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The spatial frequency and orientation selectivity of the mechanisms that extract motion-defined contours ☆

Timothy Ledgeway [a,*], Robert F. Hess [b]

[a] School of Psychology, University of Nottingham, University Park, Nottingham NG7 2RD, UK
[b] McGill Vision Research, Department of Ophthalmology, McGill University, Montreal, Que., Canada, H3A 1A1

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Abstract

The human visual system can undertake a specialized form of motion integration, one that enables the presence of extended spatial contours to be disambiguated from their backgrounds. We have shown previously that the visual system can selectively integrate local motion signals when their directions are along spatial contours and its efficiency is inversely related to the curvature of the contour involved (Ledgeway, T., & Hess, R. F. (2002). *Vision Research*, *42*, 653–659). This integration primarily involves the direction, rather than the speed, of local motion signals. In the present study, we sought to investigate both the spatial frequency and orientation tuning of this specialized contour integration process, using a path detection paradigm. The results show that the tuning for spatial frequency is very broad, in line with previous studies that have examined this issue. In contrast, the orientation selectivity of the mechanism mediating contour extraction under these conditions is relatively narrowband. Thus, spatial frequency but not orientation pooling appears to take place prior to the extraction of motion-defined contours, a situation that is different from that previously shown for spatial contours composed of static, oriented elements.

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

1. Introduction

It is well established that visual neurons in mammalian striate cortex exhibit multi-dimensional tuning to stimuli that fall within their receptive fields. Individual cells in area 17 of cat and V1 of monkey respond selectively to a limited range of spatial frequencies, orientations, motion directions and to a lesser extent temporal frequencies. As the receptive fields of these neurons are localized in space, the extraction of more global relevant image properties (e.g., overall shape of spatially extensive objects) is widely assumed to involve later visual areas or lateral/feedback modulatory neural mechanisms which serve to integrate (combine, link or pool) the outputs of earlier stages within the visual pathways. The precise nature of this global integration process is still indeterminate but nonetheless the rules by which local orientation information is integrated across the visual field to extract contour fragments in human vision has been the focus of a number of recent studies (for reviews see Hess & Field, 1999; Kovacs, 1996). These rules have been couched in terms of an "association field" somewhat akin to the notion of a "receptive field" but involving cellular networks rather than individual neurons (Field, Hayes, & Hess, 1993).

In a similar vein, we have recently investigated the rules that underlie the integration of local motion signals across space to help disambiguate the presence of simple spatial contours (Hess & Ledgeway, 2003b; Ledgeway &

☆ Some of the experiments in this study have been reported previously and published in abstract form (Hess & Ledgeway, 2003a).
* Corresponding author. Tel.: +44 115 8467343; fax: +44 115 9515324.
E-mail address: timothy.ledgeway@nottingham.ac.uk (T. Ledgeway).

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Hess, 2002). Previous work by Verghese, Watamaniuk, McKee, and Grzywacz (1999) and Watamaniuk, McKee, and Grzywacz (1995) had shown that the detectability of a moving element with a trajectory composed of multiple small jumps is enhanced relative to that of the individual constituent motions. Moreover, the shape of the trajectory has an influence (Verghese, McKee, & Grzywacz, 2000). Triplet of dots moving in a consistent direction are more detectable if their movement is along a common axis (collinear motion) than when it is perpendicular to it (but see Bex, Simmers, & Dakin, 2003). These studies, which suggest a role for sequential recruitment (interactions) between local motion detectors, highlight the importance of a specialized form of temporal integration for extracting the motion trajectories of objects.

Our approach was different in that our stimuli were in constant motion within the confines of a dense spatial array of stationary apertures and our results were interpreted within the general framework of the linking rules for motion direction somewhat analogous to those previously described by Field et al. (1993) for orientation. In particular, we demonstrated that local motion signals are integrated across space if those local directional signals are aligned along the axis of straight or moderately curved spatial contours (Ledgeway & Hess, 2002). Moreover the ability to detect such spatial contours, defined solely by motion direction, is insensitive to large differences in the speeds of the individual elements defining the contour. That is, even when adjacent contour elements had a fivefold difference in absolute drift speed, detection performance was just as good as when all the elements along the contour had the same drift speed. This finding is reminiscent of studies using random-dot patterns (e.g., Watamaniuk & Duchon, 1992) that have also shown that observers can integrate randomly distributed local speeds into a global percept of speed and discriminate that global speed as well as if all the dots in the display moved at a single speed. This therefore, is a specialized type of spatial integration, one that is very different from simple speed-based segmentation mechanisms, which delineate or segregate regions of the image that differ from each other in terms of their local speeds and thus are likely to belong to different objects in the world (Hess & Ledgeway, 2003b).

However, comparatively few studies have investigated the properties of the grouping processes that mediate the extraction of spatial contours defined solely by direction cues (e.g., Hess & Ledgeway, 2003b; Ledgeway & Hess, 2002; Ledgeway, Hess, & Geisler, 2005; Rainville & Wilson, 2004) and many fundamental issues remain unresolved. In particular the spatial frequency and orientation selectivity of both the detectors that encode the local directions of the contour elements and the mechanisms that subsequently serve to integrate those estimates to disambiguate the contour have yet to be firmly established.

