Psychophysical differences in processing of global motion and form detection and position discrimination

Benjamin M. Harvey　　Visual Development Unit, Department of Experimental Psychology, Oxford University, Oxford, UK

Oliver J. Braddick　　Visual Development Unit, Department of Experimental Psychology, Oxford University, Oxford, UK

In models of complex motion processing of expanding, contracting or rotating patterns, localization of the center of motion is regarded as an implicit function of the system, used for heading determination and achieved by coarse population encoding. The situation modeled contains an optic flow pattern that is modified by including translational motion, as occurs when the observer is not looking directly at their heading, and relies on global processing of the entire optic flow field. Our psychophysics experiments show that accurately localizing the center of a symmetrical complex motion pattern, or an analogous complex radial or concentric form pattern, relies on local processing near the center of the pattern. This contrasts with detection of the same patterns, which involves considerable spatial summation, relies on global processing, and is very tolerant of noisy stimuli. Coarse localization uses both central and peripheral information, involving some spatial summation. Some differences are seen between different pattern types. The low level of spatial summation seen in position discrimination is surprising if position discrimination is seen as an implicit function of the global processing system, and suggests modifications may be needed to models of heading determination.

Introduction

Determination of an animal's heading is an important function of the extrastriate cortex and is vital for useful interpretation of the world around them. Models of heading determination have suggested that analysis of the optic flow field caused by an animal's motion can be used to derive heading using coarse population codes, in a population of neurons each of which integrates optic flow information over an extended area (Graziano, Andersen, & Snowden, 1994; Lappe & Rauschcker, 1993; Page & Duffy, 2003; Perrone & Stone, 1998). Area MST has been widely proposed as the site for such analysis of optic flow, and microstimulation of MST has been shown to affect heading judgments (Britten & van Wezel, 1998). However, in many situations heading corresponds to the center of the expanding motion of the optic flow field, and in these situations there may be relatively local operations that can determine heading more simply and more accurately by locating this center of motion. When heading does not correspond to the center of motion (i.e. when the animal is not looking in the direction of their heading), it can only be discriminated with an accuracy of 1.5–3° (Britten & Van Wezel, 2002).

In the present study we examine observers' ability to locate the center of an optic flow pattern, compared to their sensitivity for detecting the presence of a globally coherent flow pattern. The centers of motion of rotating, expanding and contracting motions are perceptually very obvious, and our data show that their locations can be discriminated very accurately when fixated.

Neurons in macaque MSTd respond to rotating, expanding and contracting patterns of motion (Graziano et al., 1994), have very large receptive fields (Duffy & Wurtz, 1991a) reflecting considerable spatial summation, and many give position-invariant responses to optic flow stimuli (Duffy & Wurtz, 1991b; Graziano et al., 1994). Human psychophysics of global motion processing shows considerable spatial summation for radial and rotational patterns (Burr, Morrone, & Vaina, 1998), and fMRI has shown these patterns to activate the human MT complex (MT+) (Morrone et al., 2000), so it is likely that human MT+ performs a similar role to macaque MSTd. Indeed, there is fMRI evidence for an optic flow-specific region of human MT+, perhaps a human homologue of MST (Huk, Dougherty, & Heeger, 2002; Morrone et al., 2000; Smith, Wall, Williams, & Singh, 2006).

The detection of globally coherent patterns, and the localization of their centers, also arises for static equivalents of optic flow. Sensitivity to global form patterns has been found in macaque V4, whose neurons respond preferentially to radial and concentric gratings (Gallant, Braun, & Van Essen, 1993; Gallant, Connor, Rakshit, Lewis, & Van Essen, 1996), show significant position invariance (Gallant et al., 1996), and have large receptive

fields (Desimone & Schein, 1987). Human psychophysics of global form processing also shows large-scale spatial summation of concentric (Wilson, Wilkinson, & Asaad, 1997) and radial (Wilson & Wilkinson, 1998) patterns, while fMRI shows these patterns to activate an area of human cortex which may be homologous with V4 (Wilkinson et al., 2000).

In this study we investigate a series of tasks involving the localization (position discrimination) of the centers of radial and circular motion and form patterns within the visual field, and compare these to tasks involving detection of the same patterns. The use of coherence thresholds as a common metric in both tasks allows a direct comparison of the variables affecting performance. The results show that many of the properties associated with detection tasks, particularly summation over an extensive area of the visual field, are not seen for fine position discrimination tasks. Rather, fine position discrimination appears to require very local processing.

