



Snakes and ladders: the role of temporal modulation in visual contour integration

Peter J. Bex *, Anita J. Simmers, Steven C. Dakin

Institute of Ophthalmology, 11-43 Bath Street, London EC1V 9EL, UK

Received 15 May 2001; received in revised form 14 August 2001

Abstract

We investigated temporal aspects of the cortical mechanisms supporting visual contour integration by measuring observers' efficiency at detecting fragmented contours, composed of Gabor micropatterns, embedded in a field of distractor elements. Gabors consisted of a static Gaussian enveloping a sinusoidal carrier which was temporally modulated by motion or counter-phase flicker. The elements forming the path could be oriented either parallel ('snakes') or perpendicular to the contour orientation ('ladders'). Sensitivity to contour structure (estimated by measuring the maximum tolerable element orientation jitter supporting contour detection) was increased when the elements were drifting or flickering. Snakes were more detectable than ladders under all conditions. The increase in sensitivity conferred by drifting carriers was present even when the elements in the same stimulus were drifting at a range of speeds spanning almost three octaves. These results lend further support to the notion that the contour integration system receives separate transient and sustained input. © 2001 Elsevier Science Ltd. All rights reserved.

Keywords: Contour integration; Linking; Motion; Flicker; Speed

1. Introduction

Physiological and behavioural studies indicate that the receptive fields of early visual detection mechanisms are spatially limited and are highly selective for a limited range of stimulus attributes—such as spatial frequency, orientation and direction of motion (Hubel & Wiesel, 1968; Wurtz, 1969; Henry et al., 1974; Schiller et al., 1976; Anderson & Burr, 1987). This means that information about image structure over extended areas of visual space must be based on the combined responses of a number of independent, local inputs. In recent years this integration process has been extensively explored using a contour detection task introduced by Field and colleagues (Field et al., 1993). In these tasks, observers are required to detect a contour that is defined by many narrow-band elements that are embedded in a large array of identical, but randomly oriented elements (see Fig. 1 for example images). The parameters of the embedded contours, such

as length and curvature, prevent the contour from being detected by individual receptive fields (Hess & Dakin, 1997); the responses of multiple local units must be integrated in order to detect the contour.

Several studies have now identified many constraints on the stimulus parameters that support the long-range associations necessary for contour detection. Observers are able to detect considerably curved contours (up to 60° between adjacent elements) even with large separation between adjacent elements along the contour (Field et al., 1993). In general, sensitivity to contours increases with the length and straightness of the path (Field et al.; Pettet, 1999; Mullen et al., 2000), although closure of highly curved contours can increase sensitivity (Kovacs & Julesz, 1993). Sensitivity also increases with exposure duration (Roelfsema et al., 1999), and with the similarity in the phase (Dakin & Hess, 1999; Hess & Dakin, 1999; Keeble & Hess, 1999) or spatial frequency (Dakin & Hess, 1998; Dakin & Hess, 1999) of the elements defining the contour. Contours can also be integrated within and across depth with similar factors determining sensitivity (Hess & Field, 1995; Hess et al., 1997).

* Corresponding author. Fax: +44-207-608-6983.

E-mail address: p.bex@ucl.ac.uk (P.J. Bex).

In the peripheral visual field, the detection of approximately straight path stimuli could be accounted for on the basis of the maximum energy along a given orientation, without requiring any post-receptoral interactions among local element detectors. However, in the foveal and parafoveal visual field (up to about 10° eccentricity), observers are able to detect contours in spite of large amounts of positional and orientational jitter and these results require facilitatory interactions among local receptive fields at distributed locations (Hess & Dakin, 1997, 1999). These data are generally consistent with a class of models based on long-range excitatory interactions among neighbouring receptive fields with similar orientation (Field et al., 1993) and spatial frequency (Dakin & Hess, 1998, 1999) selectivity.

Most investigations of spatial grouping and contour integration have explored the spatial parameters that limit sensitivity to static images. However, a number of recent studies have examined how the temporal relationships among spatially separated elements can affect the perception of spatial structure. For example Usher and Donnelly (1998) measured sensitivity to contour stimuli composed of line elements that were flickered either synchronously or asynchronously with respect to background elements. In synchronous conditions, the contour and the background elements were presented on the same frame, interleaved with a blank frame. In

asynchronous conditions, the contour was presented alone on alternate frames interleaved with a frame containing only the background elements. At high temporal frequencies synchronous and asynchronous stimuli appear identical, however observers were reliably more sensitive to asynchronous stimuli than synchronous stimuli. This and a number of other recent psychophysical studies (e.g. Alais et al., 1998) suggest that temporal synchrony can facilitate the processes mediating spatial grouping, possibly by a mechanism of temporal binding among neurones that respond to the path elements at the same temporal intervals. Furthermore, Lee and Blake (1999) found that a simultaneous change in direction of a field of randomly oriented, drifting Gabor elements revealed apparent spatial form, suggesting that temporal synchronous changes alone can be sufficient to reveal structure in otherwise random stimuli.