A recent experiment carried out by Bex et al. (2003), using a stimulus configuration similar to that of Verghese et al. (2000), has an important bearing on the issue of spatial frequency tuning of moving contour detection mechanisms. They showed that when observers are required to detect an ensemble of spatially bandpass target dots (amongst a background of randomly moving noise dots) whose collective motion defined a translating contour-like object, performance was invariant with regard to the overall spatial frequency content of the image. Interestingly, contour visibility was also little affected when alternate target elements within the moving contour differed in spatial frequency by up to ± 1 octaves, suggesting that the integration process itself is relatively broadly tuned for spatial frequency. However, in that study, the contours themselves underwent motion across the visual field (changed spatial location over time) and did not remain in a fixed spatial location in the visual field throughout the duration of each presentation unlike the stimuli employed by Ledgeway and Hess (2002). One advantage of using our stimulus configuration (stationary apertures arranged along a contour and each containing a patch of moving texture) is that any potential differences in contour sensitivity across the visual field are minimized and it does not rely on a temporal sequence of stimulation across successive spatial locations (which could introduce temporal matching ambiguity for the local motions present). Consequently, the motion-defined contours used in our previous studies may be particularly well suited to address the spatial properties of the mechanisms that underlie the integration of local direction signals in contour detection tasks.

In the present study, we sought to investigate the spatial properties (spatial frequency and orientation selectivity) of this specialized type of integration for disambiguating motion-defined contours, similar to those we have developed previously (e.g., Ledgeway & Hess, 2002). The main objectives were fourfold: (1) To ascertain if the detection of motion-defined contours is possible across a broad range of spatial scales (frequencies) and explore the spatial frequency selectivity of the global contour integration process. (2) To elucidate the orientation selectivity of the global contour integration process. (3) To compare detection performance for contours composed of moving versus stationary orientation-filtered elements. (4) To disentangle the influences of temporal flicker cues and motion direction information on contour detection. Probing the spatial properties of the mechanisms that mediate the integration or linking of local motion signals should provide important insights into its relationship to the spatial linking proposed previously for extracting contours composed of static (Field et al., 1993) and dynamic (Bex, Simmers, & Dakin, 2001) orientation-based cues.

2. General methods

2.1. Observers

The two authors (T.L. and R.F.H.) served as observers in all of the experiments and an additional, naïve observer (I.L.S.) was used to confirm the generality of several key findings. Each observer had normal or corrected-to-normal acuity.

2.2. Apparatus and stimuli

Stimuli were generated using an *Apple Macintosh G4* computer and were displayed on a gamma-corrected monitor (*Sony Multiscan G520*) with a mean luminance of ~50 cd m^{-2} and a refresh rate of 75 Hz. Stimuli were viewed binocularly at a distance of 0.74 m and presented within a central, square display window 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 screen was homogenous and had a luminance of ~50 cd m^{-2}. Fixation was unconstrained (a fixation point was not provided) and observers were permitted to make eye movements.

To assess our ability to detect contours defined solely by motion we used displays containing multiple micropattern elements similar to those used previously (e.g., Ledgeway & Hess, 2002) to assess contour integration based on the linking of local direction signals (see Fig. 1). Micropatterns were constructed such that contours were defined 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 spatially two-dimensional (2-D), visual noise that was spatially filtered using conventional Fourier techniques to leave a restricted band of either spatial frequencies or orientations (prior to filtering the noise was spatially broadband, orientationally isotropic and composed of individual noise elements subtending 1.6×1.6 arc min). The bandpass filters used had a sharp cut-off in all cases (ideal filters) and the resulting filtered images, which had 8-bit luminance resolution, were re-scaled so that they had the same mean luminance (50 cd m^{-2}) and root-mean-square (RMS) contrast (0.22) as the original unfiltered noise. Equating RMS contrast in this manner across all conditions ensures that any gross differences in visibility and apparent contrast are minimized (e.g., Bex et al., 2003; Moulden, Kingdom, & Gatley, 1990).

For noise that was spatially-frequency filtered the bandwidth of the filters used was always 1 octaves (full width) with a centre frequency of either 0.84, 1.74, 3.54 or 7.13 c/deg. For noise that was orientation-filtered the bandwidth of the filters used was 29° (full width). The filtered noise within each micropattern was presented with the confines of a smooth, 2-D, stationary Gaussian spatial window (standard deviation 0.13°, truncated at ±0.4°). The noise could be made to drift smoothly and coherently in any desired direction, spanning the 360° range, at a drift speed of 2°/s.

The use of micropatterns containing orientation-filtered (29° bandwidth) noise avoids an otherwise severe confound that would have arisen if spatially one-dimensional (1-D) moving patterns, such as sinusoidal gratings (Bex et al., 2001), had been used instead. These latter stimuli are inherently ambiguous and suffer from the well-known "aperture problem", in that motion is only perceived perpendicular to the axis of orientation. Pilot studies (involving T.L. and naïve observer I.L.S.) confirmed that the micropatterns used in the present study did not exhibit this directional ambiguity. Direction-identification of a single, centrally-presented, micropattern containing either leftwards or rightwards motion at random on each trial, was always veridical (100% correct) for both observers regardless of whether the orientation band was centred say horizontally (parallel to the motion direction) or vertically (orthogonal to the motion direction). Thus, narrowband noise decouples spatial orientation and motion direction, enabling the orientation selectivity of the mechanisms that extract motion-defined contours to be investigated.

2.3. Procedure

The contour integration task and the procedure employed were analogous to those used previously (Ledgeway & Hess, 2002). Using a standard two-alternative-forced-choice (2AFC) task observers were required to choose which interval (separated by 1 s) contained an elongated motion-defined 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). In the other interval (path plus background) eight of the micropatterns were constrained to lie along the invisible backbone of a straight (path angle of $0 \pm 5°$ random jitter), elongated contour that was constrained to pass through a central circular inclusion region (radius 0.8°) of the display area. Background micropatterns were also permitted within this circular inclusion region and the mean spatial separation between the centres of adjacent micropattern elements was 1.6° (± a uniform random deviate of 0.53°).

