linearity at the scale of the filter employed. Straight edges receive a larger amount of inter-scale support.

4.4. Contrast

Contour integration based on orientation linking is resistant to contrast changes, be they absolute or relative. With absolute contrast, performance reaches asymptotic levels at contrasts above 10–15% [29,40]. With relative contrast, random variations of between 10% and 90% have virtually no impact on performance for contours of any curvature [41]. This is an interesting result because it bears upon how orientation linking is accomplished at the neural level, and it has implications for how orientation linking might be modeled at the computational level. It would seem that cells that are linked may not necessarily be much more active, for more overall activity would have implications for contrast coding which is thought to be related to the average neuronal firing [42]. The fact that contour and contrast coding are not intimately associated has implications for the possible relationship between the contrast facilitation effects reported for the detectability of low contrast Gabors when they are flanked by high contrast Gabors [32–34,43], and it has implications for contour integration. It would appear that the two processes may not, contrary to what was once thought [22], be connected [44]. Furthermore, in a recent study [44], we did not find that contour elements are perceived to have a different contrast to that of background elements. That is, elements that were linked into a contour were not of higher perceptual contrast compared with those that were part of the background. Thus, modeling the effects of orientation linking as overall increased cellular activity to the contour and reduced cellular activity to the background elements, may not be correct.

4.5. Temporal tuning

Contour integration does not critically depend on element temporal frequency as long as it is below the temporal resolution limit for the detection of the elements themselves [45,46]. If the contrast of the elements is modulated within a contour integration task, one observes the expected dependence on absolute contrast,
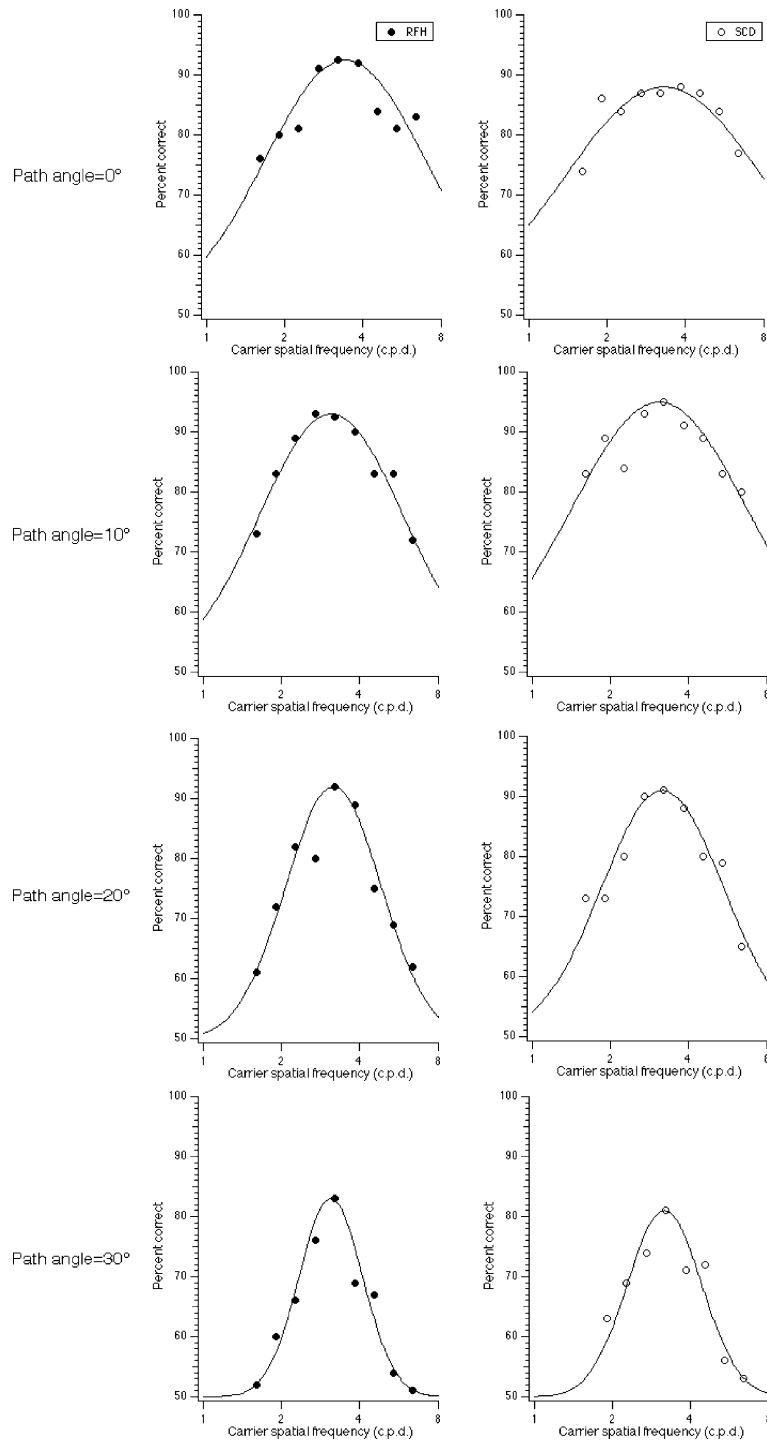
Fig. 7. Tuning of contour integration for the spatial frequency of contour components at different contour curvatures (path angle). Notice the sharpening of tuning for more curved contours (from [39]).