In a recent study, Hayes (2000) employed moving and flickering contour displays to examine whether the *physical* or *perceived* positional relationships among path elements determined contour linking. When the sinusoidal carrier of a Gabor patch is set in motion within its static Gaussian envelope, the apparent location of the Gabor is shifted in the direction of carrier motion (Devalois & Devalois, 1991). This perceived positional shift therefore moves elements away from the

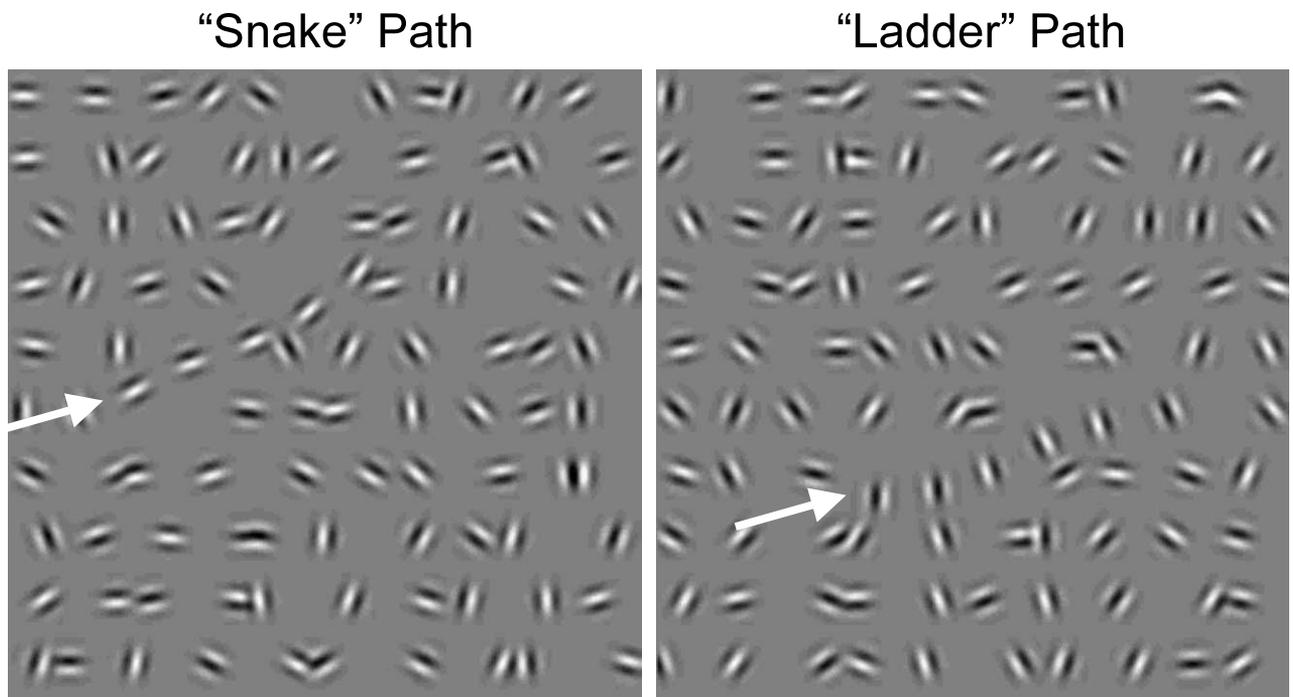


Fig. 1. Illustrations of typical stimuli. Each diagram shows a single frame from one of our stimuli. A white arrow helps the reader locate the path, but was not present in experimental trials. On the left the elements are aligned parallel to the contour—snake paths, on the right the elements are aligned perpendicular to the contour—ladder paths. In these illustrations, the elements defining the path are in phase and path curvature (a) is 10° . The elements were set in motion by drifting the sinusoidal carrier within its static Gaussian envelope. Elements defining the path moved in a coherent direction (except for the perturbations of local angle described in the Section 2), distracter elements moved in random directions.

‘backbone’ of the contour, which for static patterns is known to reduce sensitivity to the contour (Field et al., 1993). Therefore for moving contour stimuli, it is possible to align either the physical locations of the contour element (but thereby misalign their perceived locations); or to align their perceived locations (but thereby misalign their physical locations). Hayes (2000) found that contours were detected best when the perceived locations of the micro-patterns were aligned to compensate for the illusory shift, but their physical locations were misaligned. This result suggests that models of early visual processing should consider the physical and perceived location coded by early visual filters.

