Impoverished second-order input to global linking in human vision

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Abstract

Recent evidence points to the importance of global operations across spatial regions larger than individual cortical receptive fields. Studies of contour integration and motion trajectory detection suggest that network operations between local detectors underlie the encoding of extended contours in space and extended trajectories in motion. Here we ask whether such network operations also occur between second-order-detectors known to exist in visual cortex. We compared performance for stimuli composed of either first-order or second-order elements equated for visibility, and we show that unlike the first-order case, there is little or no linking interaction between local second-order detectors. Near chance performance was found for elements defined by second-order attributes when observers had to identify either an elongated spatial contour or an extended motion trajectory embedded in noise elements. This implies that the network operations thought to underlie these two global tasks receive, at best, an impoverished input from local detectors that encode second-order image attributes. © 2000 Published by Elsevier Science Ltd. All rights reserved.

Keywords: Second-order; First-order; Integration; Global linking

1. General introduction

The more we learn about the intricacies of cortical circuitry, the more our initial notions of cortical processing in terms of the local receptive field properties of single cells are being questioned. There is now ample evidence, even in V1, of not only feedforward but also lateral (Gilbert & Wiesel, 1979; Lamme, 1995; Zipser, Lamme, & Schiller, 1996) and feedback (Hupe et al., 1998) influences on the behaviour of cortical cells. The picture that is emerging highlights the importance of the rich cortical network whose dynamics may accomplish quite complex global tasks specifically involving the integration of information across large spatial regions (e.g. Field, Hayes, & Hess, 1993).

It was with this in mind that Field et al. (1993) coined the term 'association field' to distinguish the network properties from the local properties of the classical receptive field. Contour integration is a good example of the importance of linking the responses of cells tuned to different orientations in different spatial positions. This is a global process and its anatomical substrate is thought to lie in the long lateral connections between cells with similar orientation preference in the striate cortex (Gilbert & Wiesel, 1979; Rockland & Lund, 1982; Malach, Amir, Harel, & Grinvald, 1993; Bosking, Zhang, Schofield, & Fitzpatrick, 1997; Schmidt, Goebel, Lowel, & Singer, 1997). Along similar lines, recently it has been shown (Watamaniuk, McKee, & Grzywacz, 1995; Verghese, Watamaniuk, McKee, & Grzywacz, 1999) that discriminating the directional trajectory of a single element amongst many random distractor elements is also a global process which cannot be accounted for by local motion processing.

Objects in the world may be defined by variations in several image attributes including luminance (first-order characteristics) and contrast (second-order characteristics) in particular. Our ability to detect objects defined by these two attributes is well documented for spatial (Graham, Beck, & Sutter, 1992; Wilson & Wilkinson, 1996), temporal (Holliday & Anderson, 1994), motion (Badcock & Derrington, 1985; Derrington & Badcock, 1985; Chubb & Sperling, 1988) and stereoscopic (Hess & Wilcox, 1994; Wilcox & Hess, 1997) tasks. There is

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evidence that cortical cells in the mammalian cortex can process both types of information via separate low-level pathways (Zhou & Baker, 1993; Mareschal & Baker, 1998). Two previous psychophysical studies (Landy, Dosher, Sperling, & Perkins, 1991; Ziegler & Hess, 1999; Hess & Ziegler, 2000) have shown that some varieties of second-order stimuli provide poor input to tasks involving extraction of surface shape and structure. In the present study we show, using two different tasks that control for the known and marked differences in sensitivity to first-order and second-order stimulus attributes, that the second-order pathway contributes very little to global spatial interactions. We demonstrate this for both contour integration (Experiment 1) and for motion trajectory detection (Experiment 2), two very different global processes. This suggests that the network interactions within the cortex may be driven predominately by first-order (e.g. luminance-defined) information.

2. Experiment 1: global linking of contour information across space

2.1. Methods

2.1.1. Observers

Two of the authors (RFH and TL) served as observers in the experiment and each had normal or corrected-to-normal acuity. Observer TL, in particular, is an experienced observer on tasks utilising both first-order and second-order stimuli.

2.1.2. Apparatus and stimuli

Stimuli were computer generated and presented on a carefully gamma-corrected monochrome monitor with a mean luminance of ~ 18 cd m^{-2} and a refresh rate of 75 Hz. For accurate control of luminance contrast the number of intensity levels available was increased from 8 to 12 bits by combining the outputs of the three 8-bit digital-to-analog converters (DACs) using a video attenuator as described by Pelli and Zhang (1991). All stimuli were viewed binocularly at a distance of 0.58 m and presented within a square window at the centre of the display that subtended 20° both horizontally and vertically. At this viewing distance each screen pixel subtended 2 × 2 arc min. The remainder of the display area was homogenous and had a luminance of ~ 18 cd m^{-2}.