but little or no dependence on the curvature of the contour that the individual elements comprise. This suggests that as long as the elements are of high enough contrast, their temporal frequency can be as high as 30 Hz without affecting contour integration [46]. This lack of temporal dependence of the individual elements can

be contrasted with the much stronger dependence exhibited by the contour itself. Instead of varying the rate that the contrast of individual elements is modulated, one can vary the rate at which the individual element make and break contours by modulating their orientation alignments [46]. Three interesting findings
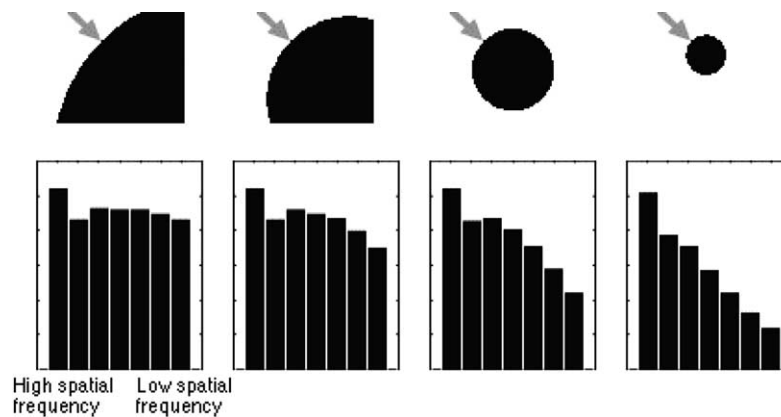
Fig. 8. The degree of scale support provided by edges of different curvature. Edge curvature increases from left to right in the figure. Histograms show the response of weighted Gabor filters at the position marked by the arrow across 3 octaves of spatial scale. For near straight edges, support is consistent across scale but drops away for more curved edges (from [39]).

emerge from this manipulation. First, the dynamics of contour integration are slow compared to that of contrast integration; second, the dynamics are dependent on contour curvature; and third, they do not depend on contrast. The critical temporal frequency for straight paths is about 10 Hz, whereas for curved paths, the frequency falls to about 2 Hz. This result is shown in Fig. 9, where the critical temporal frequency for contour detection is plotted against the curvature of the contour to be detected, for a number of contrast levels of the individual elements. Similar results showing curvature-dependent dynamics comes from a study of reaction times [47]. Furthermore, performance does not benefit from the presentation multiple cycles of temporal modulation, suggesting that contours may not be linked via a slow iterative process.