In the present investigation, we examine the effects on contour detection of motion and counter-phase flicker. We employ stimuli composed of semi-randomly positioned Gabor micro-patterns, as used in many previous studies, but here we also drift or counter-phase flicker the sinusoidal carriers within their stationary Gaussian envelopes. Previous investigations of contour integration have focused on stimuli in which the sinusoidal carriers of the path are aligned parallel to the contour, because these stimuli probe the mechanisms that identify contours that extend beyond the size of typical receptive fields. Because of the appearance of such paths, we term them ‘snakes’. Relatively less emphasis has been placed on stimuli in which the sinusoidal carriers of the path are aligned orthogonal to the contour. For static images, such ‘ladder’ paths have relatively little ecological significance and are very difficult to detect, but in moving scenes, this organisation indicates regions of common direction.

2. Methods

The observers were two of the authors (PB and AS) and a total of eight naïve volunteers, who each completed a subset of conditions. All had normal or corrected visual acuity and practised contour detection tasks before formal data collection.

Stimuli were generated on a Macintosh G4 computer by software adapted from the VideoToolbox routines (Pelli, 1997) and were displayed on a Sony PS400 monitor in greyscale at a frame rate of 75 Hz, a mean luminance of 50 cpd/m² and at 75% contrast. The luminance of the display was linearized with pseudo-12 bit resolution (Pelli & Zhang, 1991) in monochrome and calibrated with a Minolta photometer. Images were presented in greyscale by amplifying and sending the same 12-bit monochrome signal to all RGB guns of the display. The display measured 34.6 cm horizontally (832 pixels), 26 cm vertically (624 pixels), and was 57 cm from the observer, in a dark room.

2.1. Stimuli

Stimuli were composed of multiple Gabor elements pseudo-randomly positioned in a 10°*10° square region in the centre of the display. The display was divided into a 10*10 grid of equal sized cells (each 1° square). Each cell contained a Gabor element that was the product of a circular Gaussian envelope and an oriented sinusoid:

$$G(x,y) = e^{-(x^2+y^2)/2\sigma^2} \cos [2\pi*(\cos\theta*x + \sin\theta*y)/\rho + \phi],$$

where θ controls orientation, ρ the spatial frequency and ϕ the phase of the sinusoid. The spatial frequency of the elements was 3 cycles per degree (cpd) and σ , the standard deviation of the Gaussian envelope, was 0.2°.

Each trial consisted of two intervals containing 100 Gabor elements, one of which contained a path plus randomly oriented elements, the other contained only randomly oriented elements. The path was a set of six oriented Gabor elements aligned along a contour that was embedded in a background of similar, but randomly oriented Gabor elements. The construction of the path has been described in detail elsewhere (Field et al., 1993). In summary, the elements defining the path were separated by a 1.2° gap (the mean separation of the random elements, including diagonals) plus a random value between $\pm 0.12^\circ$, to eliminate periodic cues to the presence of the path. The curvature of the contour was controlled by parameter α , that determined the angular difference between adjacent elements (where $\alpha = 0^\circ$ defined a straight contour and curvature increased with α), and was fixed at 20° in the present experiments to produce paths of intermediate curvature. The first element in the path was assigned a random starting phase and a random orientation (between 0° and 360°), successive elements were placed at a location determined by the angular difference and spatial separation between adjacent elements. Paths that looped back on themselves were discarded, to avoid facilitation of path detection from closure (Kovacs & Julesz, 1993), and a new random path was generated. The spatial phase of all elements was assigned an independent random starting value (between 0° and 360°). The Gabor elements defining the path were either parallel to the contour—a ‘snake’, or perpendicular to it—a ‘ladder’, see Figs. 1 and 2.

The complete contour was randomly positioned in the display. The remaining 94 cells were then occupied by distracter elements of random orientation and with random starting phase. The distracter elements were randomly positioned within unoccupied cells with the constraint that each cell contained the centre of only one Gabor, to eliminate clumping of elements. Overlapping elements summed. In the random pattern, all 100