To assess our ability to integrate contours defined by either luminance (first-order) or contrast (second-order) information we used displays containing multiple micropatterns. Each micropattern was composed of a *carrier* and a *modulator*. The carrier was either a 1-D, randomly-oriented sinusoid of spatial frequency 7.4 c deg^{-1} or 2-D, binary noise composed of square checks

subtending 2 arc min of Michelson contrast 0.3. The modulator was a 1-D sinusoid with a spatial frequency of 1.8 c deg^{-1}. The orientation of the modulator always defined the contour to be detected. Each micropattern was presented within a smooth, 2-D, Gaussian spatial window (standard deviation 0.27°, truncated at $\pm 0.88°$). In the case of first-order micropatterns, the modulator and carrier were *added* so that the orientation was defined by *luminance modulation* (LM). In the case of second-order micropatterns, the modulator and carrier were *multiplied*, rather than added, so that the orientation was defined by *contrast modulation* (CM). The stimuli are shown in Fig. 1.

To ensure that the luminance-defined and contrast-defined micropatterns were of comparable visibility for the task we first measured orientation-discrimination thresholds for single micropatterns as a function of stimulus modulation depth using a standard two interval, 2 AFC procedure with the method of constant stimuli[1]. Since the contour integration task relies solely on orientation linking (Field et al., 1993) we sought to ensure that any loss of performance for contrast-defined micropatterns was due to their global linking rather than their local orientation resolution. Fig. 2 shows results for two observers for two different types of (i) contrast-defined stimuli at maximum modulation (open symbols), and (ii) luminance-defined stimuli as a function of contrast (filled symbols). For both contrast-defined and luminance-defined stimuli the carrier was either broadband noise (square symbols) or a 1-D sinusoid of random orientation (circular symbols). By comparing the contrast-defined results t the luminance-defined results we can derive the luminance contrast that produces similar levels of orientation-discrimination performance to that obtained with contrast-defined stimuli at maximum modulation. For the 2-D noise stimulus, similar performance is achieved for contrast-modulated micropatterns at unity modulation depth and luminance-defined micropatterns at a contrast of 0.2 and 0.175 for RFH and TL, respectively. For the 1-D carrier stimulus, similar performance is achieved for contrast-modulated mi-

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[1] Observers judged in which of two temporal intervals (each contained a single micropattern of 500 ms duration) the more clockwise-oriented stimulus occurred. The starting orientation of the micropattern (standard) in either the first or second interval was chosen randomly from a 180° range and that of the micropattern in the other interval (comparison) differed from the standard by either 0, ± 5, ± 10 or $\pm 15°$. Observers completed at least four runs of 70 trials (10 for each of the seven orientation differences examined) for a range of modulation depths. The resulting data were plotted as the percentage of trials on which the comparison stimulus was judged to be rotated clockwise relative to the standard, as a function of the angular difference between the two stimuli. Discrimination thresholds for each run were calculated as half the angular difference in orientation between the 75 and 25% response levels on the fitted Weibull (1951) function.
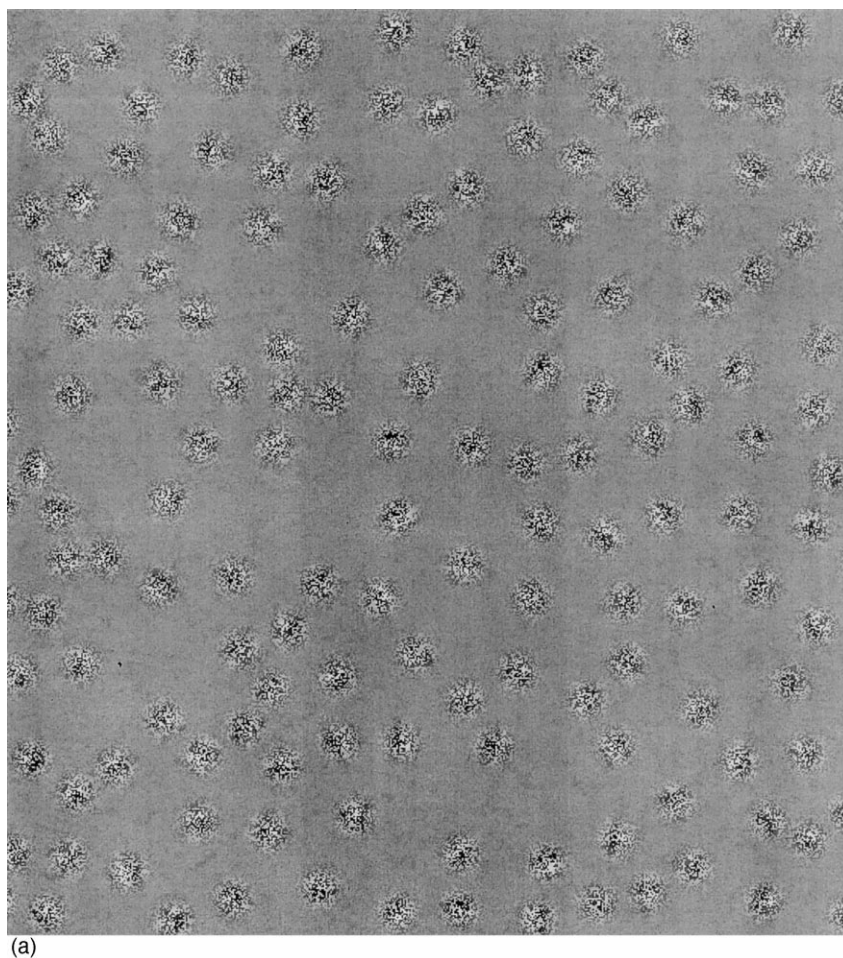
(a)

