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Rules for combining the outputs of local motion detectors to define simple contours

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Abstract

We know something about the fidelity with which motion can be detected in local regions of the visual field but nothing about how these local motion signals are combined across space to define contours. To investigate such linking rules, we measured the detectability of motion-defined contours using an adaptation of the paradigm of Field, Hayes, and Hess (*Vision Research*, *33* (1993) 173) in which subjects are asked to detect the presence of simple contours defined solely by local motion direction that are embedded in a field of otherwise random local motions. We show that contours defined by motion whose direction is along the contour are more detectable than contours defined by motions of any common direction. Furthermore, the contour configuration is important in that straight and moderately curved contours, though not highly curved ones, can support this specialized form of motion integration. © 2002 Published by Elsevier Science Ltd.

Keywords: Motion; Direction; Contours; Paths; Association field

1. Introduction

Ever since the pioneering work of Hubel and Wiesel some 40 years ago, our understanding of visual processing has revolved around the tuning properties of single cells (see Hubel & Wiesel, 1977). Such a preoccupation is understandable since cells in the primary visual cortex are selective for a number of what have been considered to be elementary stimulus properties such as orientation, direction of motion, color and disparity.

While it is true that some elementary detection tasks can be understood in terms of the activation of a limited subset of cortical cells with specific properties, most visual tasks require more than a single cell explanation. There is now a realization that any deeper comprehension of visual processing must involve an understanding of how the outputs of these locally tuned detectors are combined to encode elementary perceptual features. A first attempt at this was taken by Field, Hayes, and Hess (1993) in an investigation of how the outputs of local detectors tuned for orientation are combined to facilitate the detection of elementary spatial contours. This and subsequent work (for reviews, see Kovacs, 1996; Hess & Field, 1999) provided evidence that the outputs of detectors tuned to different orientations are integrated to define simple first-order curves. The concept of an 'association field' was proposed, similar to that of a receptive field except applying to a cortical network.

Here, we apply a similar approach to the issue of how the outputs of local, motion-tuned detectors are combined across space to describe or help disambiguate simple spatial contours. Watamaniuk, McKee, and Grzywacz (1995) have shown that the detectability of an element with a trajectory composed of many small jumps is enhanced relative to the detectability of the individual elementary motions. Moreover, the shape of the trajectory has an influence (Verghese, McKee, & Grzywacz, 2000). Local motions are more detectable if they are along a common axis than if they are perpendicular to it. These studies, which suggest a role for sequential recruitment, highlight the importance of a specialized form of temporal integration in global motion. Our question is similar though our methods are different. We are interested in the spatial integration of local, steady-state motion signals and specifically the linking rules that define how local motion signals are combined to define spatial contours of different