Methods

Observers

Four observers participated overall, with three in each experiment. All had normal vision. BH, JS and AW participated in Experiments 1 and 2. In Experiment 3, AW was unavailable and CB acted as the third observer. BH is an author of this study, whereas JS, AW and CB are paid volunteers who were naïve to the purpose of the experiment.

Further subjects were not used as results from the three subjects used were qualitatively very similar for almost all experiments. The main exception to this was for coarse position discrimination in Experiments 2 and 3, where no consistent pattern of results was seen across the subjects tested. It is unlikely that testing further subjects would have revealed any consistent pattern.

Small differences between subjects were also seen for fine position discrimination in Experiment 2, where replacing the center of the pattern with noise affected performance statistically significantly for JS only. However, this effect was small, and has little bearing on our findings.

Apparatus and stimuli

Although each experiment had different stimuli, all consisted of random dot kinematograms (RDKs) presented on a Sony GDM-FW900 monitor in a 13.33° by 10.16° (17.97° diagonal) rectangular region. Dynamic sequences were generated on-line at 60 Hz and at 1600 × 1200 resolution using custom software written in Lua (Ierusalimschy, 2003). Each stimulus consisted of 3000

circular white dots (4.4 min of visual angle diameter) on a black background. Stimuli were viewed binocularly at a distance of 150 cm. Observers sat in a quiet, dimly lit room.

All dots moved at the same speed of 1.9°/s, irrespective of distance from the center of motion. No radial speed gradients were used and so the motions did not simulate the motion of a rigid object. However, this allowed dot density and speed to remain constant across the stimulus. An increase in density or decrease in speed at the center of motion (as occurs in rigid objects) could have been used as an additional cue for position discrimination tasks; we wished to focus our investigation on the processing of patterns of directional information. Also, as speed drops to zero in the center of a rigid flow field, no motion information would have been available here to perform position discrimination.

This relatively low dot speed was chosen for a number of reasons. If dots moved at 15°/s, a fairly optimal speed for producing responses from MT neurons in owl monkeys (Felleman & Kaas, 1984) and macaques (Mikami, Newsome, & Wurtz, 1986), the distance between two dot positions on consecutive frames is 0.25° at 60 Hz. As the dots were 4.4 min of visual angle (0.073°) in diameter, this leaves a large space between consecutive dot positions. First, this motion does not appear smooth. Furthermore, in a display with as many dots as ours (required to provide accurate position information even at low coherence levels) such a space makes correspondence relationships between moving dots difficult. Also, we wanted to produce form stimuli analogous with our motion stimuli, with the same size of dots and lines of the same length as the motions made by the dots in the motion stimuli. If a high speed was used, the lines would have had gaps between consecutive dot positions. And with such a gap between dot positions even in the center, rotating patterns would have consecutive dots near the center crossing the center of motion, difficult for correspondence, and useless for accurate localization of the center.

Despite these considerations, we wanted to show the main finding regarding spatial summation in position discrimination of motion patterns held even at high speeds. Thus, pattern detection and fine position discrimination tasks were repeated by BH with a dot speed of 15°/s.

Dots had a lifetime of five frames (0.083 s). To minimize coherent stimulus flicker, dots were replaced asynchronously by randomly distributing initial dot lifetimes among the first five frames.

In radial motion stimuli, if the starting location of dots had been randomly distributed, there would have been a net movement of randomly placed dots toward or away from the center of motion which would respectively increase or decrease density there. Therefore, in radial stimuli, the random location was assigned to the third (middle) frame of a dot's lifetime.

Incoherently moving dots followed the same motion pattern as coherently moving dots, but around a randomly

placed center of motion, so that for rotating patterns, discriminations could not be made based on the local curvature of single dot paths. If the movement of a signal dot caused it to exceed the boundaries of the display, reach the center of motion, or at the end of the dot's lifetime, it was replaced at a new, random position with a full, five-frame lifetime.

After every sixth test trial, a 100% coherent stimulus was shown to help maintain the subjects' attention. The results from these trials were not analyzed.

The difficulty of pattern detection or position discrimination was quantified as the minimum proportion of coherently moving dots that allowed correct discrimination on 75% of trials (coherence threshold). This was determined by an adaptive staircase method (Kontsevich & Tyler, 1999) over 30 trials. Each block of 30 trials contained only one stimulus presentation condition and blocks for the conditions under comparison were displayed in a random order until all had been displayed once in a set. Seven such sets of blocks were repeated to give a mean and standard deviation of the coherence threshold for each block condition. These were used to make comparisons between conditions using 2-tailed Student's *t*-tests.