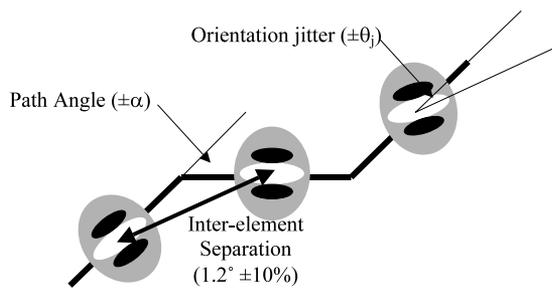


Fig. 2. Illustration of the parameters determining the relative placement of the elements defining the contour. The mean inter-element separation was 1.2° , equal to the mean separation of distracter elements, \pm up to 10% at random to eliminate periodic cues to the presence of the path. Adjacent elements along the path were randomly oriented $+\alpha$ or $-\alpha$, which controlled the curvature of the path. Thus where $\alpha = 0^\circ$ produced a straight path and curvature increased with α . In the present experiments α was set to 20° . The orientation jitter θ , controlled the orientation of the element with respect to the contour, where $\theta = 0^\circ$ was in perfect alignment. For any path element, θ was randomly selected from $-\theta_j$ to $+\theta_j$ the range of which (j) was determined by a staircase under computer control.

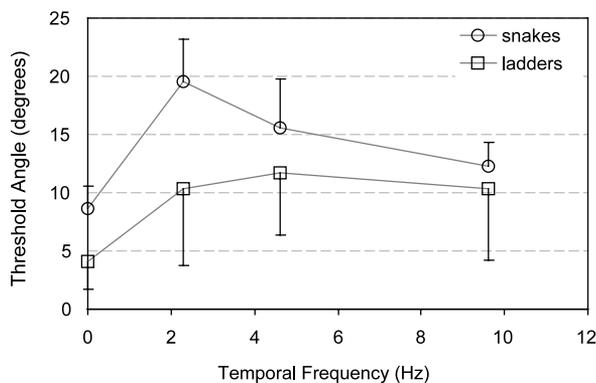


Fig. 3. Sensitivity to drifting paths as a function of temporal frequency. Circles show the mean threshold angle for 'snake' paths for seven observers (two authors and five naïve observers). Squares show mean threshold angle for 'ladder' paths for four observers (two authors and two naïve observers). Error bars show ± 1 s.e.m. (to eliminate overlap).

cells contained a randomly positioned element of random orientation and with random starting phase.

The elements were set in motion by advancing the phase of the sinusoidal carrier of each element independently by an appropriate angle to produce drift at the desired temporal frequency. The direction of motion of all elements was orthogonal to their orientation. Thus the elements forming the contour whose orientations were similar, moved in a similar direction, whereas distracter elements whose orientations were random, moved in random directions. Counter-phase flicker was achieved by modulating the contrast of each element independently according to a sinusoidal modulation of the desired temporal frequency.

The observers' task was to fixate a central cross and to identify with a button press which of the intervals contained the path. Auditory feedback followed incorrect responses.

2.2. Psychophysical manipulations

We developed a psychophysical procedure to measure observers' sensitivity to paths. Sensitivity is greatest when the elements are aligned to the contour and decreases as the orientation between adjacent path elements increases (Field et al., 1993). Therefore, we measured the amount of local orientation 'jitter' that produced 75% correct performance in the detection task, and used this as our sensitivity estimate. Each path element was aligned to the contour plus a random orientation jitter selected from a uniform distribution, the range of which was under the control of a QUEST staircase procedure (Watson & Pelli, 1983) from $-\theta_j$ to $+\theta_j$. The staircase increased the range when observers correctly identified the interval containing the path, and decreased the range when observers were unable to identify the interval containing the path. During practise runs, we established that all observers were able to perform the contour detection task at 100% correct levels when the jitter was 0° , to ensure there were no floor effects. In all experiments, the levels of the parameter of interest (i.e. the level described along the x-axis of each graph) were randomly interleaved in a single run and at least four runs for each condition were completed in random order.

3. Results

3.1. Detection of moving paths

Fig. 3 shows the sensitivity to drifting path stimuli as a function of temporal frequency. Circles show data for snake paths (contours in which elements were aligned parallel to the contour), for seven observers (two authors and five naïve observers). Squares show data for ladder paths (contours in which elements were aligned perpendicular to the contours) for four observers (two authors and two naïve observers). Factorial Analysis of Variance showed that observers were significantly more sensitive to snakes than to ladders at all speeds [$F(1, 36) = 5.80$, $P < 0.025$]. Observers were also significantly more sensitive to moving snakes than to static snakes [$F_{\text{contrast}}(1, 36) = 6.35$, $P < 0.025$], but this effect failed to reach significance for drifting ladders [$F_{\text{contrast}}(1, 36) = 3.23$, $P > 0.05$], possibly because of the smaller number of subjects in this condition.