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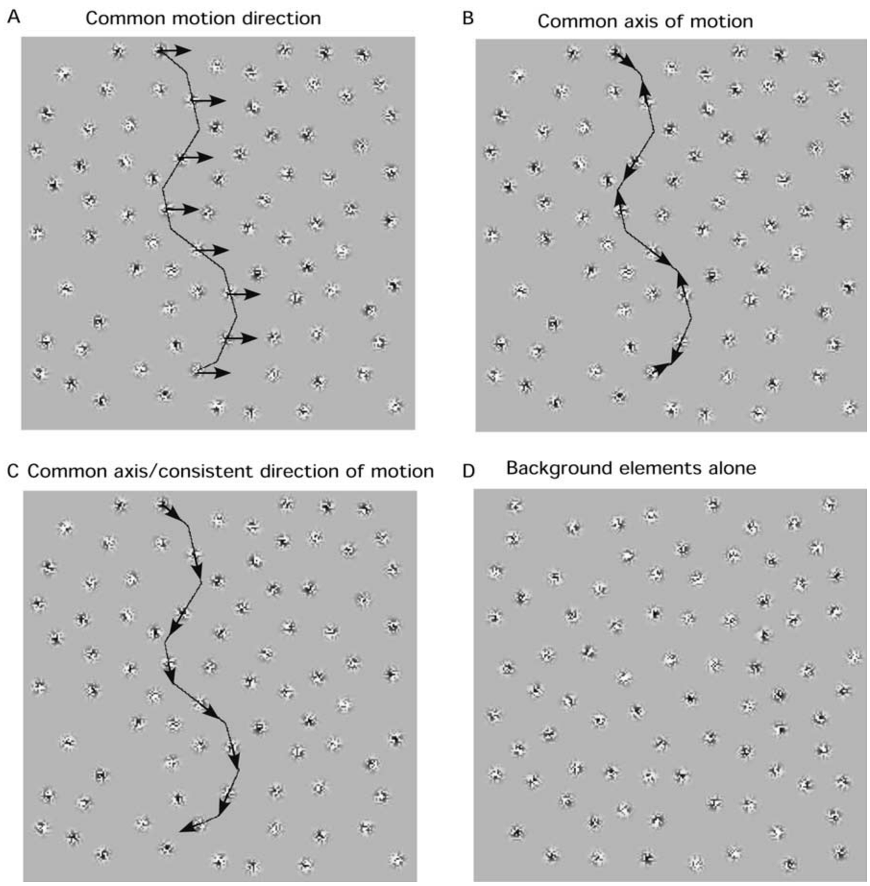

Fig. 1. Illustration of a number of different motion-defined contours. In A–C, contours and the motion direction of their constituent micropattern elements are displayed embedded in background elements having random directions: the contour in A is defined by a common motion direction, in B, by motion along its axis, in C, by motion along its axis in a consistent direction. In D, just background elements are displayed whose motion directions are random. The normally invisible backbone on which the motion-defined path was constructed is displayed for illustrative purposes only. In the experiments, each aperture was stationary and contained a patch of noise in motion. The subject's task was to detect which of two intervals (e.g. C vs. D) contains the motion-defined contour.

curvature. To separate the influences due to space, time and motion direction we have adapted the paradigm of Field et al. (1993). This involved measuring the detectability of a motion-defined contour embedded in a field of random motion directions, using a stimulus in which the local motions were present simultaneously in all parts of the field. We show that there are rules of association for motion direction as there are for orientation; contours composed of elements all of which have the same direction (Fig. 1A; common fate) are less detectable than contours composed of elements all of which have a different direction but consistent with that of the contour (Fig. 1C; consistency).

2. General methods

2.1. Observers

The authors (TL and RFH) served as observers in the experiment and each had normal or corrected-to-normal acuity.

2.2. Apparatus and stimuli

Stimuli were computer generated and presented on a γ-corrected monitor with a mean luminance of $\sim$50 cd m^{-2} and a refresh rate of 75 Hz. All stimuli were viewed binocularly at a distance of 0.74 m and presented within a square window at the center of the display that subtended 16.9° both horizontally and vertically. At this viewing distance each screen pixel subtended 1.6×1.6 arc min. The remainder of the display area was homogenous and had a luminance of $\sim$50 cd m^{-2}.

To assess our ability to integrate contours defined solely by motion we used displays containing multiple micropattern elements that were analogous to those used previously (e.g. Field et al., 1993) to assess contour integration based on the linking of local spatially-distributed orientation signals. However, in the present experiment our micropatterns were constructed such that there were no explicit local orientation cues and contours were defined instead solely on the basis of the local direction signals present, within each micropattern, along the contour's length. Each micropattern was composed of a patch of isotropic, spatially 2-D, random noise (prior to any manipulations, each square noise element subtended 3.2×3.2 arc min) that was presented within a smooth, 2-D, stationary Gaussian spatial window (S.D. 0.13°, truncated at ±0.4°). The Michelson contrast of the noise, prior to spatial windowing with the Gaussian, was 0.5. The presence of the Gaussian window entailed that each patch of noise was rendered with eight-bit luminance resolution. The noise within each micropattern could be made to drift smoothly and coherently in any desired direction, spanning the 360° range, at a drift speed of $4° \ s^{-1}$. To achieve accurate control of drift speed and ensure that it remained constant regardless of the direction of motion standard bilinear interpolation techniques were used to obtain subpixel shifts.