We used a relatively small display area, compared to many optic flow experiments, as in our results only the central few degrees of the visual field seem to be useful for position discrimination. Burr et al. (1998) show spatial summation for optic flow direction discrimination goes up to 70° of visual angle. We also used a relatively low dot velocity. These parameters were chosen to make fine position discrimination relatively easy for subjects. Future work may be needed to generalize our results for a wider range of parameters.

Experiment 1: Position discrimination of the center of motion at various distances

This experiment examined subjects' performance at discriminating the position of the center of motion of expanding, contracting and clockwise rotating patterns. The coherence thresholds for position discrimination were measured with the possible positions of the center of motion at a range of distances to the left or right of the center of the screen. For comparison, subjects also had to detect the presence of the pattern in a 2IFC task.

Methods

For each type of motion pattern (expansion, contraction, or clockwise rotation) six or seven different distances between possible center of motion positions

were examined. Due to the large number of conditions, each session could not contain a randomized sequence of all these conditions. The detection task was run first, followed by blocks of trials on position discrimination with a given motion pattern, including different center of motion separations in a randomized sequence. Tests with the different patterns were performed in separate sessions.

As the most accurate possible position discrimination was likely to occur when subjects fixated the center of motion, a 3-s presentation time was used so that subjects would have plenty of time to find the center and be sure of its position. For valid comparisons of coherence thresholds, the same presentation time was used for the pattern detection tasks, and again eye movements were allowed to give subjects the best possible chance of good performance.

It is likely that subjects' eye movement strategies for the two tasks would be different. They were well practiced with each task, with feedback given during practice, so a good search strategy for each task could be found. This should make the best use of the available information necessary to perform each task, which we expected to be different. Restricting eye movement would thus be likely to affect the two tasks differently.

Motion directions were not randomized in this experiment. Expansion and contraction were presented separately and rotation was always in a clockwise direction.

Position discrimination stimuli

Each stimulus presentation started with a series of three squares with randomly flashing colors, attracting the subject's attention to the center of the otherwise blank screen. Each square measured 25 min of visual angle on each side and they were arranged vertically above each other in the center of the screen with 12.5 min of visual angle spaces between them. When ready, the subject pressed the down arrow key on a keyboard placed on their lap. An RDK then appeared with the expanding, contracting or rotating pattern centered randomly to the left or right at a distance of 4.5–114 min arc from the center of the screen. While the stimulus RDKs were being shown no fixation or reference markers were shown as these could influence perception of the RDKs themselves. The pattern filled the entire screen so that the subject could not use the outer perimeter of the coherent region as a cue. Small white lines at the top and bottom edges of the display indicated the position of the center of the screen (although subjects reported making little use of these as they were concentrating on the center of the screen). The stimulus was displayed until the subject made a choice, using the left and right arrow keys. If no choice was made within 3 s, the RDK was replaced by a blank screen with a small green square in its center; subjects reported comparing the position of the perceived center of motion with the position of this square for difficult position
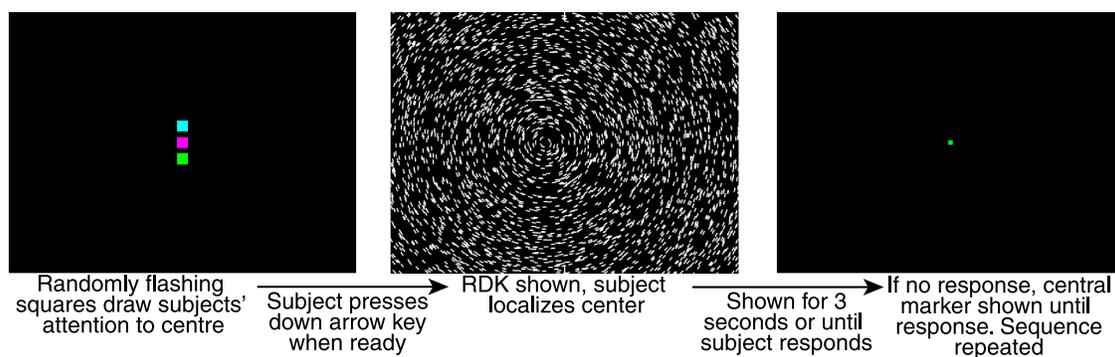
Figure 1. Order and timing of stimulus presentation events in position discrimination tasks in Experiments 1, 2, and 3.

discriminations. The flashing center spots then appeared ready for the next trial. A schematic of these events and their timing schedule is shown in Figure 1. An example is shown in Movie 1.