Fig. 1. First-order and second-order stimuli used in the contour integration task. The first-order stimuli consisted of a 1-D sinusoid (1.8 c deg^{-1}) added to either (a) a 2-D noise carrier (noise size 2 arc min) or (b) a higher frequency sinusoid (7.4 c deg^{-1}) of 0.3 contrast (shown in a and b, respectively). The orientation of the 1-D carrier was randomised. The second-order stimuli (shown in c and d) were composed of the same components except they were multiplied, rather than added, together. Each resulting micropattern was presented within a smooth, 2-D, Gaussian spatial window (standard deviation 0.27°, truncated at ± 0.88°). Each of the panels (a–d) contains a straight contour in which the orientations (defined by either first-order or second-order image characteristics) of a subset of the elements (eight) are aligned along an elongated path and the remainder have random positions and orientations.

cropatterns at unity modulation depth and luminance-defined micropatterns at a contrast of 0.175 and 0.0875 for RFH and TL, respectively. Since these luminance contrasts resulted in similar levels of orientation discrimination to those obtained with the contrast-defined stimuli at maximum modulation, we used these to assess sensitivity for the more global aspects of contour integration. In addition luminance-defined micropatterns set to (approximately) half of each of these contrast values were also employed, in order to confirm that any differences in contour integration performance found with luminance-defined and contrast-defined stimuli are not due to a gross mismatch in their effective visibility.

2.1.3. 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, 2AFC task observers were asked to choose which interval contained the elongated contour (path) (see Fig. 1). One interval chosen at random on each trial (duration 500 ms) contained 169 micropatterns of random position and orientation (background micropatterns) and in the other interval (path plus background) some (eight) of the background micropatterns had orientations that were aligned along an elongated contour that was constrained to pass through a central circular region of the display area of radius 1°. There were no local element density differences between the two presentations. Performance was measured for contours of varying straightness (defined by a uniform random variable ± 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 results are plotted
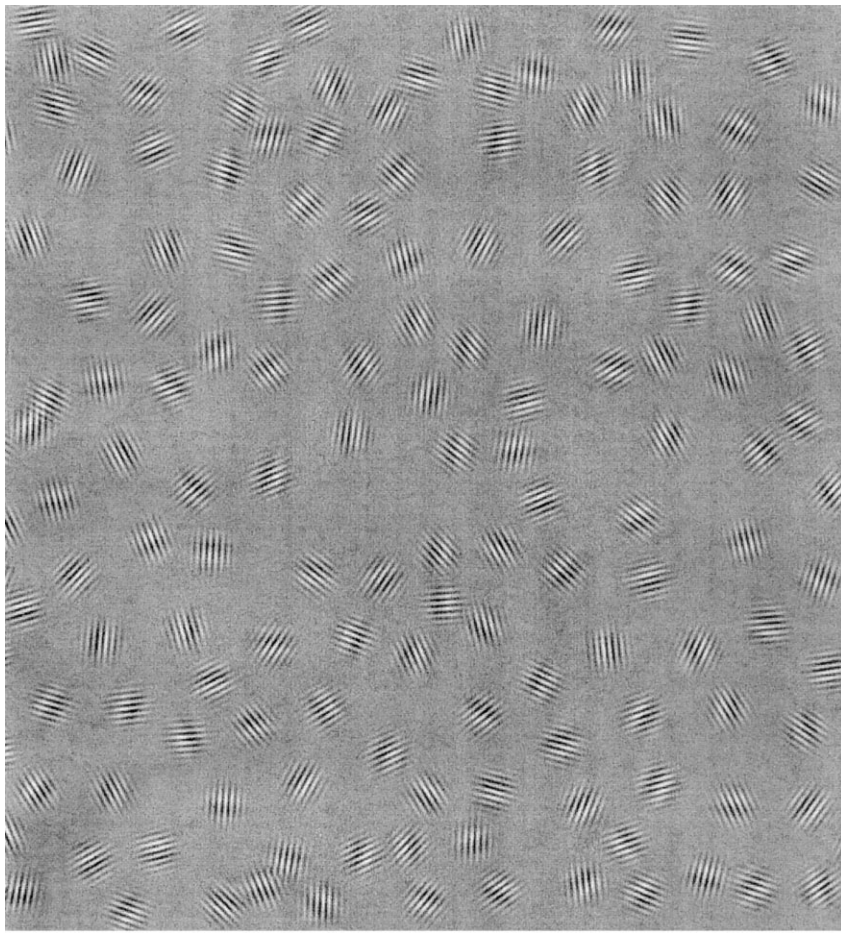
(b)