The spatial location and orientation of the contour's axis were randomized on each presentation. The directions of motion of the micropatterns making up this straight contour were always aligned along (and consistent with) the axis of the contour, a configuration that produces optimal performance for motion-defined contour stimuli (Ledgeway & Hess, 2002). There were no

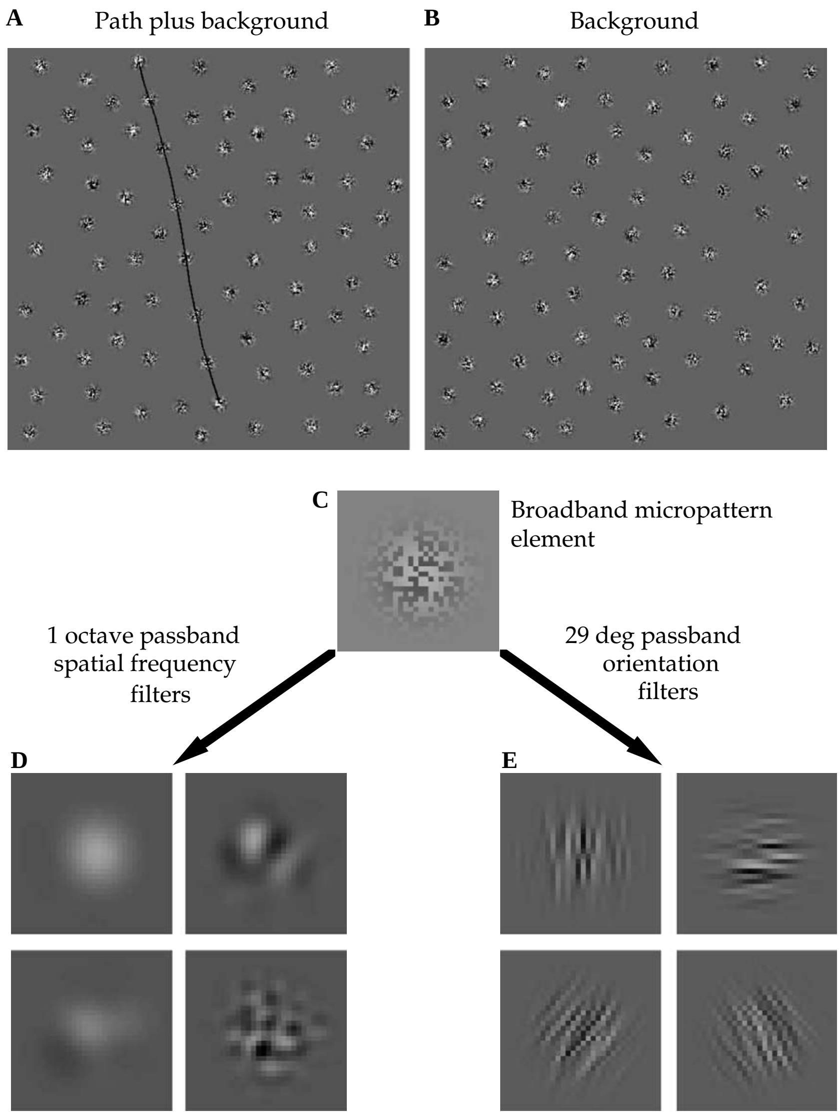

Fig. 1. Illustration of the contour detection task and stimuli used in the present study. (A) Contour composed of constituent micropattern elements (in this case broadband elements) in which the motion direction would be along the axis of the contour (shown by the normally invisible backbone on which the motion-defined path was constructed). The contour is embedded in a background of similar elements that have random motion directions. (B) The same elements are displayed but the motion directions of all elements are random. In the experiments, each aperture was stationary and contained a patch of filtered visual noise in continuous motion. The observer's task was to detect which of two intervals (e.g., A versus B) contained a motion-defined contour. (C) A magnified view of a single broadband (unfiltered) micropattern element. (D) Illustrative examples of a micropattern element that has been subjected to bandpass spatial-frequency filtering with a 1 octave (full width), ideal filter centred at one of four different frequencies. (E) Illustrative examples of a micropattern element that has been subjected to bandpass orientation filtering with a 29° (full width) ideal filter centred at one of four orientations. These filtered micropattern elements were used in displays analogous to those depicted in (A) and (B) to investigate the spatial frequency and orientation selectivity of the mechanisms that mediate the detection of motion-defined contours.

element density differences between the two intervals and both intervals contained exactly the same number and range of micropattern directions. Each run consisted of 100 trials and both observers completed at least two runs of trials for each condition tested. The percentage of correct detection scores and corresponding SEM values were calculated separately for each observer and condition tested.

3. Results

3.1. Experiment 1: Spatial frequency selectivity

To investigate if local motion signals at different spatial scales can support contour detection we first measured the detectability of straight contours (paths) composed of 2-D elements with different spatial frequency spectra. The contour and background elements were composed of two different intermingled populations whose spatial frequency spectra could differ. When the elements making up the two populations have the same narrow range of spatial frequencies, then the extent to which the detection of motion-defined contours depends on absolute element spatial frequency can be gauged. When the elements making up these two populations contain different (and non-overlapping) bands of frequencies, the spatial frequency tuning of the motion-linking process can be ascertained.