3.2. Detection of counterphase flickering paths

Fig. 4 shows the mean sensitivity to counter-phase flickering path stimuli as a function of temporal frequency for four observers (two of the authors and two naïve observers). Filled circles show data for snake paths in which the elements forming the contour flickered in phase. Open circles show data for conditions in which the relative temporal phase of the contour elements was random. The background elements of the display flickered in random temporal phase in all conditions. Factorial Analysis of Variance showed that observers were significantly more sensitive to flickering paths than static paths overall [$F_{\text{contrast}}(1, 9) = 19.41$, $P < 0.01$] and for in phase conditions in isolation [$F_{\text{contrast}}(1, 9) = 21.65$, $P < 0.01$], however there was no significant difference between flickering and static paths

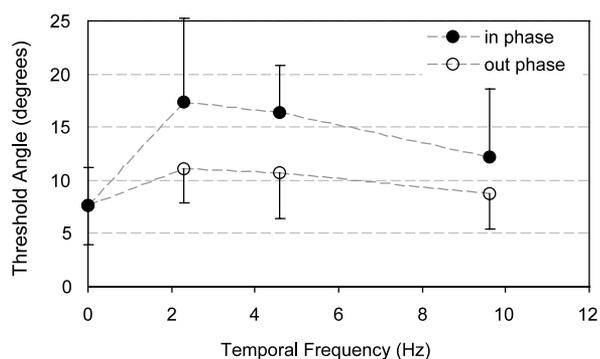


Fig. 4. Sensitivity to counter-phase flickering 'snake' paths as a function of temporal frequency for four observers (two authors and two naïve observers). Filled circles show the mean threshold angle for stimuli in which the elements forming the path flickered in the same relative phase. Open symbols the mean threshold angle for stimuli in which the elements forming the path flickered in random relative phase. Error bars show ± 1 standard error.

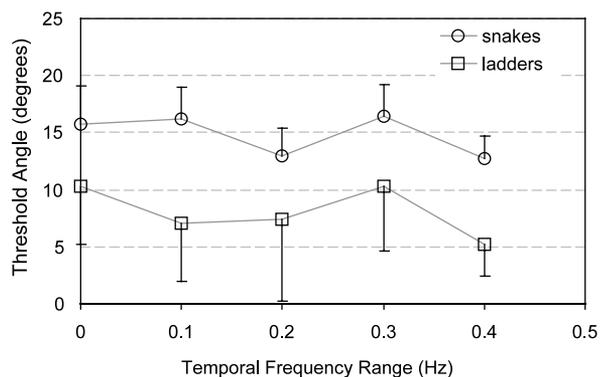


Fig. 5. Sensitivity to drifting paths in which the elements drifted at different speeds. The speed of each element was randomly selected from the distribution centred on 4.6 Hz, spanning the range shown by the x axis. Circles show the mean threshold angle for 'snake' paths for seven observers (two authors and five naïve observers). Squares show mean threshold angle for 'ladder' paths for two observers. Error bars show ± 1 standard error.

for out-of-phase conditions alone [$F_{\text{contrast}}(1, 9) = 2.49$, $P > 0.05$]. A t test also showed that observers were more sensitive to in-phase flicker than to random phase flicker [$t = 3.92$, $P < 0.005$]. (A t test was necessary for this comparison because the 0 Hz condition for in- and out-of-phase conditions were the same).

Although motion and sinusoidal counter-phase flicker of sine-wave elements produce identical luminance changes at any single point of the stimulus, only counter-phase flicker modulates the contrast of the stimulus. At low temporal frequencies, this gave rise to the perception of wave-like changes in contrast across the display, but this was not noticeable at high temporal frequencies. The authors ran additional trials in which the temporal profile of the counterphase flicker was square-wave, rather than sine-wave in profile. Thus the elements abruptly reversed phase, rather than slowly reversing through zero contrast, thereby maintaining constant image contrast locally and globally. The results were not significantly different for these observers than for sine-wave flickering stimuli. This confirms that contrast changes do not account for the weak effect of random-phase flicker on contour detection.

3.3. Detection of moving paths as a function of speed range

The results of Experiments 1 and 2 show that sensitivity to contours increased when the elements comprising them were set in motion or were flickering in phase, but with little or no advantage for counter-phase flickering elements in random temporal phases. We wondered whether the advantage was based on the common speed/temporal frequency of the path elements or on their common direction. In Experiment 3 therefore, we varied the temporal speed range of the elements forming the stimulus. The temporal frequency of each element (path and distracter) was independently selected at random from a uniform log distribution of temporal frequencies centred on 4.6 Hz. The range from which the temporal frequency of each element was selected from the range $10^{\pm 0.0}$ (where all elements moved at 4.6 Hz), $10^{\pm 0.1}$ (each element moved at a temporal frequency randomly selected from a distribution from 3.7–5.8 Hz), $10^{\pm 0.2}$ (2.9–7.3 Hz), $10^{\pm 0.3}$ (2.3–9.2 Hz), or $10^{\pm 0.4}$ (1.8–11.6 Hz). The temporal frequencies of target and distracter elements were selected from the same distribution, ensuring that the path could not be detected by identifying a single element that was noticeably slower or faster than the rest.