2.3. Procedure

The contour integration task is illustrated in Fig. 1 and the procedure employed was analogous to that used previously by Field et al. (1993). Specifically using a standard two interval, Two-Alternative-Forced-Choice (2AFC) task observers were asked to choose which interval (separated by 1 s) contained the elongated contour (path). One interval chosen at random on each trial (duration 507 ms) contained 158, non-overlapping micropatterns of random position and direction (background micropatterns) and in the other interval (path plus background) some (eight) of the background micropatterns were constrained to lie along the invisible backbone of an elongated contour that was constrained to pass through a central circular region of the display area of radius 0.8°. The directions of motion of the noise within the micropatterns making up this contour could be varied independently of those of the background micropatterns according to a number of rules (see Fig. 1A–C). There were no local element density differences between the two intervals and importantly both intervals contained exactly the same number and range of micropattern directions. Performance was measured for direction-defined contours of varying straightness (defined by a uniform random variable with a range of $5° \pm$ path angle; where a path angle of 0° indicates a straight path and a path angle of 40°, for example, indicates a curved path). Each run consisted of 100 trials and both observers completed at least two runs of trials for each condition tested.

3. Results

To understand how local motion signals are combined across space we first measured the detectability of contours (paths) of different curvature where the motion

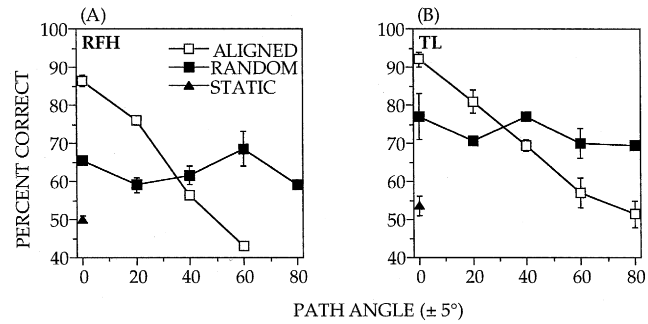

Fig. 2. Percent correct performance for contour detection for two subjects is plotted against the curvature of the contour (specified as path angle) for these conditions. In the first, the motions defining the contour are aligned along the contour and their directions are consistent (unfilled squares). 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 contaminating spatial cues, a static version of the stimulus was 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.

of the micropattern elements comprising the path was constrained to be aligned along the axis of the contour (Fig. 1C). These results, for two subjects, are shown in Fig. 2 as unfilled squares. Best performance is obtained with straight paths and performance falls off progressively with path curvature with chance performance being reached for path curvatures of between 60 and 80°. That this phenomenon is indicative of motion processing is seen by comparing performance in the case where only one frame of the motion sequence was presented (i.e. a static version of the same stimulus with the same total duration) as shown by the filled triangle. Performance in this case is at chance.

This result raised a number of questions. First, *does motion along the contour represent a special case*? Second, *is the fall-off in performance with path angle due to a spatial limit or a directional variance limit*? Third, *if the aligned motion condition is special, is the axis of motion or the direction of motion important*? Finally, *what are the spatial and temporal limits of this integration*?

3.1. Does motion along the contour represent a special case?

To address this question we compared performance (Fig. 2), for two subjects, for paths of different curvature. The motions of the elements comprising the contour were either always aligned along (consistent with) the contour (Fig. 1C and unfilled squares in Fig. 2) or all in the same (common) direction (Fig. 1A and filled squares in Fig. 2), which was randomized from trial to trial independently of the particular path curvature. Performance on the former case is substantially better for less curved paths but worse for more curved paths.

That is, only in the aligned case is performance strongly dependent on path curvature. In the case where all of the path elements have identical but random motion directions, there seems to be only a weak dependence on the spatial distribution of the elements. There is clearly something special about local motion direction being along the axis of the contour, especially when the contour is straight or moderately curved.