The results, for two observers (R.F.H. and T.L.), are shown in Fig. 2. Percent correct detection performance is plotted against the difference in octaves between the centre spatial frequencies of the two, spatially intermingled, populations of elements. Each centre frequency, referred to one of the element populations, is depicted by a different symbol and line style. To gauge the absolute spatial frequency dependence of this specialized form of motion integration, the relevant results are those when the two populations had identical spatial frequencies (0 octaves difference). It appears that in general there is remarkably little dependence on spatial frequency over most of the 3 octaves range of frequencies investigated. Detection performance does fall to some extent, however, at the lowest centre spatial frequency tested (i.e., 0.84 c/deg), especially for observer R.F.H. who exhibits uniformly lower performance overall than T.L. Thus, under the conditions of the present experiment motion information at the coarsest spatial scales appears to be a somewhat impoverished stimulus for driving contour detection mechanisms. Nonetheless the finding that performance is reasonably invariant with absolute spatial frequency, at least for narrowband elements $\geqslant 1.74$ c/deg, is in good agreement with the results of Bex et al. (2003) and allows us to measure the spatial frequency tuning of the contour integration process itself by varying the spatial frequency difference between alternate elements in both the contour and the background. Again, it is clear that there is, if anything, only a very weak dependence on the spatial frequency content of alternate elements for the motion-defined contour stimuli used in the present experiment. For both observers detection performance typically declines as the spatial frequency difference between adjacent elements comprising the contour increases, but this effect is relatively modest and by no means universal. Indeed, one striking feature of the results depicted in Fig. 2 is that when 0.84 c/deg elements are intermixed with those centred at a higher spatial frequency, the visibility of the resulting motion-defined contour can actually be enhanced compared to when all the elements are centred at 0.84 c/deg.

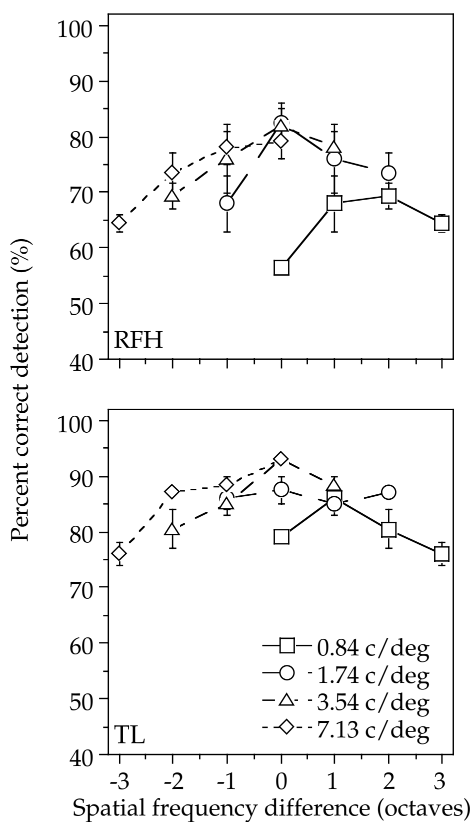

Fig. 2. Plots for two observers showing the effect of the element spatial frequency of motion-defined contours where the motion of all contour elements is aligned along the contour. Two-dimensional spatial noise was filtered into octave passbands and the detectability, in terms of percent correct, of straight contours is plotted as a function of the difference (in octaves) between the centre spatial frequencies of alternate elements in the contour (and background). Each centre frequency, referenced to one of the element populations, is depicted by a different symbol and line style. The vertical bars above and below each datum (where visible) represent the SEM indicating variability between different runs of trials. See text for details.

In order to be sure that the performance levels measured in Fig. 2 required the linking of every adjacent element defining the contour (rather than say every other element), a control experiment was carried out in which the motion directions of alternate elements were randomized. This manipulation is known to effectively disrupt performance on this task when spatially broadband elements are used (Ledgeway & Hess, 2002). The results (Fig. 3) are plotted in exactly the same format as those in Fig. 2. Regardless of the spatial frequency difference between elements, performance falls uniformly to near chance levels under these conditions, suggesting that the performance levels reported in Fig. 2 for this task depended critically on the linking of motion information from adjacent neighboring contour elements. Thus, we are confident that the results shown in Fig. 2 do indeed reflect the integration of motion along a contour.

3.2. Experiment 2: Orientation selectivity

Next we sought to establish the orientation tuning of the motion integration process underlying contour

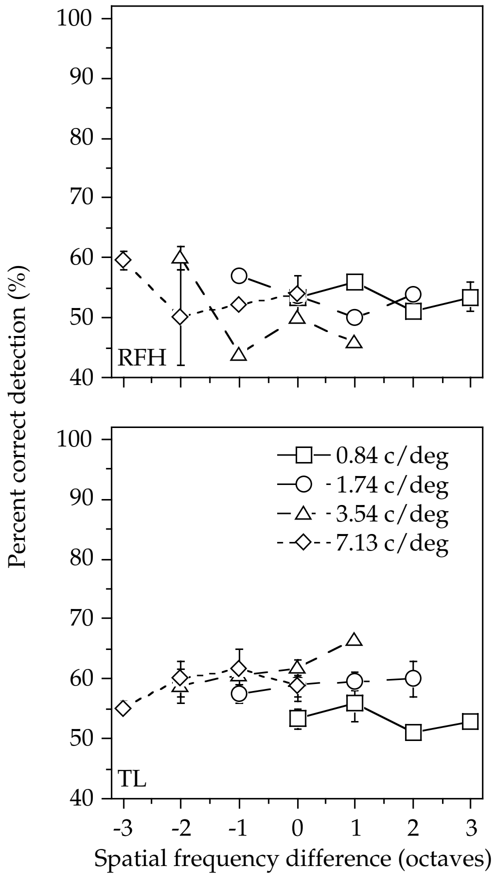

Fig. 3. Similar to Fig. 2 with the exception that for half (every other) of the elements comprising the contour, the motion directions were aligned along the contour axis and for the other half the motion directions were random.