4.6. Correlation and synchrony

Purely temporal synchronous differences [48] in correlation between figure/ground elements have also been shown to provide an additional cue to integration (other than orientation), though the effects of this temporal difference on its own is relatively weak (compared with orientation). Early evidence suggested that contour detection was facilitated if the elements comprising the contour were presented in synchrony and temporally separated from that of the background elements [49]. This temporal difference between contour and background elements could be as little as 13 ms, well within the visual system's temporal integration period. More recent evidence suggests that this result may be artefactual. Beaudot [50] argues that the order of presentation is important. He observed the previously reported facilitation only when the contour elements preceded the background elements in the first cycle of stimulus presentation. This finding suggests that what are important are the initial transients, rather than asynchrony per se [50,67].

4.7. Smoothness

Early work on contour integration, using the paradigm described in Fig. 3, was done with contours for which the sign of the angle between the contour segments varied. It was later shown that contours with a single sign of inter-element angle—i.e., contours that curved in only one direction—were more detectable than contours that changed curvature direction [36,37,51]. Similar results are seen in Fig. 10 where performance on the contour integration task is compared for curvature-direction varying contours (circles) and for single direction-of-curve contours (crosses). The performance difference between single-curve and multiple-curve contours is only seen for path angles greater than 20°, and even at 30° the facilitation produced by single-curve contours is modest, though significant. The non-monotonic behaviour seen for the 45° path angle is a consequence of contour closure, and not smoothness per se (there are eight elements comprising this contour and when they vary in a single-curve direction with a path angle of 45° they form a close circle). Closed contours are a little more detectable [30,38,51], presumably because they form a more conspicuous and recognizable object shape. The extent to which single-curve contours are more detectable than multiple-curve ones of the same path angle, suggests that the "association field" description shown in Fig. 4 is not completely accurate. The strength of the linking associations between two cell must be also modulated by much longer range interactions. Whether this is done by long-range lateral interactions or feedback from higher levels is at present unknown.

4.8. Polarity

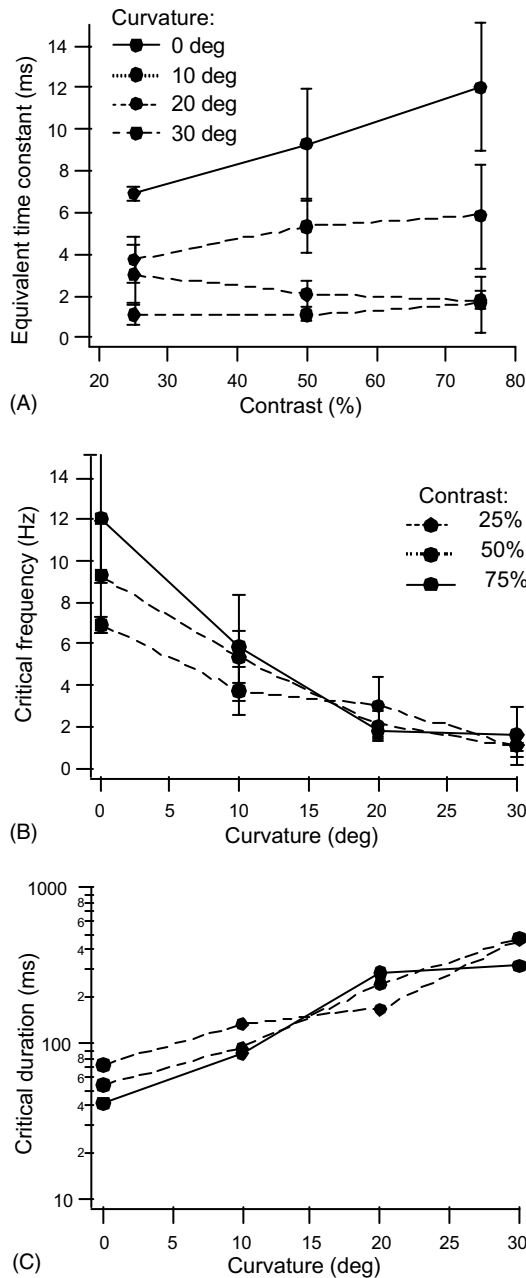The effect of the contrast polarity of elements for contour integration is important for a number of

(A)

Fig. 10. Contour integration as a function of contour curvature (path angle) compared for smooth (crosses), jaggered (circles) and closed contours (rightmost cross symbol). Performance is better for smooth contours but only when they are considerably curved (above a 20° path angle). The non-monotonic behaviour of the smooth contour is due to the fact that, for this particular stimulus comprising eight contour elements, once the path angle is 45°, the contour becomes closed. Closure accounts for an extra increment in detectability above that of smoothness per se.