Fig. 1. (*Continued*)

as the percent correct responses for the contour integration task, as a function of the path angle, for each of the two observers.

2.2. Results and discussion

In the case where the Gabor micropatterns were defined by luminance contrast, and presented at a modulation depth producing comparable orientation discrimination to the contrast-defined stimuli, similar results (Fig. 3) were found to those previously reported by Field et al. (1993). Performance was flawless for straight paths (path angle of 0°) but declined for very curved paths (e.g. path angle of 40°). The carrier (either broadband noise or a higher frequency sinusoid of random orientation) had little disruptive influence on performance. A substantial reduction (factor of two) in the luminance contrast of the micropatterns had a moderate effect on performance, in that it was typically worse overall, but exhibited the same dependence on path angle. Indeed for straight paths performance for

both observers was still clearly very good and close to 100% correct.

When the carrier was multiplied by the component defining the contour to produce contrast-defined micropatterns (set to maximum modulation amplitude), performance was dramatically reduced for both types of second-order stimuli. Performance with straight paths was only significantly above chance for one observer (TL), even though the individual micropatterns and their local orientation were clearly visible and well defined, suggesting that the breakdown is in the global linking process itself. Importantly, additional observations (data not shown) showed that these levels of performance for TL did not deteriorate until the number of micropatterns comprising the path was decreased to two to three, a result consistent with this observer using only a small number of adjacent contour micropatterns in the main experiment rather than the eight available in the path. Interestingly performance for luminance-defined micropatterns began to deteriorate at much longer path lengths, when the number of
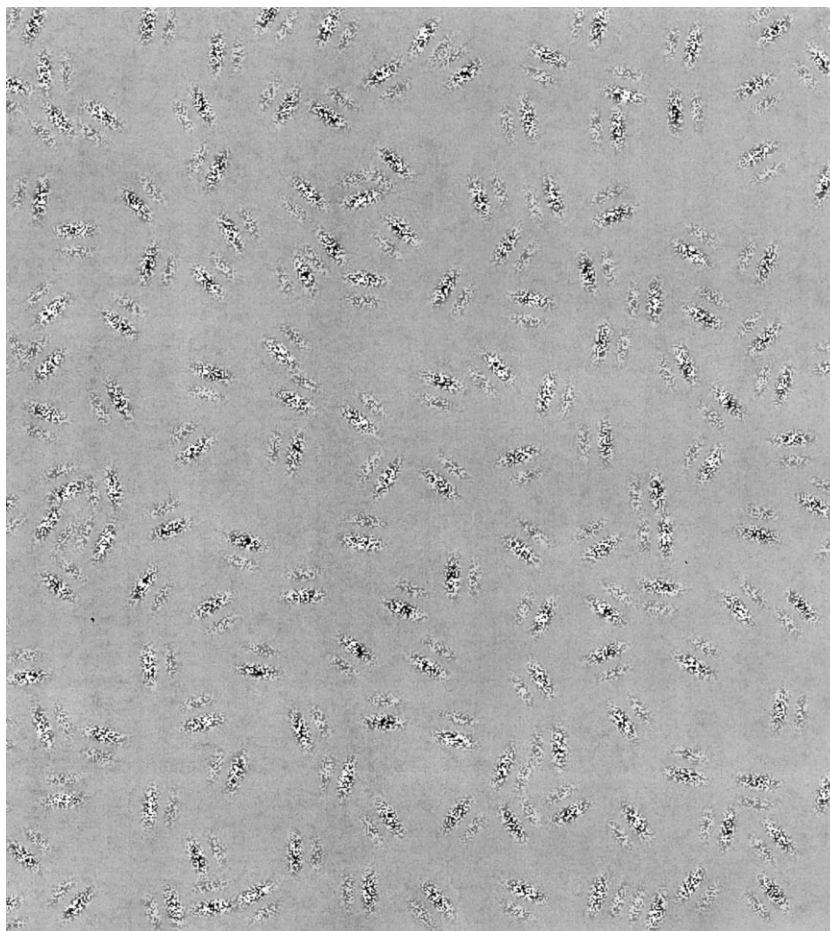
(c)

Fig. 1. (*Continued*)

adjacent micropatterns in the path was reduced to less than six. This demonstrates clearly that any contour integration for contrast-defined stimuli is at best predominantly local.