detection. Due to the fact that the straight contours used had a random configuration (overall orientation of the elongated contour axis with respect to the display) from trial to trial (see Section 2), the most appropriate manipulation is to vary element orientation in relative terms (i.e., the local orientation of each element relative to the axis of the contour to be detected). This is certainly the case for motion direction using broadband micropatterns, in that it is direction of motion relative to the contour that defines this specialized form of integration (Ledgeway & Hess, 2002; Ledgeway et al., 2005). Consequently, we measured the effect of varying the micropattern element orientation relative to the contour for spatial frequency broadband stimuli with an orientation bandwidth of 29° (see cartoons at the top of Fig. 4 which represent the central orientation of the 2-D noise within each element of a contour relative to a hypothetical straight vertical contour). In this case, the centre (median) orientations of all the contour elements have some fixed relation to the axis of that contour, that their motion directions define.

Performance is plotted as a function of the element orientation relative to that of the straight contour in

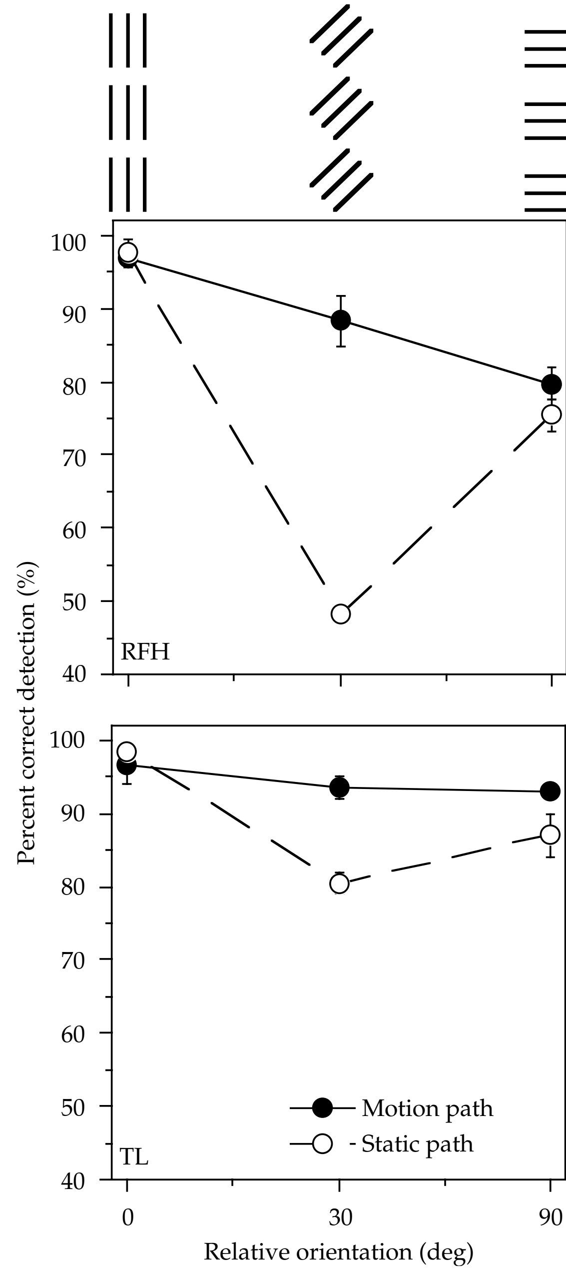

Fig. 4. The effect of varying the relative (i.e., with respect to the contour axis) orientation alignment of elements on the detection of motion-defined contours (filled symbols), where the motion direction of contour elements was aligned along the contour axis, and static contours (unfilled symbols). The texture within each element was spatial frequency broadband noise whose orientations were restricted to a 29° passband. The cartoon at the top of the figure represents the relationship between the centre orientation of the contour elements and the elongated axis of the contour, for the case where the contour itself was vertical. In the actual experiments the overall orientation of the contour was randomized from trial to trial. The vertical bars above and below each datum (where visible) represent the SEM indicating variability between different runs of trials.

Fig. 4 (note that the motion direction of the elements comprising the contour was again always along the axis of that contour). For the two observers (R.F.H. and

T.L.) detection of straight motion-defined contours (filled symbols and solid line) is comparable to levels previously seen for spatially broadband, isotropic stimuli (Ledgeway & Hess, 2002). There is a clear but weak dependence of performance on the orientation structure of the elements relative to the contour that their motions define. Detection is best when the moving orientation structure is aligned with the contour (0° relative orientation) and worst when it is orthogonal to the contour (90° relative orientation). It is important to emphasize that because a purely 1-D motion stimulus (e.g., a sinusoidal grating) cannot physically have motion along its orientation axis (the aperture problem), it must be the case that only "off-axis" orientations in the filtered noise contribute to perception in the 0° relative orientation condition.