Fig. 5 shows the sensitivity to drifting path stimuli as a function of the speed range of the elements. Circles show data for snake paths for seven observers (two authors and five naïve observers). Squares show data for ladder paths for four observers (two authors and

two naïve observers). Factorial analysis of variance confirmed that observers were significantly more sensitive to snakes than to ladders [$F(1, 45) = 16.48$, $P < 0.01$]. However, there was no significant effect of the speed range [$F(4, 45) = 1.04$, $P > 0.05$], showing that observers were equally sensitive to drifting paths even when the elements forming the path moved at very different speeds.

4. Discussion

4.1. Speed, temporal frequency and direction

The results of Experiment 1 show that observers were more sensitive to contours composed of drifting elements than to contours composed of static elements (up to $9.4 \text{ Hz} = 3.1^\circ/\text{s}$ at 3 cpd in these experiments). However, Experiment 2 shows that observers are more sensitive to counter-phase flickering contours only when the elements flicker in the same temporal phase. Counter-phase flicker in random temporal phase did not significantly affect sensitivity to contours. This was not simply based on any contrast changes introduced by sinusoidal counter-phase flicker because equivalent results were found when the counter-phase modulation was square wave. In Experiment 3, we found that sensitivity to contours composed of drifting elements was increased even when the elements defining the contour and distracters drift at speeds differing by as much as three octaves. In this case individual elements defining the contour (and the distracter elements) moved at temporal frequencies ranging from 1.8 to 11.6 Hz. Sensitivity under these conditions is approximately equal to sensitivity for the fastest conditions with elements at the same speed. This suggests that the cortical processes responsible for linking the elements of a drifting contour are broadly tuned for temporal frequency.

The observation that motion increases sensitivity to contours while counter-phase flicker in random phase does not affect sensitivity demonstrates that temporal modulation per se is not sufficient to facilitate the processes of contour linking. In fact, Experiment 3 shows that common temporal frequency is not even necessary to facilitate contour detection. The finding that in-phase counter-phase flicker increases sensitivity to contours is consistent with previous investigations showing that in-phase temporal modulation promotes grouping (Usher & Donnelly, 1998; Alais et al., 1998).

In Experiment 3 the speed difference also leads to a large variation of temporal phase among the contour elements mean. Taken together these results suggest that the facilitatory effect of motion is based on the common direction of motion of the elements, rather than their common speed, temporal frequency or phase.

This is consistent with early Gestalt laws of grouping by common fate (Wertheimer, 1912) and extends the concept of association fields to include common direction as well as common orientation and spatial frequency.

4.2. Snakes and ladders: effects of contour element orientation

Previous investigations of contour integration have focused on snake stimuli (the sinusoidal carriers of the path are aligned parallel to the contour), because these stimuli probe the mechanisms that identify contours that extend beyond the size of typical receptive fields. Relatively few studies have examined contour linking in ladder stimuli (the sinusoidal carriers of the path are aligned orthogonal to the contour). Our results confirm previous studies showing that observers are significantly less sensitive to ladders than snakes in static images (Field et al., 1993). In dynamic scenes, the organisation of ladder contours indicates regions of common direction. There is a small, but non-significant increase in sensitivity once the carriers of the elements defining snake contours are set in motion, and we find that observers remain significantly more sensitive to snakes than ladders in all conditions. The resistance to detection of ladder patterns, whether static or dynamic, suggests that the most effective camouflage may be achieved with orthogonal texture.

4.3. Perceived or physical location of contour elements

It has recently been shown that observers are more sensitive to drifting contours composed of elements that are *perceptually* aligned but *physically* misaligned than to drifting contours that are *physically* aligned but *perceptually* misaligned (Hayes, 2000). These results are based on the observation that a drifting sinusoidal carrier within a static Gaussian envelope produces an illusory shift in the static envelope in the direction of the carrier (Devalois & Devalois, 1991). The results in Fig. 6 confirm this result of Devalois and Devalois for one of the authors and are in very good agreement with their data showing that the bias increases with temporal frequency (their Fig. 3). These results mean that the *perceived* locations of the contour elements will be offset from the backbone of the contour by differing (albeit small) amounts. In static contours, this spatial variation is known to reduce sensitivity to contours e.g. (Field et al., 1993). Here we find that not only is contour sensitivity unaffected by large differences in the speed of the individual elements forming the contour, but this is in spite of the spatial jitter in the *perceived* locations of the contour elements introduced by speed-based illusory shifts. This result is difficult to reconcile with Hayes' (2000), finding that that observers were