(B)

(C)

Fig. 9. Critical temporal frequency for orientation modulation obtained by modulating the orientation alignments of elements comprising an embedded contour. The dynamics of contour integration are relatively slow and vary with contour curvature (B and C) but not contrast (A) (from Hess et al. [46]).

reasons. Firstly, if contours are detected by unitary neural mechanisms which linearly sum (i.e., simple cells but not complex cells) information across their receptive fields (whatever their shape), then alternating the polarity of alternate elements should reduce performance to chance. Secondly, simple cells in V1 are polarity specific, and it is of interest to know whether orientation linking can occur between cells with different polarity sensitivities. While there are situations in the
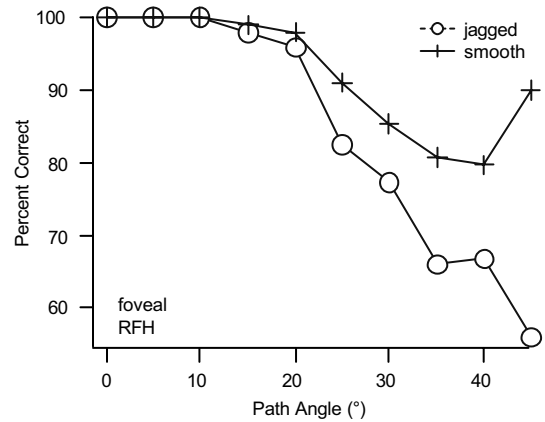
natural environment when such a combination would make ecological sense, as in the situation where the polarity of a contour can often go through contrast reversals due to occluding objects [52], there are other situations where the polarity of border contrast needs to be preserved, as in the situation where there exists a shadow border [53]. A number of studies have now been published on the phase sensitivity of contour integration [28,40,52]. The consensus is that, for central vision, the absolute phase of the contour elements affects performance very little. Contours composed of even symmetric elements are as salient as those composed of odd-symmetric elements, and this is true for both on and off varieties. These is, however, a loss of performance when elements having a phase difference of 180° are alternated. This is true for both even- and odd-symmetric elements. Typical results are seen in Fig. 11A where four phase conditions were randomized within the same testing interval. The foveal phase-alternation conditions display a consistent reduction in performance. What is of interest is that performance for curved contours is still well above chance for the alternating condition, suggesting that a simple linear filtering model (i.e., simple cells) for contour detection is inappropriate; there is a need to integrate the information from different cells with different preferred orientation preferences.

These relationships are different in the mid-far periphery where the 180° phase-alternation condition is much more disruptive, resulting in just above chance performance for straight contours. Hess and Dakin [52] suggested that this may be because peripheral contours, unlike their foveal counterparts, involve less contour
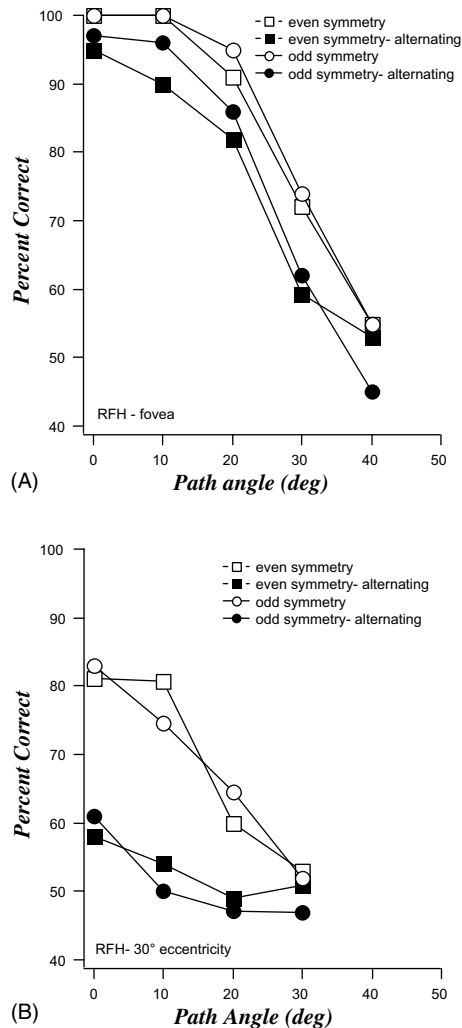
Fig. 11. The effect of the local spatial phase of contour elements for foveal and peripheral stimulation. For foveal vision, there is a small decrement in performance particularly when there is a relative phase change of 180° between alternate elements (filled symbols). For peripheral vision, this effect is even greater rendering all but straight paths undetectable.