Pattern detection stimuli

Each stimulus block started with a blank, black screen. When ready for the first trial, the subject pressed the down arrow key on a keyboard placed on their lap. After a 1-s presentation of a central small red square, two RDKs were presented for 3 s each, separated by a 500 ms interval containing a black screen with a central yellow square. In one RDK interval the motion had 0% coherence, with the other interval containing a partially coherent motion pattern. The subject used the left and right arrow keys to choose whether they judged coherent motion to be present in the first or second interval respectively. When both RDK intervals had been presented, a green square was shown in the center of the screen until a response was given.

In all pattern detection tasks the center of coherent motion was exactly in the center of the screen. While the stimulus RDKs were being shown no fixation or reference markers were shown as these could influence perception of the RDKs themselves. A schematic of these events and their timing schedule is shown in Figure 2. An example is shown in Movie 2.

Results

Figure 3 shows individual subjects' coherence thresholds for position discrimination with different degrees of required precision, and for the detection task (isolated data points on right). Coherence thresholds for even very coarse position discrimination tasks (8.71–18.11) were statistically significantly higher than for detection (3.26–7.92) tasks, typically with ratios of 1.67 to 3.49 (Figure 3). The one exception to this is detection of expansion for AW which gave particularly poor performance, which was not statistically significantly lower than for coarse position discrimination of expansion.

Interestingly, though AW was particularly poor at detecting expansion, his position discrimination coherence thresholds for expansion were very similar to those for contraction and rotation. Indeed, there was little relation between how well a subject performed at detecting a pattern and localizing it.

Furthermore, subjects can discriminate between centers of motion positions very finely with high coherence. AW could discriminate positions less than 5 min of visual angle apart at 75% coherence.

As the separation between possible center of motion positions increases, coherence thresholds decrease sharply, appearing to approach an asymptote for separations of 60 min and above. However, when the coherence threshold for position discrimination is plotted against separation on a log–log plot (Figure 4), the data fall on a
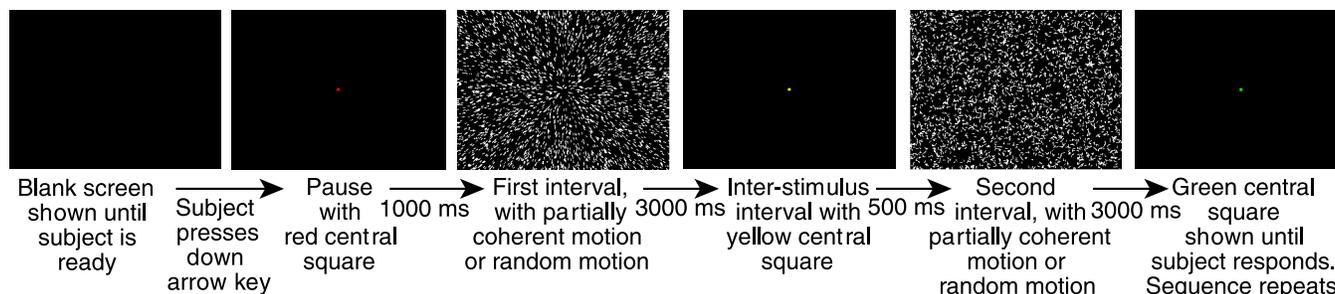

Figure 2. Order and timing of stimulus presentation events pattern detection tasks in Experiments 1, 2, and 3.
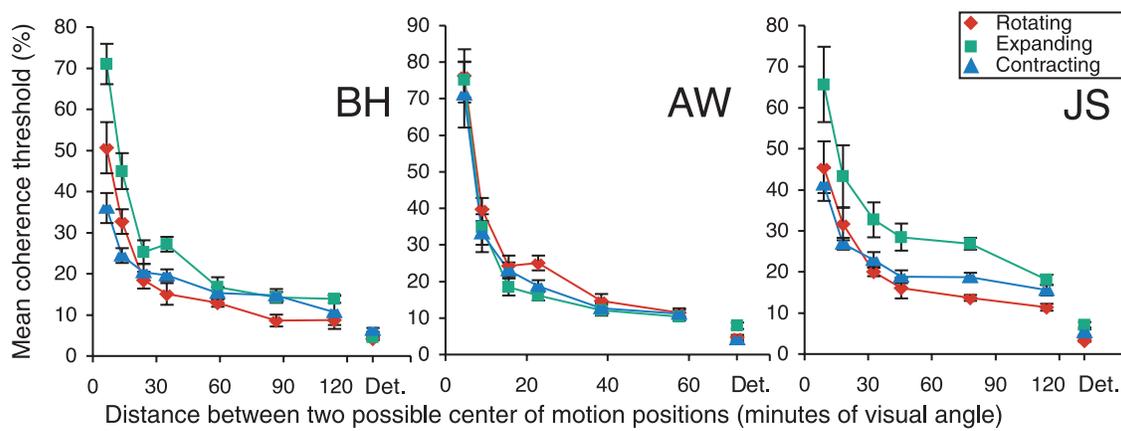
Figure 3. Mean position discrimination coherence thresholds with varying distances between the two possible center of motion positions, and detection (Det.) coherence thresholds for rotating, expanding and contracting patterns for BH, AW, and JS.

single straight line, suggesting that that both coarse and fine position discriminations lie on the same continuum of performance.