An interesting and possibly special case of contour integration occurs when the orientation of the path micropatterns are all orthogonal to the path itself. For first-order micropatterns, Field et al. (1993) demonstrated that this results in much reduced, albeit above chance, performance. It is interesting to ask whether this form of orientation linking is preserved for second-order stimuli. To answer this, we compared performance for our two first-order and our two second-order stimuli when the micropatterns defining a straight path were orthogonal to that path. Our first-order stimuli always produced above chance performance levels (61% for TL and 65% for RFH) whereas performance for the second-order stimuli was never above chance (50% for TL and 49% for RFH). It is presently not known what drives the above chance performance for first-order stimuli on this task but it could be mediated either by weak orientation linking

or some qualitatively different process. Whatever the mechanism it does not work for second order stimuli.

3. Experiment 2: global linking of direction information over space and time

We wondered whether the deficit for spatial contour integration demonstrated in Experiment 1 using contrast-defined micropatterns was an example of a more general deficiency of second-order information in global tasks. To address this issue we used a motion task similar in principle to contour integration which has also been shown to be accomplished via global/ network interactions (Verghese et al., 1993). The task involves detecting the global trajectory of a single element (circular spot), drifting in a consistent direction embedded in a field of similar elements having random local trajectories. We used conditions that have previously been shown by Verghese et al. (1993) to give optimum performance for luminance-defined stimuli.
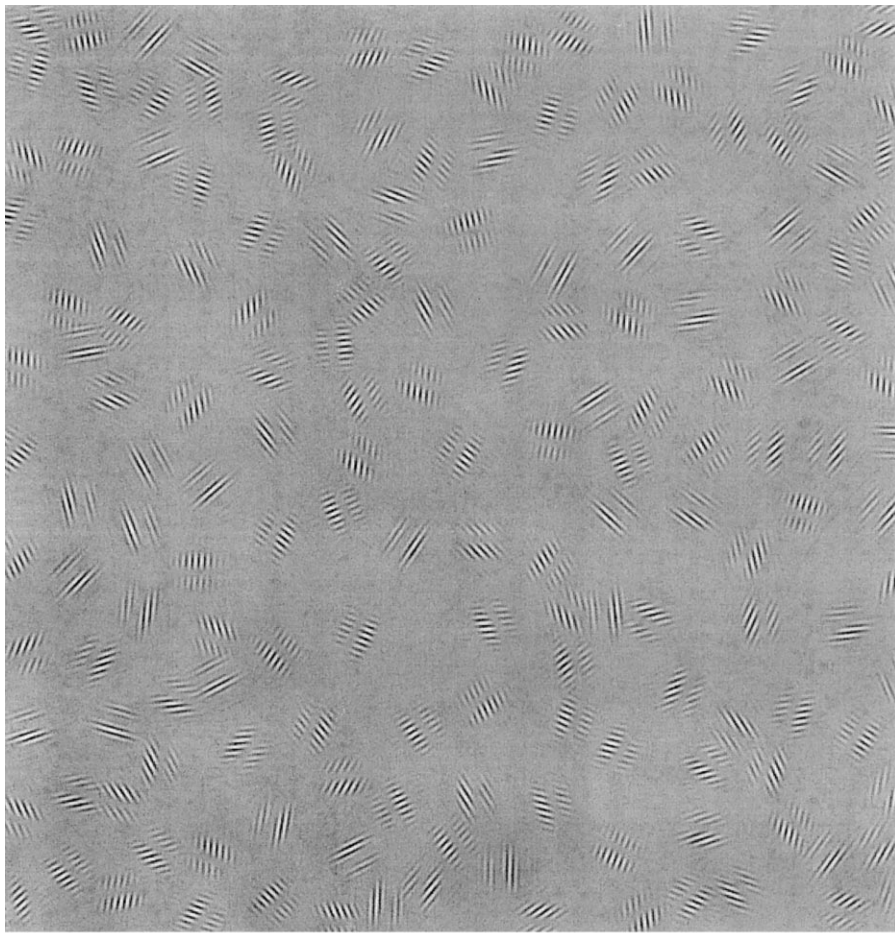
(d)

Fig. 1. (*Continued*)

3.1. Methods

3.1.1. Observers
RFH and TL were the same observers that participated in Experiment 1.

3.1.2. Apparatus and stimuli
The apparatus and stimuli were similar to those used in Experiment 1 with the following exceptions. Motion stimuli were composed of either luminance-defined or contrast-defined circular elements (see Fig. 4). The first-order elements consisted of circular regions (diameter 7 arc min) whose space-averaged luminance was less than the mean (18 cd m^{-2}) of the 2-D, static, binary noise background (carrier) to which they were added. The second-order elements consisted of circular regions whose space-averaged contrast was different to the mean contrast of the 2-D noise field with which they were multiplied.