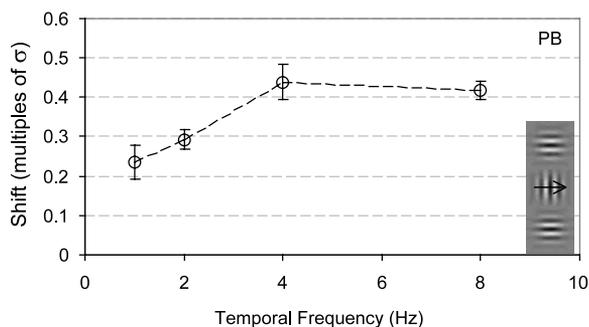


Fig. 6. Shift in the perceived location of a static Gaussian envelope containing a drifting sinusoidal grating carrier, as a function of drift rate (after Devalois & Devalois, 1991). A QUEST Yes/No staircase procedure determined the point of subjective alignment of a centrally fixated, vertical drifting Gabor element with two flanking, static horizontal Gabor elements, illustrated by the inset. These orientations forced observers to align the Gaussian envelopes, without influence of the phase of the grating carriers. Data show the 50% point of a cumulative normal function fitted by least χ^2 to the combined data of four runs of 32 trials, error bars show $\pm 95\%$ confidence intervals.

more sensitive to drifting contours composed of *perceptually* aligned than *physically* aligned elements.

4.4. Related studies of grouping processing in temporally modulated stimuli

Previous investigations of global integration of local motion cues have typically employed patterns with few elements, with few motion directions and with no distractors present—e.g. barber-pole (Wallach, 1935), lines (Shimojo et al., 1989; Castet et al., 1993), masked diamond stimuli (Lorenceanu & Shiffrar, 1992), plaid patterns (Adelson & Movshon, 1982), optic flow stimuli, (Gurney & Wright, 1996; Bex et al., 1998, 1999), samples of single or multiple objects (Verghese & Stone, 1995, 1996), and plaid barber-poles (Castet & Zanker, 1999) for review see Lorenceanu and Shiffrar (1999). These studies have identified global interactions among local motion detectors. The global interactions find plausible real-world solutions from ambiguous or competitive local motion signals based on pooling the local velocity signals across the pattern, including those signals at the edges of the aperture.

The present study examines the integration of motion signals in stimuli with multiple distracter elements that allow many more false correspondences among neighbouring elements. The results show that observers are able to extract moving paths from chaotic moving stimuli in a manner similar to that reported in previous investigations with equivalent static stimuli. The results are consistent with models of path detection that are based on long-range interactions among local detectors (Field et al., 1993). The increase in sensitivity to moving paths suggests that directional cues facilitate the interactions among local detectors.

Acknowledgements

AJS was supported by a fellowship from the MRC. SCD was supported by a fellowship from the Wellcome Trust.