Discussion

The difference in coherence thresholds suggests that the processes involved in locating the center of an optic flow pattern are less tolerant of noisy stimuli than those detecting it. Coherence thresholds for detecting optic flow are generally presumed to reflect the noise reduction resulting from spatial integration in areas MT and MST. The lower noise tolerance for position discrimination raises the question of whether a different, possibly earlier motion processing area is implicated in this task.

Our subjects' mean coherence thresholds for detecting optic flow patterns (3.26–7.92%) are similar to those seen in macaques with rigid optic flow stimuli of the same area (about 10%) by Heuer and Britten (2004). However, our patterns were not rigid, and contained a far higher number of dots than those of Heuer and Britten.

While the data can be considered in terms of distinct mechanisms determining the coherence thresholds for coarse and fine position discrimination, the log–log plot in Figure 4 suggests a continuum of performance. Qualitatively, subjects report that the coarse discriminations are easier and can be made without accurately fixating the center of motion, suggesting some involvement of less local processing, but results from this experiment cannot provide conclusive evidence on a unitary vs. separate mechanisms. Experiments 2 and 3 were designed to investigate more directly the degree of local vs. global processing involved in the two types of task. For all subjects, 12 min arc separation between positions fell into the 'fine position discrimination' region of Figure 3, while still giving measurable thresholds, and 1.5° fell into the asymptotic region of 'coarse position discrimination'. These two values of separation were therefore used for subsequent experiments.

It is possible that the higher coherence thresholds seen for position discrimination tasks, compared to detection tasks, result from the positional uncertainty found in the position discrimination task. As subjects have to attend to
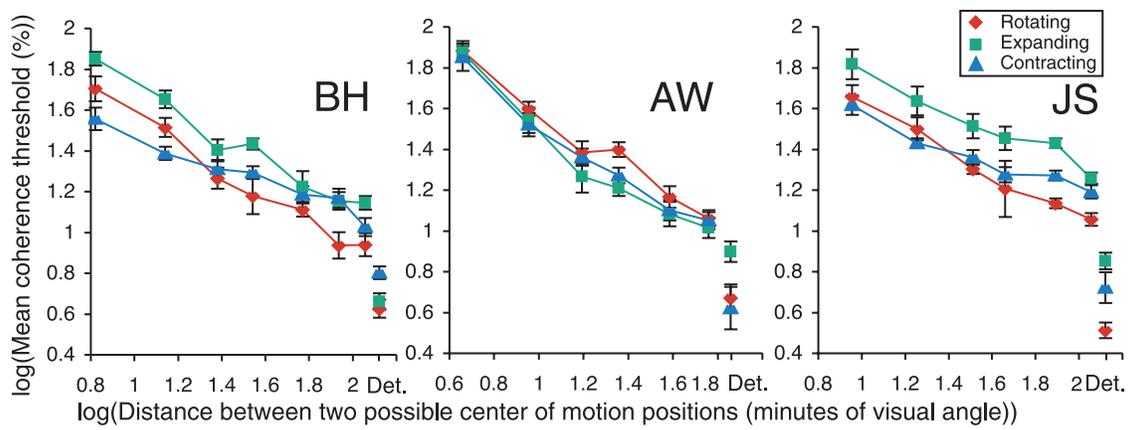

Figure 4. Log–log graph of mean position discrimination coherence thresholds with varying distances between the two possible center of motion positions, and detection (Det.) coherence thresholds for rotating, expanding and contracting patterns for BH, AW, and JS.

a larger area as the position of the stimulus is unknown, this may increase the coherence threshold. Pilot studies in out lab show that positional uncertainty raises coherence thresholds for pattern detection.