integration and more simple linear filtering, that is processing within rather than between cells that are of different orientation preferences (see Fig. 3).

4.9. Monocular/binocular

The available evidence suggests that the cells involved in contour integration receive binocular connections. It has been shown that contours that oscillate between two different depths, 6 min apart, can be integrated efficiently [54]. This finding suggests that binocular cells are involved in contour integration, since performance in this task could not be explained by purely monocular processing, and it also implies that the distance metric of the association field is in terms of binocular, rather than

monocular, space. An interesting question to ask is whether purely monocular cells, which are known to exist in input layers of the striate cortex, provide any input to contour integration.

5. Contrast modulation

Another source of contour information in the real world is that of a texture boundary [55]. Cells in the early visual areas respond to not only the boundaries defined by luminance but also those defined by contrast [56]. In fact, both individual simple and complex cells in cat can respond to both of these image features, but each cell operating at different scales [57–59] for each feature. An individual cell may respond to both the carrier and envelope frequencies of a contrast-modulated stimulus, each with a bandpass response, but at a scale that may be up to a factor of 10 apart. It is clearly of relevance to know whether both of these sources of information are available to the contour integration network. One problem is that contrast-modulated stimuli are less visible than their luminance-defined counterparts, so it would not be appropriate to compare their respective performances at the same physical contrast or modulation depth. To counter this Hess et al., [60] measured the contrast of luminance modulation that equated the orientation discrimination performance of an isolated 100% contrast-modulated element. They reasoned that since contour integration depends exclusively on orientation linking of a number of elements, performance should be equated for the orientation discrimination for any one of these elements. Typically, orientation discrimination performance for a 100% contrast-modulated element was around 5–7°. An equivalent (having the same spatial components) luminance-defined stimulus of around 10–12% contrast produced similar levels of performance. Results were obtained for both types of stimuli composed of either 1-D or 2-D carriers. Performance for contour integration was compared for these two stimuli (an array of luminance- and contrast-defined elements) at their respective orientation discrimination-equated contrasts (4–17% luminance contrast and 100% contrast modulation). The results were clear-cut: even straight contours composed of contrast-modulated elements were undetectable (i.e., at chance). "Equivalent" luminance-defined stimuli were at a ceiling level of performance (100%). Contour integration mechanisms in vision operate on luminance-not contrast-defined information.

6. Chromaticity

Since colour is derived from a surface property, it may be expected that a mechanism that extracted contours

should be particularly sensitive to chromatically-defined contours. The contour interaction mechanisms in human vision are capable of operating on contours defined exclusively by colour. McIlhagga and Mullen [40] examined contour interaction for red/green isoluminant Gabor elements, and later Mullen et al. [29] extended this work to investigate performance with blue/yellow isoluminant elements. They found good performance for contour integration with similar estimates of internal noise and sampling efficiency. They also found that the contour integration mechanisms are sensitive to the chromaticity of their input. Contours composed of alternating red/green and luminance-defined elements, and blue/yellow elements alternated with luminance elements or alternated with red/green elements, were much harder to detect. This chromatic input sensitivity did not depend on whether the chromaticities were along cardinal or non-cardinal colour axes—it was simply a chromatic/non-chromatic differential sensitivity. However, they found no evidence that colour was more sensitive in defining contours than luminance. They found similar results when they introduced colour alternation to luminance-defined contours as they did when they introduced luminance alternation to colour-defined contours [40]. These results fall between two alternate explanations: that of separate contour integration mechanisms for colour and luminance (i.e., a cortical independence for colour and luminance contour processing), and a common contour integration mechanism that is chromatically sensitive at its input. Normally we think about contours being segregated from their backgrounds via orientation linking; colour, however, is itself an important competing linking feature for segregation [61]. A complicating factor is that these two forms of segregation (i.e., orientation and colour) may compete [40]; this could explain why sensitivity depends on colour, but not on a particular colour, and it may explain why colour alternation of luminance-defined contours is not more disruptive than visa versa.