3.3. Experiment 3: Comparing performance for moving versus stationary orientation-filtered (band limited) stimuli

Superficially the results of Experiment 2 suggest that the detectability of motion-defined contours depends on the relative orientation of the contour elements. This in turn suggests that it may well be mediated by the same mechanisms that Field et al. (1993) showed, were responsible for the detection of 1-D static stimuli. To better understand the relationship between the motion and static cases, performance was measured using the same orientation-filtered elements as in Experiment 2 with the exception that the texture within each element was stationary rather than moving.

The results for two observers (R.F.H. and T.L.) are displayed in Fig. 4 as unfilled symbols and dashed lines. While it is true that performance levels for contours composed of either static or moving elements is similar when the peak of the orientation band is either aligned or orthogonal to the contour, somewhat different results are obtained when the orientation band is centred obliquely (30°) relative to the contour that it defines. In this case, the detection of static stimuli is at chance (R.F.H.) or substantially reduced (T.L.), consistent with previous studies that have investigated contour detection with obliquely oriented stationary elements (e.g., Dakin & Hess, 1998; Ledgeway et al., 2005). However, motion-defined contours remain highly detectable under these conditions and this provides compelling evidence that the mechanisms responsible for integrating static contours exhibit different properties to those that integrate contours defined by motion.[1]

[1] Additional observations by a naïve observer (I.L.S.) confirmed this difference in performance for contours composed of static (54% correct, SEM ±2%) and moving (82% correct, SEM ±2%) elements, when the orientation band is centred obliquely (30°) relative to the contour.

An interesting issue that is still indeterminate is whether or not the mechanisms responsible for integrating contours defined by motion direction can pool or link information across different orientations, as previously shown to be the case for spatial frequency (Experiment 1). To address this issue we adopted a similar procedure of manipulating the centre orientation of each alternate element of the contour, as depicted schematically by the cartoon at the top of Fig. 5 for the hypothetical case where the contour is vertical.

In Fig. 5 percent correct detection is plotted as a function of the orientation difference (i.e., difference in

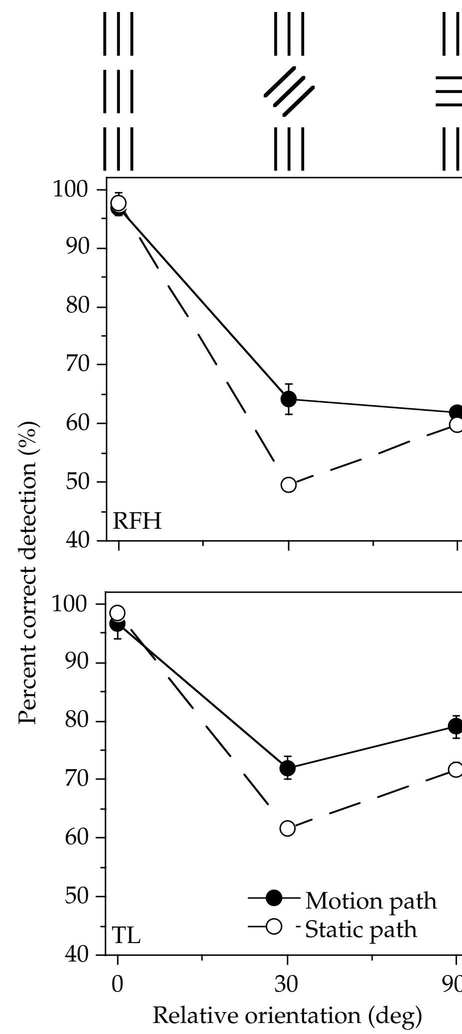

Fig. 5. The effect of varying the relative (i.e., with respect to the contour axis) orientation of alternate elements in the display on the detection of motion-defined (filled symbols) and static contours (unfilled symbols).The texture within each element was spatial frequency broadband noise whose orientations were filtered such that they were restricted to a 29° passband. The cartoon at the top of the figure represents the relationship between the centre orientation of each contour element and the elongated axis of the contour, for the case where the contour itself was vertical. In the actual experiments, the overall orientation of the contour was randomized from trial to trial. The vertical bars above and below each datum (where visible) represent the SEM indicating variability between different runs of trials.

the centre orientation of a 29° orientationally-bandpass filtered image) between alternate contour elements, separately for observers R.F.H. and T.L. The results for motion-defined paths (filled symbols and solid lines) show a rapid drop in performance for a 30° orientation difference between alternate elements. Similar results were obtained for a static version of the same stimulus, except that performance levels fall to near chance levels for a 30° difference but are above chance for a 90° rotation. The residual above chance levels of performance found for both motion-defined and static contours for an orientation difference of 90° between neighboring adjacent elements is consistent with probability summation between two populations of elements each effectively at half density. Table 1 displays the separate measurements of the detectability of these contours when only half the number of elements are present and subsequent probability summation predictions according to two different models, one involving simple statistical summation and the other involving d' summation (see Graham, 1989; Green & Swets, 1966).

However, probability summation cannot readily explain the exceptionally poor levels of performance found for static contours when there was an orientation difference of 30° between neighboring adjacent elements (in this case performance is worse than the probability summation prediction). One possibility is that the presence of texture elements oriented obliquely with respect to the contour axis (for which orientation linking is poor), actively interferes with or inhibits the spatial linking of interspersed elements that are parallel with that axis. Further research is needed to address this issue (which is beyond the scope of the present paper), but at present it is sufficient to conclude that the mechanisms responsible for integrating contours defined by motion direction cannot combine information derived from very dissimilar orientations.