Experiment 2: Spatial summation in motion detection and position discrimination tasks

Optic flow direction discrimination tasks show considerable improvements in performance as a greater stimulus area is presented (Burr et al., 1998), a result taken to reflect the spatial summation seen in visual areas such as MSTd, which have receptive fields up to 100° (Duffy & Wurtz, 1991a). Performance in Burr et al.'s experiment was predicted by the stimulus area, but was insensitive to which parts of this area were presented. In our fine position discrimination tasks, subjects reported watching and fixating the center of motion, while ignoring peripheral regions, while for detection tasks they reported looking around the display, not using any specific point. Therefore, we compared performance with the full stimulus area and with two stimuli with certain areas replaced with dynamic noise, selectively restricting the information available to the observer. In one restricted condition, the diameter of the partially coherent region was reduced, while in the other the center of the stimulus was made incoherent, producing an annulus. We examined these three stimulus area conditions for a 2IFC detection task, a fine position discrimination task, and a coarse position discrimination task to see if the spatial summation involved in each task was different.

While stimuli were very similar to those in Experiment 1, we also wanted to eliminate a potential confound in the position discrimination task. For a given motion pattern, the position of its center of motion can be determined by examining the direction of motion between the two center locations being discriminated. For example, in an expanding pattern local dot motions in this region will be moving away from the center of motion, and contracting patterns will have dots moving toward the center (subjects did not report using this strategy). To control for this, we randomized the direction of rotating patterns between stimulus presentations. With a constant pattern, subjects could potentially make a discrimination based on whether dots in the central region moved up or down, but randomizing the direction would make this impossible. However, we did not randomize the direction of radial motions as neurophysiological studies of optic flow processing in macaque MSTd (Graziano et al., 1994; Tanaka & Saito, 1989) show greater numbers of expansion- than contraction-sensitive cells. Thus human psychophysical differences between the processing of these patterns are possible, and indeed occur in this experiment (fine position discrimination, annulus condition). No such neurophysiological differences are known between clockwise and counterclockwise rotating patterns, allowing randomization of direction.

As it was potentially possible for subjects to discriminate position based on the directions of unidirectional motion of single dots in very restricted areas for expanding and contracting patterns, a control experiment was performed with BH as the subject. Here, coherence thresholds for fine position discrimination were compared when expanding and contracting motions were tested separately and when they were tested with stimuli for each direction randomly interleaved so that the subject did not know the direction of radial motion beforehand. If subjects were basing decisions on the directions of single dots very restricted areas, we would expect coherence thresholds to be higher when they could not use this strategy, for example when the direction of radial motion was changed at random.

Methods

For each type of motion pattern (expansion, contraction, or rotation) and each task (detection, coarse discrimination, and fine discrimination), comparisons were made between the full stimulus and the reduced area or missing center, annular, condition. The order of all blocks was randomized with respect to task (detection or coarse or fine position discrimination), motion pattern (rotation, expansion and contraction) and spatial configuration (9.5°, 3° or annular window). Subjects were informed which task they were about to do and for which motion pattern, but not which spatial configuration condition would be used, though this would be obvious from the presentation of the first trial, which was shown at 100% coherence. A staircase was completed for each combination of conditions before the next randomly chosen combination. However, within each staircase the direction of rotational motion was randomized between single stimulus presentations.

Position discrimination stimuli

Stimulus parameters were very similar to those described for Experiment 1 (Figure 1, Movie 1). However, in this experiment we wanted to control the area of the partially coherent pattern, so this was restricted to circles and annuli, with incoherent noise in the rest of the display. To avoid the possibility of discrimination based on the position of these circles and annuli, they were centered on the center of the screen, rather than the center of the motion pattern.

To distinguish the fine and coarse position discriminations examined in Experiment 1, two distances between the possible center of motion positions were examined; 12 min (fine) and 1.5° (coarse) of visual angle.
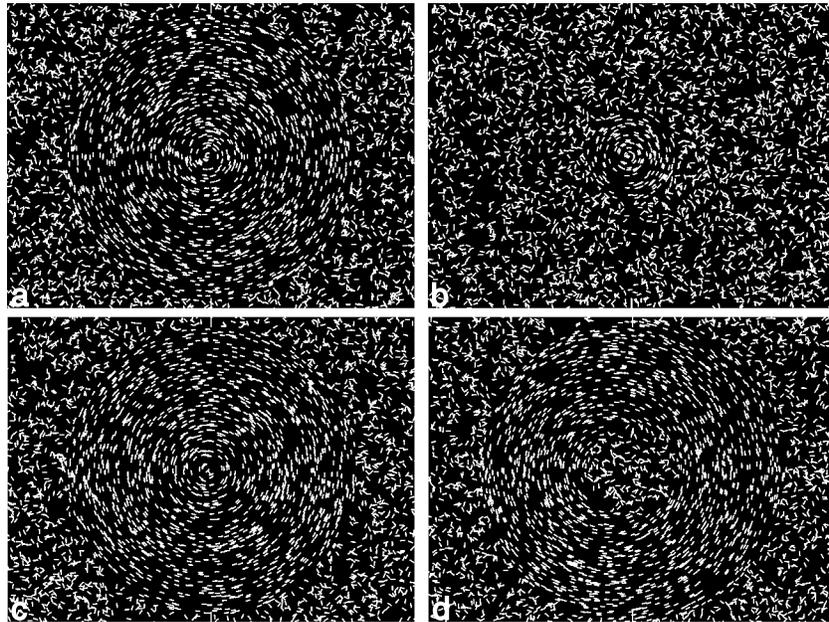
Figure 5. Restricted stimulus area conditions used in Experiments 2 and 3. Panel (a) shows the 9.5° diameter area. Panel (b) shows the 3° diameter area used in all detection and position discrimination tasks. Panel (c) shows the annulus area used in the fine position discrimination task. Panel (d) shows the annulus area used in the pattern detection and coarse position discrimination tasks.