7. An association field for other modalities

7.1. Stereo

Integration can occur between isotropic elements located at different depths along a common depth-defined contour [62]. Though contours at one fixed depth are more detectable, contours that are represented only by disparity are also detectable. This finding suggests that the outputs of disparity-selective neurons can be integrated in an analogous way to that discussed above for orientation-sensitive neurons in 2-D space. That linking is very much weaker in the former case may reflect the fact that contours in the natural environment are never defined by depth alone.

7.2. Motion

Local motion directional signals can be linked to define spatial contours. This is true for contour elements composed of 2-D spatial noise where local orientation linking is not operating [63]. It is also true when local orientation linking is operating as in the case of 1-D signals [45], though the underlying mechanisms responsible for these two cases might be different. In the former case where orientation linking does not occur [63], it is not the absolute direction of these local signals that is
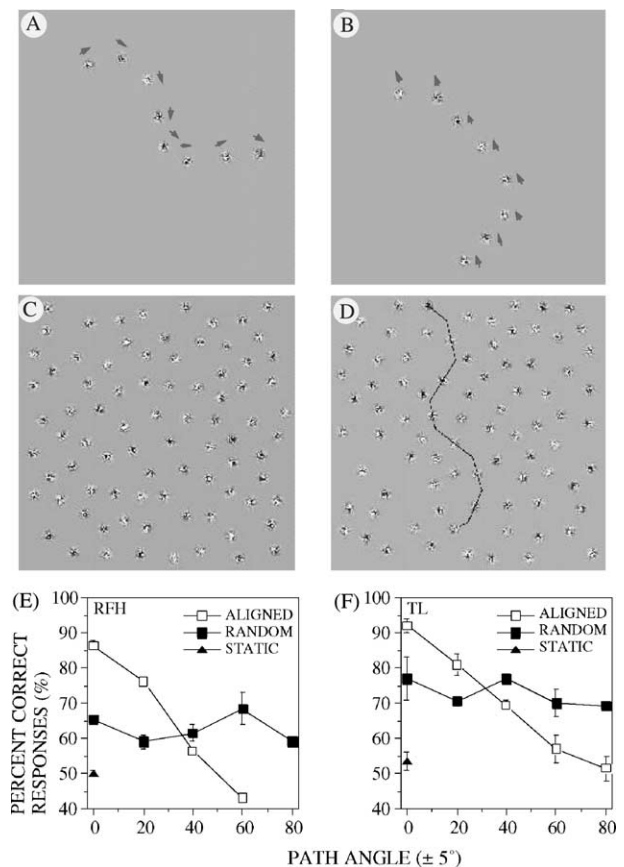

Fig. 12. Motion-defined spatial contours. In A and B, local motion directions are either along the contour or all the same and not aligned along the contour. In C these motion-defined contours are embedded in an array of background elements having random local motion directions. D represents the same directional signals distributed randomly. Detection of the contour is now based purely on the linking of local motion directional signals. In E and F, percent correct performance for contour detection is plotted for two subjects against the curvature of the contour (specified as path angle) for three conditions. In the first, the motions defining the contour are aligned along the contour and their directions are consistent (unfilled squares). In the second condition, the motions defining the contour all have a common direction that is randomized from trial to trial (filled squares). In the third condition, as a control for any spatial cue, a static version of the stimulus is displayed (filled triangle). Performance is best in the aligned case but only for straight and moderately curved contours. Chance performance is obtained when the contour is not defined by motion (from [63]).

important, or indeed even their relative directions to the notional contour that they define, but solely their alignment along the contour that is all important. This is shown in Fig. 12 where psychophysical performance is plotted against contour curvature (defined as above for the spatial case) for three different conditions. First, where all the local directional signals are the same but random with respect to the contour (filled squares), second where they are aligned with the notional contour (unfilled squares) and third, where only one frame of the multi-frame display is presented (filled triangle). Performance is much better when the local motion directions are aligned with straight contours, and performance shows a clear dependence on the curvature of the contour. What is important is the relative (to the contour) directional variance, not the absolute directional variance. Chance performance is obtained in the static version of the stimulus, thus confirming that the contour is defined by motion alone.