3.4. Experiment 4: The roles of temporal flicker and motion direction in contour detection

A potentially important issue not taken into account in the comparison of performance for static and motion-defined contours concerns the role played by temporal factors apart from motion. Static and motion-defined contour stimuli are different in their temporal properties and Bex et al. (2001) have shown that simple counterphase flicker per se can enhance sensitivity for detecting contours composed of 1-D elements. Thus, it is possible that the enhanced performance found for motion-defined contours, composed of elements with oblique relative orientations (Fig. 4), is due simply to the temporally varying nature of the stimuli. The purpose of Experiment 4 was to address this interesting issue.

Contour detection was measured for orientation-filtered stimuli (29° full bandwidth) in which the constituent elements contained substantial flicker, but no consistent direction information. This was achieved by replacing the texture within each element with a new stochastic sample of filtered noise on each frame. This ensured that there were no coherent local motion cues within the temporally changing stimulus. The results (for observers R.F.H. and T.L.) are compared to those previously obtained for elements whose motion was aligned along the contour (Fig. 6). Similar sensitivity was found for flickering and motion-defined contours when their constituent orientations were either aligned with or orthogonal to the contour. The results are, however, very different for elements oriented obliquely to the contour. In this case, the abolition of consistent motion direction information renders the flickering contours much harder to detect. Thus, the mere presence of flicker within each element (a temporally changing luminance distribution) cannot fully account for the pattern of results found. Direction information plays an important role that is most evident when the relative orientations of the elements are oblique with respect to the contour on which they lie.

4. Discussion

Using a paradigm that allowed us to readily separate out the influences of direction, orientation and spatial frequency, we investigated the spatial rules that govern the integration of local motion direction signals to define

Table 1
Results for two observers showing percentage correct detection performance for motion-defined and static contours where half of the orientation-filtered elements are either aligned (0°) or orthogonal (90°) to the contour axis

Condition (contour type and observer)	1/2 Density population 0°/90° (% correct)	Simple statistical probability summation (% correct)	d' Probability summation (% correct)
Motion (R.F.H.)	57.5/56.5	63.03	59.87
Static (R.F.H.)	57.5/55.5	62.18	59.26
Motion (T.L.)	75/67	83.5	78.97
Static (T.L.)	69/64.5	77.99	73.23

Two probability summation models are used to predict the performance when contours are composed of twice the number of elements where alternate elements have local relative orientations of either 0° (aligned along the contour) or 90° (orthogonal to the contour). Performance in the two-population case (orientation difference of 90° in Fig. 5) is consistent with the predictions of probability summation.

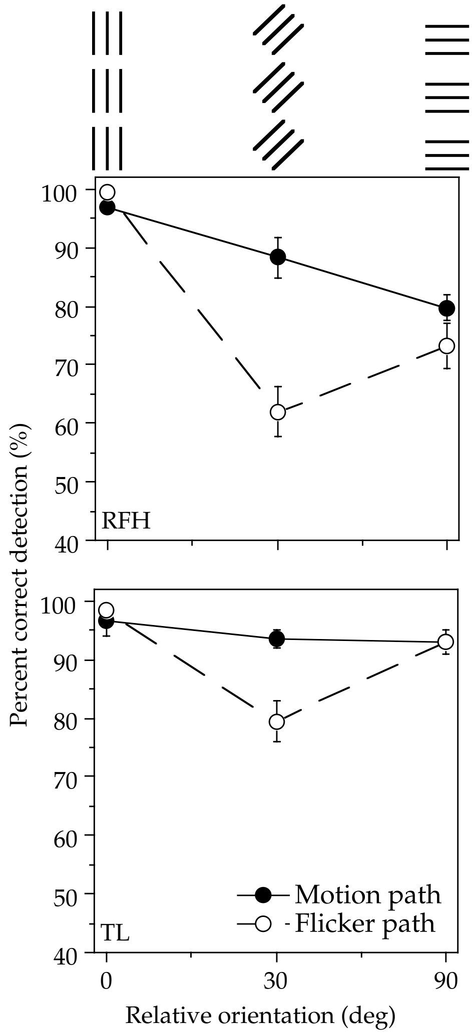

Fig. 6. Same as Fig. 4 with the exception that detection performance is plotted for motion-defined (filled symbols) contours and contours composed of flickering elements (unfilled symbols) that contain no net direction information (achieved by replacing the orientation-filtered noise present within each element with a new sample on each image update).

simple spatial contours. Previous studies have shown that the spatial integration of local motion signals depends crucially on both the relationship of those motion directions to the contour's axis and shape and also the variance (degree of similarity) of the local direction signals present (see Hess & Ledgeway, 2003b; Ledgeway & Hess, 2002). When 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 motion directions that define it are of prime importance. When the contour is highly curved, however, performance is limited by the variance of the composite directional signals without regard for their precise spatial arrangement along the contour. Thus, there are rules for combining local motion directions across space in a manner that is somewhat analogous to the rules that determine how local orientation signals are combined to define static contours (Field et al., 1993). As for orientation, there is an association of motion direction and spatial position (i.e., an "association field" for motion).

In the present study, we delineate the spatial frequency and orientation dependencies of this specialized form of integration (i.e., for motion along the contour). In terms of spatial frequency selectivity of the contour detection process, the situation is relatively straightforward. There is very little dependence on either the absolute (i.e., of all the elements) spatial frequency of the elements or differences between (i.e., of alternate elements comprising the contour) element spatial frequency. This suggests a broad spatial frequency tuning consistent with the idea that the integration process underlying the extraction of contours can combine motion information across a range of spatial scales.