We first measured direction discrimination for a single luminance-defined element drifting with a displacement size of 7 arc min frame^{-1} (corresponding to a drift speed of 8.75° s^{-1} at the image update rate of 75 Hz) either horizontally or vertically, as a function of its contrast (luminance difference with respect to the noise background), using a standard single interval discrimination procedure with the method of constant stimuli[2]. The luminance-defined elements were then set to be at the same multiple of threshold as that found for a contrast-defined element at unity modulation. For RFH, a contrast-modulated element with a modulation depth of 1.0 was found to be at approximately 2.85 times threshold. Performance for a luminance-defined element that is 2.85 times its threshold for this task has a modulation depth of 0.068. For TL, performance for a contrast-defined element of unity modulation depth was found to be about 4.31 times threshold. For a luminance-defined element this corresponds to a modu-

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[2] Observers indicated, using one of two response buttons, whether the axis of an isolated element's motion (displaced 7 min arc frame^{-1}) trajectory was vertical or horizontal. The duration of the motion sequence was 500 ms. Observers completed four runs of 50 trials in total and thresholds were determined by fitting Weibull (1951) functions to the data for each run and finding the modulation depth corresponding to the 75% correct performance level.

lation depth of 0.072. This ensured that in the main experiment we used contrast-defined elements and luminance-defined elements that were of comparable visibility for accomplishing the trajectory detection task.

3.1.3. Procedure

A two-interval-forced choice procedure was used and the observer's task was to identify the interval which contained an extended motion trajectory. Within one of the intervals, chosen at random on each trial, a single first-order or second-order element with an extended trajectory (i.e. a consistent direction of motion that was either horizontal, vertical or oblique and chosen at random on each trial) was presented for a duration of 500 ms centrally in the visual field (within a square area subtending $4 \times 4°$) embedded in a field of 400 background elements whose directions of motion (speed 7 arc min frame^{-1}) were chosen at random on each displacement from a range spanning 360°. In the other interval *all* elements had random local trajectories that

Fig. 3. Percent correct responses for the contour integration task for luminance-modulated (LM — first-order) and contrast-modulated (CM — second-order) stimuli of the type depicted in Fig. 1(a–d), as a function of the path angle, for two observers. The modulation depths of the LM stimuli were either equal to (filled 'black' symbols) or less than (filled 'grey' symbols) that required to produce comparable orientation-discrimination performance to the CM stimuli (open symbols) at maximum modulation (see Fig. 2) and as such all stimuli were equated, conservatively, for visibility. The vertical bars above and below each data point (where visible) are standard errors that reflect variability in performance across runs of trials.

were assigned stochastically on each displacement from a range spanning 360°. The stimulus type (either first-order or second-order) was randomised between each run of trials and observers completed at least three runs of 100 trials for each.

3.2. Results and discussion

For first-order (luminance-defined) elements, performance for both observers was high (84.66% for RFH, SEM 2.02% and 95.5% for TL, SEM 0.65%). However when the elements were defined by second-order (contrast) variations, performance dropped dramatically (57.66% for RFH, SEM 2.72% and 74.24% for TL, SEM 1.65%). Considered in isolation, it is difficult to deduce from this result whether the second-order input is simply weaker or non-existent because like the spatial contour integration task, local detectors, though not responsible for optimal performance, may still be able to support the reduced levels of performance that we found for second-order stimuli.