3.2. Is the fall-off in performance with path angle due to a spatial limit or a directional variance limit?

In principle, the fall-off of performance with path angle could be due to the fact that when the local motion direction signals are aligned along a contour, the more curved the contour is the wider the range of directional signals that need to be integrated to extract the contour. The efficiency with which local motion signals are combined may depend solely on the absolute variance of the local directional signals present irrespective of how they are distributed across space. On the other hand, performance may depend not only on the absolute directional variance of the local motion signals but also on their relative alignment along a putative contour. The results of Fig. 2 imply that both of these factors may limit performance. Not only there is a fall-off in performance as a function of contour curvature for perfectly aligned local motions (i.e. absolute directional variance increases with curvature), but performance is also reduced when the local motions all have a common direction (i.e. zero absolute directional variance) but are misaligned with the contour. This suggests that the spatial arrangement as well as the absolute directional variance of the local motions are important. To demonstrate the importance of the spatial nature of this special form of integration, rather than just the absolute directional variance of the constituent motion signals per se, we compared performance, for two subjects, in three conditions (Fig. 3). In the first, the local motion directions were along the contour (Fig. 1C and unfilled squares are the same data as in Fig. 2). In the second condition, the contour was always straight (0°) but the constituent local motions were chosen to be aligned along 'dummy' contours (contours that were generated but not actually presented) whose curvature was varied (Fig. 3, unfilled circles). Finally, the contour was always highly curved (60–80°) and the local motion directions chosen to be aligned along dummy contours whose curvature was varied (unfilled triangles). For any particular contour curvature (i.e. path angle), these conditions have identical absolute directional variance of the constituent motion signals. They were manufactured specifically for this purpose and we subsequently verified this by simulation. Although the absolute directional variance of the constituent motion signals comprising the contour at each curvature was identical in each of

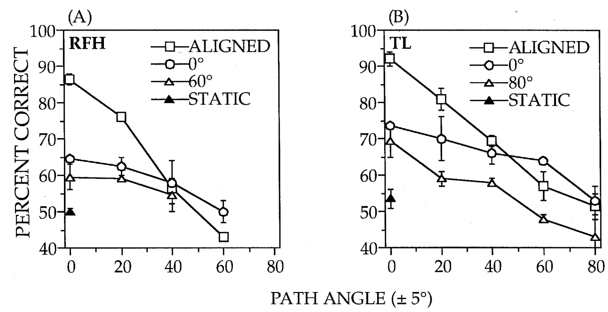

Fig. 3. Percent correct performance for contour detection for two subjects is plotted against the curvature of the contour (specified as path angle) for three conditions. In the first, the motions defining the contour are aligned along the contour and their directions are consistent (i.e. Fig. 1C; unfilled squares). In the second condition, a straight contour has its constituent motion directions taken from dummy contours of different curvature (unfilled circles). In the third condition, a curved contour (60–80°) has its constituent motion directions taken from dummy contours of different curvature. Although the range of directional signals needing to be integrated along the contour is the same in all three cases at each particular path angle, performance is best in the aligned case for straight and moderately curved contours. The filled symbol represents performance on a static version of the task. Chance performance is obtained when the contour is not defined by motion.

these three cases, performance was not constant. The results show that performance is best, at least for straight and moderately curved contours (up to 40–60° path angle), when the local motion directions of elements comprising the contour are aligned along the contour, suggesting a role for the spatial configuration of the local motion signals. However, at large path angles when contours are very curved, performance is similar in these three cases suggesting a primary dependence on the absolute directional variance of the local motion signals comprising the contour.