This finding is in stark contrast to the pattern of results found by studies that have explored the spatial frequency dependence of contours defined by static orientation cues. In that case, the spatial tuning of the linking process is spatial frequency narrowband (Dakin & Hess, 1998). The bandwidth (half width at half height in a percent correct space) was $\sim$1.3 octaves for straight contours. For motion-defined contours, the results of the present study agree with those of Bex et al. (2003) in suggesting that the spatial tuning of the linking mechanism is much broader. Indeed in the present study, contour detection was readily possible even when the spatial frequencies of the elements comprising the contour differed by over 3 octaves. Thus, although there are some similarities concerning the specific rules that determine how the local information is integrated to enable extended contours to be detected, importantly these rules are not identical for contours defined by motion and those defined by static orientation cues.

Investigating the orientation selectivity of the mechanisms that integrate local motion signals to extract contours is a relatively more complex issue. Importantly, the results of the present study (Experiment 2) demonstrate that it is the orientation of the elements relative to the contour that is critical. In terms of relative (i.e., with respect to the contour axis) orientation, the situation is complicated mainly because, for orientationally band limited elements, contour integration mechanisms based purely on the presence of orientation cues can contribute to the detectability of contours containing motion. In other words, contours are no longer solely defined by the consistent motion directions of their constituent elements if those elements are filtered in the orientation domain.

However, it is possible to conclude that the influence of orientation-based cues is at least equal to that provided by motion direction for orientations that are aligned with or orthogonal to the contour that they represent. For oblique orientations (i.e., relative to the contour), however, Experiment 3 demonstrated that motion-based contour extraction mechanisms can support good performance levels close to those previously observed for unfiltered elements (Ledgeway & Hess, 2002), whilst the contribution of orientation-based mechanisms under these conditions is minimal (see Fig. 4). To illustrate further the separate effects of static orientation and motion on contour detection, Fig. 7 shows the performance of two observers (T.L. and I.L.S.) for moderately curved contours (path angle of 20°) composed of orientation-filtered noise that was either static (unfilled columns) or in continuous motion (filled columns). The orientation band of the noise within each micropattern was aligned with the curved axis of the contour (0° relative orientation). The use of curved, rather than straight, contours avoids the performance ceiling effects found previously in Experiments 2 and 3. It is evident that for both observers performance improves significantly with the addition of motion along (and consistent with) the depicted contour, bolstering our conclusion that both orientation- and direction-based cues contribute to contour detection. It is important to emphasize that this advantage for contours containing motion is not simply due to the temporally changing patterns of stimulation (flicker) provided by motion stimuli, as evidenced by the results of Experiment 4.

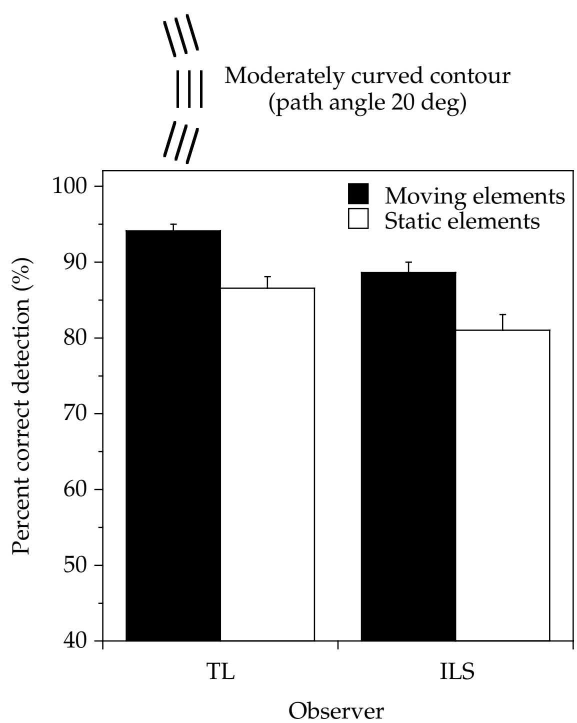

Fig. 7. Same as the 0° relative orientation condition of Fig. 4 with the exception that the motion-defined (filled columns) and static contours (unfilled columns) were moderately curved (20 ° path angle) rather than straight. The orientation of the noise within each micropattern was always centred on the curved axis of the contour and in the case of motion-defined contours the drift direction was also along (consistent with) that axis. See text for further details.

In terms of the orientation tuning of contour detection, the results of Experiment 3 (where the relative orientations of alternate contour elements were varied) suggest that the mechanism that underlies contour detection from motion signals does not collapse information across orientation prior to its analysis. Performance fell sharply when the orientation difference between alternate elements was 30° and was close to chance levels when alternate elements differed in orientation by 90°. Interestingly, a similar pattern of results was found when each element in the display contained stationary, rather than moving, texture (see Fig. 5). This latter finding is in good agreement with previous studies in that orientational noise (increased relative orientational variance of contour elements) has been shown to degrade greatly the detectability of static contours (Field et al., 1993). Thus, in both cases the mechanisms that mediate contour extraction appear to exhibit narrowband orientation selectivity. An important additional finding that emerges from the current study is that although static contour mechanisms are highly efficient at processing contours defined by elements that are oriented either parallel or orthogonal to the contour axis, they are much less sensitive to obliquely oriented elements. However, motion-based contour mechanisms appear able to efficiently process contours composed of all orientations (although information is not combined across different orientations) as long as the motion direction is along the contour axis. This results in a strong detection advantage for contours containing motion, when the local texture information is oriented obliquely with respect to the contour.

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