The possibility that above chance performance for the second-order stimuli is based on the responses of independent local motion sensors is supported by the additional finding that the detectability of a single extended 200 ms trajectory (51% for RFH, SEM 4.51% and 61.5% for TL, SEM 1.85%) is comparable to that of two, successive (temporally abutting), non-overlapping 100 ms trajectories (56% for RFH, SEM 8% and
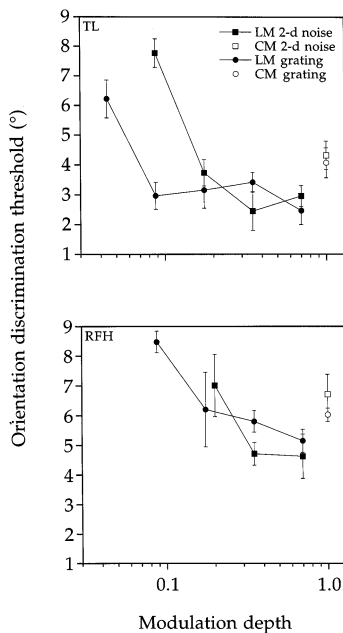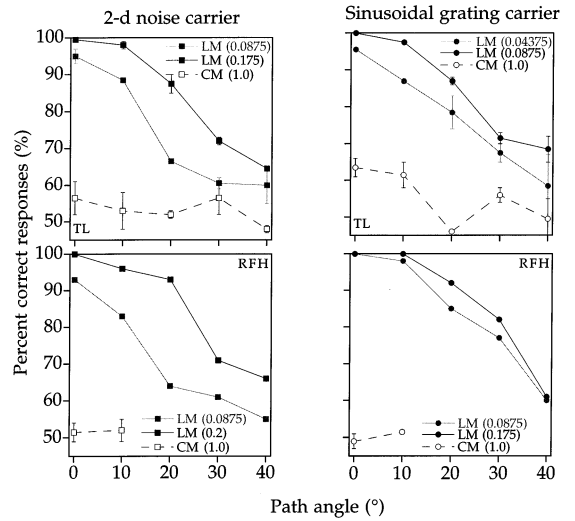

Fig. 2. Orientation-discrimination thresholds for two observers measured using two types of isolated first-order stimuli and two types of second-order stimuli as a function of the modulation depth. First-order stimuli were composed of either luminance-modulated (LM) 2-D noise (indicated by the filled squares) or a LM grating of random orientation (filled circular symbols). Second-order stimuli were composed of either contrast-modulated (CM) 2-D noise (open squares) or a CM randomly-oriented grating (open circles). The vertical bars above and below each data point (where visible) are standard errors that reflect variability in the calculated threshold across runs of trials. To ensure that the LM and CM micropatterns used in the contour integration task were of comparable visibility, the modulation depths of the LM stimuli that produced similar levels of performance to the CM patterns at maximum modulation were derived separately for each observer and used for the stimuli depicted in Fig. 1.
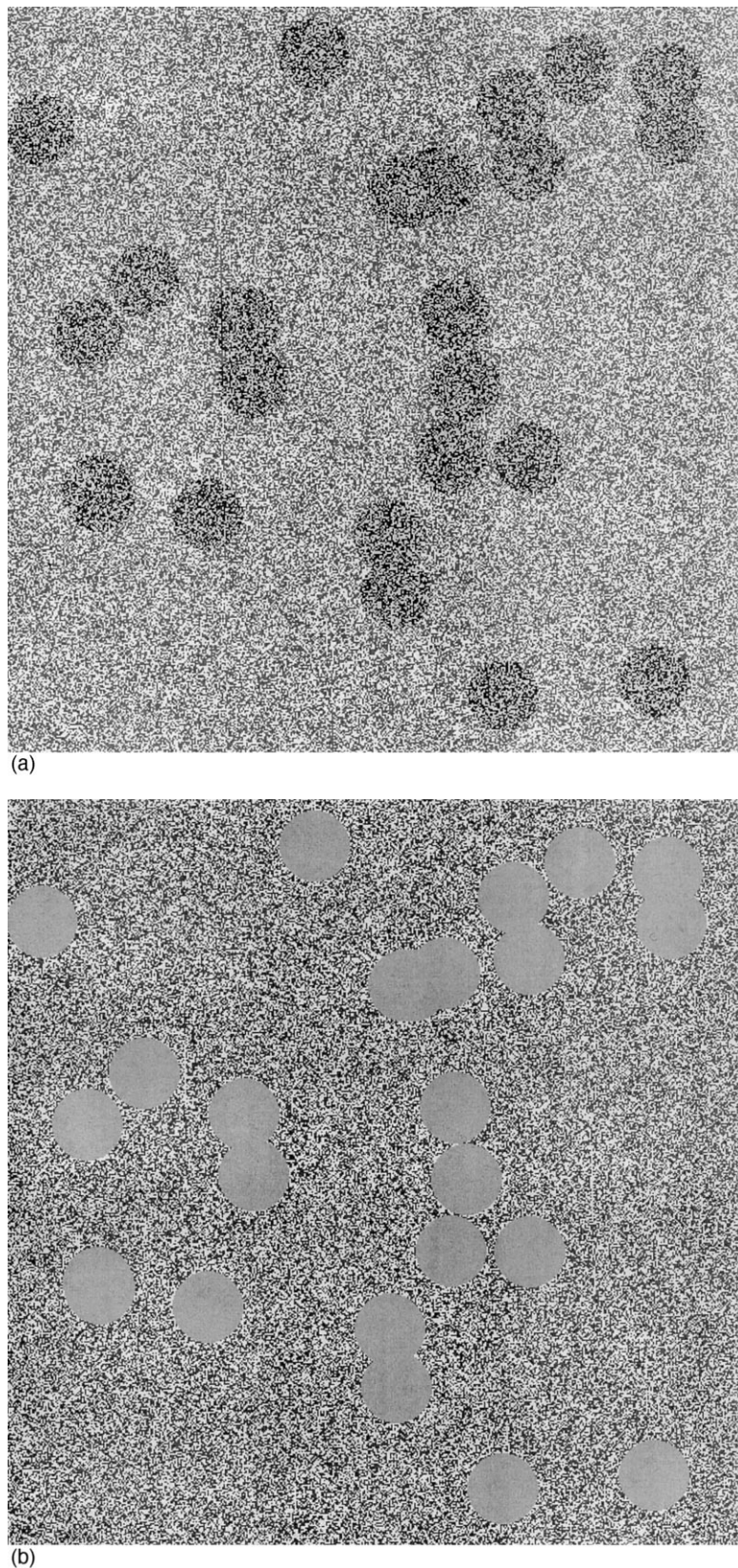
Fig. 4. Schematic diagram (a magnified section, for clarity) of the first-order and second-order stimuli used in the motion trajectory task. The first-order elements (a) consisted of circular regions (diameter 7 arc min) whose space-averaged luminance was less than the mean of the 2-D noise background (carrier) to which they were added. The second-order elements (b) consisted of circular regions whose space-averaged contrast was different to the mean contrast of the 2-D noise field with which they were multiplied. In the motion sequences a single first-order or second-order element underwent an extended trajectory (had a constant velocity) and each of the remaining elements was displaced in a random direction spanning a 360° range. The 2-D noise carrier was stationary.