The above results suggest that both the degree of alignment of local direction signals with respect to a contour's axis and the absolute directional variance of those signals are important factors that influence the ability to extract motion-defined contours. When the constituent local motions are aligned along a contour the loss of performance with curvature is likely due to the increase in the absolute directional variance. This leads to a straightforward prediction: if the fall-off in performance with contour curvature in the aligned case is limited by the absolute directional variance of the constituent local motions then a similar dependence should be seen for a straight contour (0° path angle) whose local motion directions are randomly jittered about the contour. The only common factor in these two cases is a comparable change in the absolute directional variance. The results shown in Fig. 4A and B are for the case where the directional jitter of local motion signals comprising a straight contour is systematically varied (unfilled circles). This dependence, for two subjects, is similar to that previously observed in Fig. 2 for local

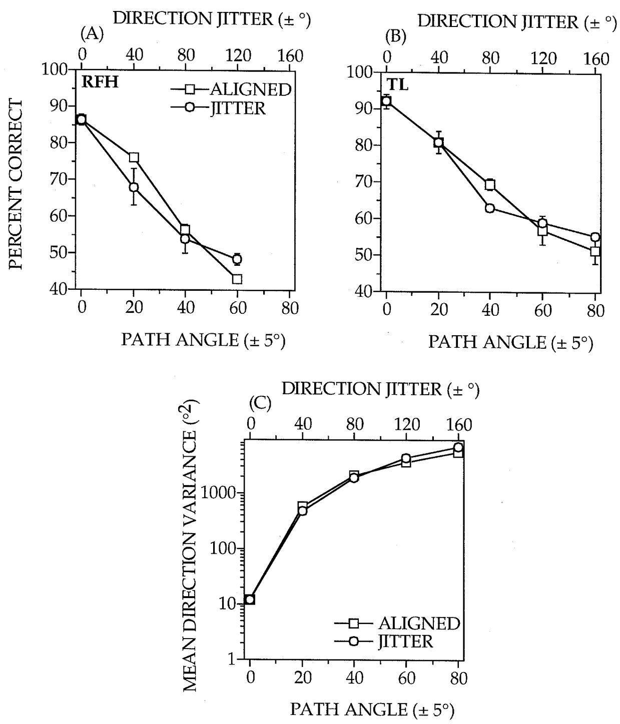

Fig. 4. In A and B performance for contour detection for two subjects is compared for the case where the motions comprising the contour are perfectly aligned and in a consistent direction but the curvature of the contour varies (unfilled squares) with the case where the contour is always straight but the constituent motions that are consistent in direction, vary (are randomly jittered) about true alignment (unfilled circles). In C, the computed mean directional variance (degree square) is compared for the two kinds of stimuli (i.e. the conditions depicted in A and B above). The results indicate that if the local motion directions are aligned along the contour and have a consistent direction then the fall-off in performance with contour curvature is due to the increased directional variance of the motion signals that need to be integrated.

motion signals perfectly aligned along contours of different curvature (unfilled squares). On geometric grounds one would expect the directional variance to be comparable in both conditions when the directional jitter in Fig. 4A and B equals twice the path angle in Fig. 2. Our simulation in which we calculated the mean square deviation (variance) of the directional signals of the elements defining the contour in the above two cases shows that this is true (Fig. 4C; compare unfilled circles and squares). This clearly suggests that jittering the local motions about a straight path is the same as altering path angle for elements perfectly aligned along a contour, a prediction based on the primary importance of the absolute directional variance of the local motion signals aligned along a contour.

3.3. *Is axis of motion or the direction of motion important?*

In all of the above cases when the local motion signals were aligned along the contour, their direction was consistent in that it was along the contour. Is this an important requirement or is it just the axis of motion that is important? To address this issue we varied the local motion direction of alternate elements comprising a straight contour. At one extreme they were in the same direction along the contour (0° directional difference), whereas at the other extreme, they were moving in opposite directions along the contour (180° directional difference, see Fig. 1B). The results for two subjects, which are shown in Fig. 5, show that there is a marked reduction in performance in these two extreme cases indicating that it is the alignment along the contour of direction of motion rather than just axis of motion per se that is important. The filled square in Fig. 5 indicates that performance is close to chance when every alternate element along the contour's length is independently assigned a random motion direction (so that only half of the path elements present have motion directions aligned along the contour). This is consistent with the visual system having to integrate the motion signals of adjacent neighboring contour elements (rather than say every other element) in order to detect the contour. Performance levels can just exceed this when the motion directions of alternate contour elements are in opposition (180° direction difference)—a result that may be consistent with probability summation (e.g. Verghese, Watamaniuk, McKee, & Grzywacz, 1999) of two effectively half density contours defined by opposing local motions. The fact that performance is not the same when the constituent local direction signals are all in the same direction (0°) as compared with the case when alternate elements contain motion in opposite directions (180°), suggests that any implicit spatial orientation cue derived from motion smear (Geisler, 1999) does not determine performance.