References

- Adelson, E. H., & Movshon, J. A. (1982). Phenomenal coherence of moving visual patterns. *Nature*, *300*, 523–525.
- Alais, D., Blake, R., & Lee, S. H. (1998). Visual features that vary together over time group together over space. *Nature Neuroscience*, *1*, 160–164.
- Anderson, S. J., & Burr, D. C. (1987). Receptive field size of human motion detection units. *Vision Research*, *27*, 621–635.
- Bex, P. J., Metha, A. B., & Makous, W. (1998). Psychophysical evidence for a functional hierarchy of motion processing mechanisms. *Journal of the Optical Society of America, A* *15*, 769–776.
- Bex, P. J., Metha, A. B., & Makous, W. (1999). Enhanced motion aftereffect for complex motions. *Vision Research*, *39*, 2229–2238.
- Castet, E., Lorenceanu, J., Shiffrar, M., & Bonnet, C. (1993). Perceived speed of moving lines depends on orientation, length, speed and luminance. *Vision Research*, *33*, 1921–1936.
- Castet, E., & Zanker, J. (1999). Long-range interactions in the spatial integration of motion signals. *Spatial Vision*, *12*, 287–307.
- Dakin, S. C., & Hess, R. F. (1998). Spatial-frequency tuning of visual contour integration. *Journal of the Optical Society of America, A* *15*, 1486–1499.
- Dakin, S. C., & Hess, R. F. (1999). Contour integration and scale combination processes in visual edge detection. *Spatial Vision*, *12*, 309–327.
- Devalois, R. L., & Devalois, K. K. (1991). Vernier acuity with stationary moving gabors. *Vision Research*, *31*, 1619–1626.
- Field, D. J., Hayes, A., & Hess, R. F. (1993). Contour integration by the human visual system: evidence for a local ‘association field’. *Vision Research*, *33*, 173–193.
- Gurney, K., & Wright, M. J. (1996). Rotation and radial motion thresholds support a two-stage model of differential-motion analysis. *Perception*, *25*, 5–26.
- Hayes, A. (2000). Apparent position governs contour-element binding by the visual system. *Proceedings of the Royal Society of London Series B-Biological Sciences*, *267*, 1341–1345.
- Henry, G. H., Bishop, P. O., & Dreher, B. (1974). Orientation axis and direction as stimulus parameters for striate cells. *Vision Research*, *14*, 767–777.
- Hess, R. F., & Dakin, S. C. (1997). Absence of contour linking in peripheral vision. *Nature*, *390*, 602–604.
- Hess, R. F., & Dakin, S. C. (1999). Contour integration in the peripheral field. *Vision Research*, *39*, 947–959.
- Hess, R. F., & Field, D. J. (1995). Contour integration across depth. *Vision Research*, *35*, 1699–1711.
- Hess, R. F., Hayes, A., & Kingdom, F. A. A. (1997). Integrating contours within and through depth. *Vision Research*, *37*, 691–696.
- Hubel, D. H., & Wiesel, T. N. (1968). Receptive fields and functional architecture of monkey striate cortex. *Journal of Physiology*, *195*, 215–243.
- Keeble, D. R. T., & Hess, R. F. (1999). Discriminating local continuity in curved figures. *Vision Research*, *39*, 3287–3299.
- Kovacs, I., & Julesz, B. (1993). A closed curve is much more than an incomplete one: effect of closure in figure-ground segmentation. *Proceedings of the National Academy of Science*, *90*, 7495–7497.
- Lee, S. H., & Blake, R. (1999). Visual form created solely from temporal structure. *Science*, *284*, 1165–1168.

- Lorenceau, J., & Shiffrar, M. (1992). The influence of terminators on motion integration across space. *Vision Research*, *32*, 263–273.
- Lorenceau, J., & Shiffrar, M. (1999). The linkage of visual motion signals. *Visual Cognition*, *6*, 431–460.
- Mullen, K., Beaudot, W. H. A., & McIlhagga, W. H. (2000). Contour integration in color vision: a common process for the blue-yellow, red-green and luminance mechanisms? *Vision Research*, *40*, 639–655.
- Pelli, D. G. (1997). The Video Toolbox software for visual psychophysics: transforming numbers into movies. *Spatial Vision*, *10*, 437–442.
- Pelli, D. G., & Zhang, L. (1991). Accurate control of contrast on microcomputer displays. *Vision Research*, *31*, 1337–1350.
- Pettet, M. W. (1999). Shape and contour detection. *Vision Research*, *39*, 551–557.
- Roelfsema, P. R., Scholte, H. S., & Spekreijse, H. (1999). Temporal constraints on the grouping of contour segments into spatially extended objects. *Vision Research*, *39*, 1509–1529.
- Schiller, P. H., Finlay, B. L., & Volman, S. F. (1976). Quantitative studies of single-cell properties in monkey striate cortex I. Spatiotemporal organization of receptive fields. *Journal of Neurophysiology*, *39*, 1288–1399.
- Shimojo, S., Silverman, G. H., & Nakayama, K. (1989). Occlusion and the solution to the aperture problem for motion. *Vision Research*, *29*, 619–626.
- Usher, M., & Donnelly, N. (1998). Visual synchrony affects binding and segmentation in perception. *Nature*, *394*, 179–182.
- Verghese, P., & Stone, L. S. (1995). Combining speed information across space. *Vision Research*, *35*, 2811–2823.
- Verghese, P., & Stone, L. S. (1996). Perceived visual speed constrained by image segmentation. *Nature*, *381*, 161–163.
- Wallach, H. (1935). Über visuell Wahrgenommene Bewegungsrichtung. *Psychologische Forschung*, *20*, 325–380.
- Watson, A. B., & Pelli, D. G. (1983). QUEST: A Bayesian adaptive psychometric method. *Perception and Psychophysics*, *33*, 113–120.
- Wertheimer, M. (1912). Experimentelle studien über das sehen von bewegung. *Zeitschrift für Psychologie*, *61*, 161–265.
- Wurtz, R. H. (1969). Visual receptive fields of striate cortex neurons in awake monkeys. *Journal of Neurophysiology*, *32*, 727–742.