For both distances, the full stimulus condition had a 9.5° diameter circle of partially coherent motion (Figure 5a). For the reduced area condition, this was reduced to 3° (Figure 5b). For fine discrimination, the annulus condition had a central incoherent area of 24 min of arc diameter, with the outer diameter increased to 9.08° to maintain the same stimulus area as the full stimulus condition (Figure 5c). This very small central area was chosen to minimize the difference in the stimulus while still easily covering the center of motion. For coarse discrimination, the annulus condition had a central incoherent area of 3° diameter, with the outer diameter increased to 9.96° to maintain the stimulus area (Figure 5d). As well as being the same area as the circle used in the reduced area condition (so that the two contained mutually exclusive information), this gave a diameter in the fine and coarse conditions which was the same multiple of the separation to be discriminated.

Pattern detection stimuli

Again, stimulus parameters were very similar to those described for Experiment 1 (Figure 2, Movie 2). However, this stimulus was also spatially restricted in the same ways as for the position discrimination tasks (Figures 5a, 5b, and 5d). For pattern detection, the annulus condition had the same dimensions as for the coarse position discrimination condition. The annulus with an incoherent central 3° was chosen as this region had the same area as the circle used in the reduced area condition and because this

stimulus was closely comparable with the coarse position discrimination task.

Higher speed stimuli

As our stimuli contained dots moving at relatively low speeds, we repeated the fine (12 min) position discrimination and pattern detection tasks for one subject (BH) using dot speeds of 15°/s, considerably faster than the 1.9°/s used in the rest of our experiments.

Randomly mixed directions of radial motion

As it was theoretically possible for subjects to discriminate the position of the centers of pattern motion by looking at the direction of unidirectional dot motion in a small area, we repeated the fine position discrimination task, comparing coherence thresholds when the direction of radial motion was constant throughout the test to thresholds when trials for expanding and contracting patterns were randomly interleaved during the test. When trials were randomly interleaved, the test contained 60 trials, rather than 30, so that both expansion and contraction tests could be run to their full length.

Results

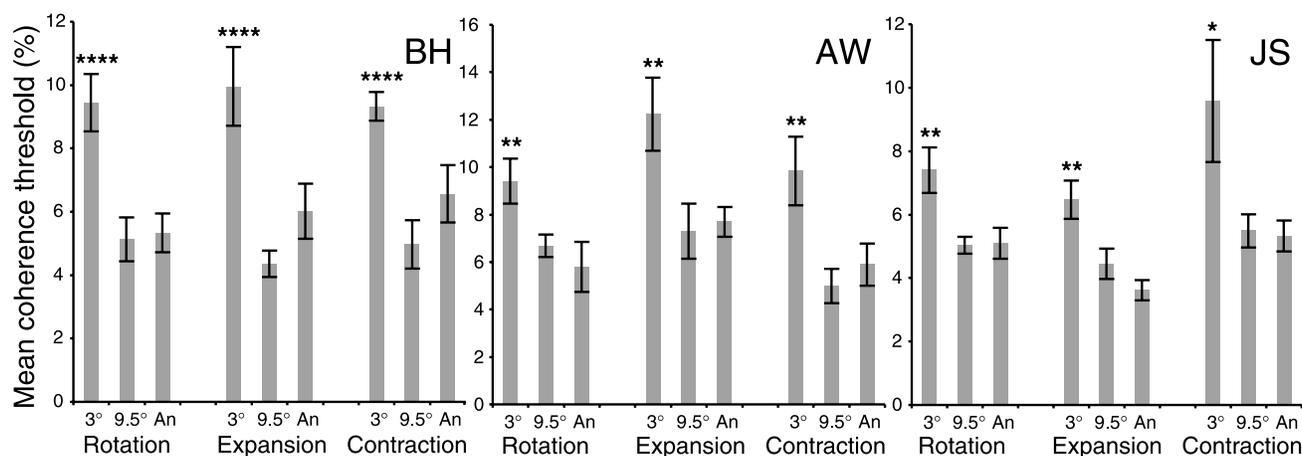Different patterns of results across the stimulus area conditions were seen for detection and coarse and fine