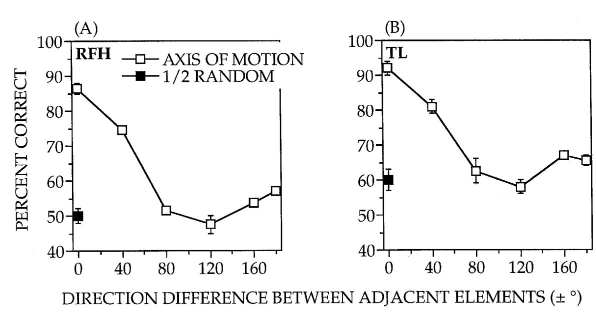

Fig. 5. Performance for two subjects is plotted for detecting a straight contour where the local axis of motion is along the contour but the direction between alternate signals comprising the contour is varied (unfilled squares). Comparison of performance in the 0° (consistent direction) and 180° (opposing directions) case for the directional difference of alternate elements comprising the contour reveals the importance of having the constituent local motions not only along the axis but also in a consistent direction. The filled square represents the case where every alternate contour element has a random motion direction. The fact that chance performance results suggests that the visual system needs to integrate across adjacent contour elements to solve this task.

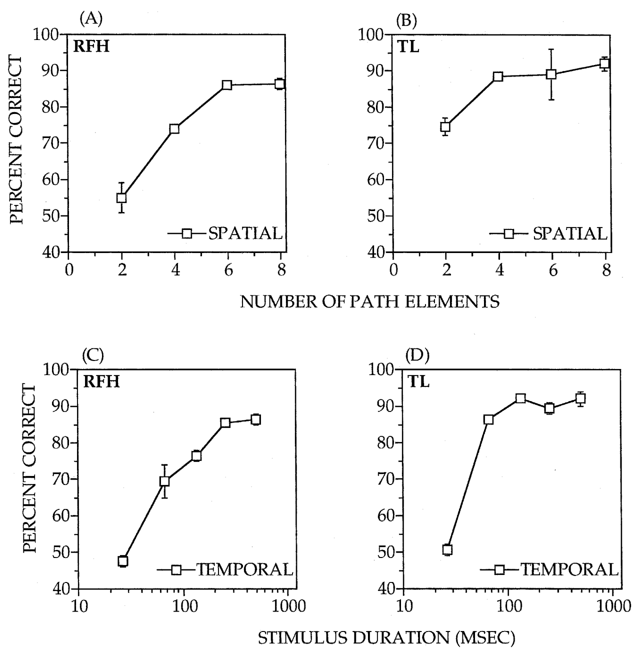

Fig. 6. In A and B spatial summation is shown for detecting a straight motion-defined contour where the direction of the constituent motion signals is aligned with the contour and in a consistent direction (e.g. Fig. 1C) for two subjects; four to six spatial motion samples are required for asymptotic performance. In C and D temporal summation associated with detecting the same motion-defined straight contour is shown; 133–256 ms is required for asymptotic performance. In the original experiments we used motion-defined paths of eight elements, presented for 506 ms.