54.75% for TL, SEM 1.32%). The marginal improvement in performance for the single 200 ms trajectory found for observer TL is entirely consistent with simple probability summation between the outputs of local motion detectors (Verghese et al., 1993). However, for first-order motion stimuli a single 200 ms trajectory was much more detectable (65.5% for RFH, SEM 6.5% and 83% for TL, SEM 0.82%) than two 100 ms trajectories (50.5% for RFH, SEM 1.5% and 67.5% for TL, SEM 1.56%) occurring in the same temporal interval, a result consistent with global facilitatory interactions between local motion units tuned to similar directions of motion as previously suggested by Verghese et al. (1993).

4. General discussion

Second-order (contrast-defined) information has been shown to be an effective cue that can be used in tasks involving spatial processing (Graham et al., 1992; Wilson & Wilkinson, 1996), motion processing (Chubb & Sperling, 1988; Cavanagh & Mather, 1989) and stereoscopic processing (Hess & Wilcox, 1994; Wilcox & Hess, 1997). Single cell recording from cat and monkey have shown that a substantial number of both simple and complex cells in visual cortex are involved (Zhou & Baker, 1993, 1994, 1996) in what is thought to be a separate pathway for second-order processing. The present results suggest that the second-order input to both spatial contour integration and motion direction processing is also, at best, very weak. The reason for this is unclear at present though it is known that there is not a fixed relationship between the orientation of the first-order input and the orientation selectivity of envelope-sensitive neurones (Mareschal & Baker, 1998). This in itself may not provide a satisfactory explanation as it merely enables the neurones to exhibit some degree of form cue-invariance (Albright, 1992). The answer may lie in the relationship between first-order and second-order statistics of natural images, a topic yet to be addressed. We do not feel that these results can be explained by a differential fall-off of sensitivity of second-order detectors, relative to first-order detectors, as a function of eccentricity. First, there is evidence at least for moving patterns that sensitivity to spatial structure declines at the same rate with eccentricity for both first-order and second-order motion stimuli (Smith, Hess, & Baker, 1994; Smith & Ledgeway, 1998). Second, in the present study fixation was not controlled and subjects were permitted to make eye movements during the stimulus presentation.

There is also evidence that second-order information cannot be used reliably to extract surfaces whether defined by relative motion (Landy et al., 1991; Hess & Ziegler, 2000) or disparity (Ziegler & Hess, 1999). Optic flow and visual search, two tasks which may involve global processes, have also been shown to be deficient for second-order stimuli (Allen & Derrington, 1999; Seiffert & Cavanagh, 1999). Since all of these disparate tasks are believed to involve global spatial processes one is left to conclude that the second-order input to such processes may be impoverished. While the exact nature of these global linking processes is not well understood, it is thought to involve a network of lateral interactions within visual cortical areas as well as feedback signals from higher visual areas (Hupe et al., 1998). Our results suggest that such intra-cortical interactions only occur in the processing of first-order information.

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