These results suggest a similar type of association field to that already described for orientation linking, namely strong co-circular associations, but in this case for local motion directions. More recently we (Hess and Ledgeway, unpublished) that a similar though much weaker linking occurs for the speed of motion. In this case the contour is defined by a correlation between the speeds of elements rather than correlations between their individual orientations.

8. An association field: one or many

The idea that the visual system supports a generic, cue-invariant association field is unlikely. Firstly, the association fields for spatial and motion domains appear to have important differences that would suggest different sites in the pathway. Orientation linking appears to operate within scales and prior to feature extraction [64], whereas motion directional linking is velocity dependent and operates on multi-scale input, which suggests a later stage of visual processing. Another argument against a generic association field is that not all visual information is able to be linked. For example, elements whose orientation is defined by contrast variation are not able to be linked [60]; this is also true for elements composed of two orthogonal orientations [64].

9. The neurophysiological substrate

The properties of contour integration discussed so far provide the edge pieces of the puzzle of the neurophysiological substrate of an "association field" for spatial contours. Neurons in the early stages (e.g., V1) of visual processing that exhibit strong spatial frequency tuning and orientation tuning are prime candidates for orientation linking because psychophysical data suggests that orientation linking occurs within separate spatial scales. We know that there are long-range connections between cells of similar orientation preference in V1, and this is another requirement for contour integration. Psychophysical results also suggest that the neurons involved receive binocular input, are located within the central visual field, and respond to luminance-defined information. Contours can emerge from linkage via any one of a number of attributes (e.g., contrast, texture, motion, colour, stereo), and while it seems that higher visual areas such as LOC must also be involved, the present evidence suggests that higher visual area responses are to the contour per se, irrespective of how it is defined [65,66]. Thus contour integration must involve a number of visual areas, but it would appear likely that V1 plays a special role in orientation linking.

How would this claim best be verified? Ideally one would measure the extracellular activity from the target population of neurons in V1. The local properties of these neurons' receptive field could be determined using as a stimulus an isolated Gabor element (varying in size, spatial frequency, absolute orientation). Then, one would compare its extracellular response for the same matched stimulus element embedded in an array of similar but random elements, when the matched element is part of a contour compared to when it part of the background. If the work of Lamme and coworkers [1–3] is applicable to contour integration, then the overall activity of the neuron in these two situations would not be that different since we know that perceived contrast (and by association, the averaged neuronal activity) does not change. However, the temporal pattern of the spike train may differ between these two experimental situations. In particular, the latter part of the spike train may be modulated by the contour context. A finding such as this would help explain why the psychophysical results suggest the linking operation is sluggish, yet not iterative [46]. Unfortunately, until this experiment is done the above are merely speculations derived from 'distant' psychophysics.

9.1. Unresolved questions

As each new door is opened, many more present themselves. Chief amongst these is the relationship between contour integration via orientation linking and contextual modulation. Another related question concerns the relative importance of lateral connections versus feedback processes. Finally, how global are the orientation interactions that underlie contour interaction? These questions may be best answered using neurophysiological approaches, although psychophysical experiments may, as they often have in the past, also provide some of the answers.

10. Conclusion

Orientation linking appears to be a basic visual process designed to explicate spatial contours. The rules that govern this process appear to be tightly matched to the statistics of contour information found in natural images. The psychophysical properties of contour integration suggest a special role for neurons in early visual areas, particularly V1. While it is thought that the underlying linking operations involve lateral as well as feedback connections, the relative importance and relationship of these two processes is presently unknown.

Acknowledgements

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