3.4. What are the spatial and temporal limits of this integration?

The contours that we have used in the previous experiments comprised eight elements and were presented for a total duration of 506 ms. To ascertain the number of local motion positions (the spatial integration) and the critical duration (the temporal integration) used by the visual system to integrate local motion directions, we varied both the number of contour elements and the duration of presentation for a motion-defined, straight contour (Fig. 1C). The results, for two subjects, which are shown in Fig. 6 demonstrate that performance approaches asymptotic levels, most clearly shown in the data of observer TL, for four to six elements spatially and 133–256 ms temporally.

4. Discussion

Using a paradigm that allowed us to readily separate out the influences of direction, space and time, we investigated the rules that govern the spatial integration of local motion direction signals to define 2-D spatial contours. The spatial integration of local motion signals depends crucially on both the relationship of those motion directions to the contour's 2-D orientation and shape and also the absolute variance of the local direction signals present. When these local motions are aligned along a contour of straight or moderate curvature, the detection of that contour is greatly enhanced. This suggests that the spatial layout of the contour and the directions which define it are of prime importance. When the contour is highly curved, performance is determined solely by the absolute variance of the composite motion signals without regard for their precise spatial arrangement along the contour. Thus there are rules for combining local motion directions across space in a way that is analogous to the rules that determine how local orientation signals are combined to define simple contours (Field et al., 1993). As for orientation, there is an association of motion direction and distance that is consistent with first-order curves. We envisage this as representing the functional connections between a number of spatially localized, motion-sensitive neurones within an adaptive cortical network. It would be interesting to know if there are similar long-range connections between motion direction columns in MT (Albright, Desimone, & Gross, 1984), as there are between orientation columns in V1 (Gilbert & Wiesel, 1979; Rockland & Lund, 1982; Malach, Amir, Harel, & Grinvald, 1993; Bosking, Zhang, Schofield, & Fitzpatrick, 1997; Schmidt, Goebel, Lowel, & Singer, 1997), that could form the anatomical substrate for this specialized type of integration. However, there is as yet no pertinent neurophysiology suggesting where in the visual system these interactions occur.

Watamaniuk et al. (1995) have conducted experiments on a related theme. They measured the detection of a motion trajectory defined by the sequential displacement of a single element embedded in a field of elements undergoing random motion. These experiments, which investigated the temporal aspects of the integration of local direction signals, are complimentary to ours which focus primarily on the 2-d spatial aspects of this linking. In particular, the present study has a number of novel aspects.

1. Our use of stationary apertures containing motion allows us to disentangle local direction cues from global contour shape.
2. Because we were interested primarily in the spatial aspects of the integration of local direction signals, our global spatial contour was composed of local directional information whose spatial and temporal properties were constant and do not rely on a temporal sequence of stimulation across successive spatial locations.
3. As a consequence of the way that we constructed our spatial contours we ensured that there was no net global flow in the image containing the contour.

4. Because we used static local apertures, each of which contained constant motion, there is no temporal matching ambiguity for these local motions. The only matching ambiguity is at the level at which local motion directions are linked between micropattern elements to define a global contour.
5. Our stimulus allows the disambiguation of contour length from duration of stimulation.

Verghese et al. (2000) were the first to show that detection of a straight trajectory defined by motion along its axis is more detectable than motion perpendicular to its axis. We have taken this a step further by disambiguating on the one hand, direction from contour shape and on the other hand, direction of motion from axis of motion, to delineate the spatial constraints. We have shown that (1) it is the linking of motion direction rather than axis of motion that is crucial and (2) motion along the contour is preferred to that in any other common direction by the visual system, but only for contours of moderate curvature.

The results of experiment 1 show that contours of moderate curvature, defined by a common (but random) direction of motion, are less detectable than those defined by motions whose directions are aligned along the axis of the contour. Put another way, this particular form of motion integration depends on the degree of similarity between each of the direction signals present and the contour's local spatial orientation, as well as the absolute direction variance of the local motion signals. This does not mean that real contours in rigid motion are less detectable than contours defined by motion along their axes. Real contours are defined by more than just motion information. It does mean that objects or animals that are camouflaged against their backgrounds can be detected more easily if motion occurs along their contour: a camouflaged snake being a good example.

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