Figure 6. Mean coherence thresholds for detecting rotating, expanding and contracting motion patterns when presented in circular windows with 3° or 9.5° diameter or in an annulus (An). *P*-values for differences compared to 9.5° window condition. *Note*: *$p < 0.05$, **$p < 0.01$, ****$p < 0.0001$.

discrimination tasks. For all subjects and all motion types, coherence thresholds for detection were statistically significantly increased by reducing the size of the partially coherent stimulus presentation area to 3° (Figure 6). Mean coherence thresholds of 4.35–7.30% were increased to 6.46–12.23%, with ratios of the two results ranging from 1.41–2.29. However, when the stimulus was presented in an annulus with no change in area, performance was unaffected.

In contrast, fine position discrimination was unaffected by reducing the size of the stimulus presentation area (Figure 7). When the stimulus was presented in an annulus with the central 24 min of visual angle replaced with dynamic noise, coherence thresholds were statistically significantly increased for all subjects with expanding or rotating motion patterns. Mean coherence thresholds of 15.35–35.09% were increased to 26.90–62.10%, with ratios of the two results ranging from 1.38 to 2.06.

Performance was not statistically significantly affected by replacing the center of contracting motion patterns with noise for subjects BH and AW, and was reduced less, but still statistically significantly for subject JS. For contracting patterns, JS's coherence thresholds increased from 27.83% to 34.86%, a ratio of only 1.25, the smallest seen. This difference was only significant at $p = 0.0265$ and was statistically significantly smaller than effects of the same manipulation on rotating and expanding patterns. As such, this result still supports the finding that performance for fine position discrimination of the center of motion is less affected (when at all) by replacing the center of the pattern with noise in contracting patterns than rotating and expanding patterns. This is anyway a minor finding of this paper.

Coarse position discrimination results were mixed, with some conditions and subjects affected by reducing the area of the circle, and others by replacing its center with
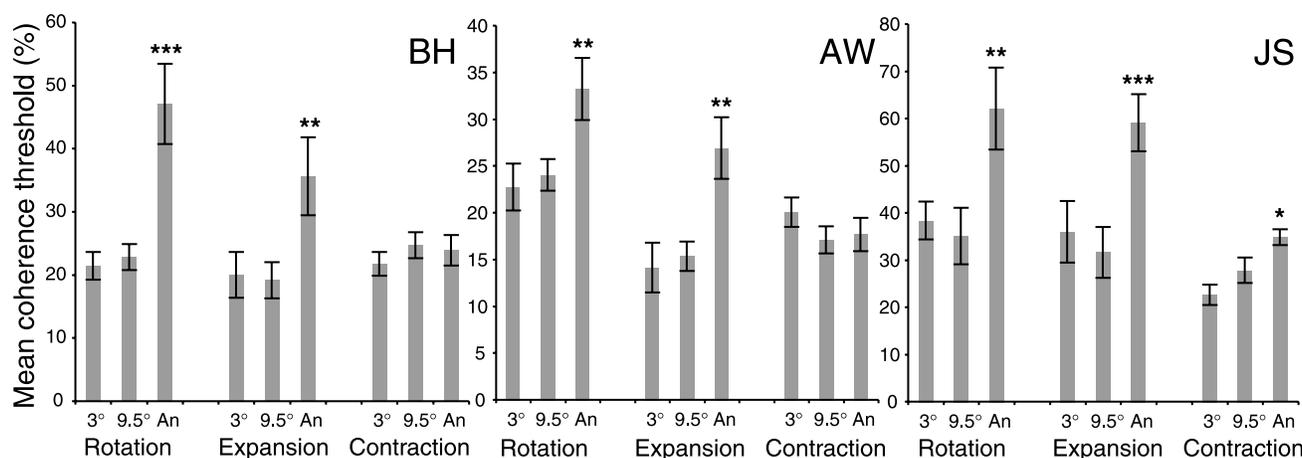

Figure 7. Mean coherence thresholds for position discrimination of rotating, expanding and contracting motion patterns when presented in circular windows with 3° or 9.5° diameter or in an annulus (An). Possible center of motion positions were 12 min of visual angle apart. *P*-values for differences compared to 9.5° window condition. *Note*: *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.
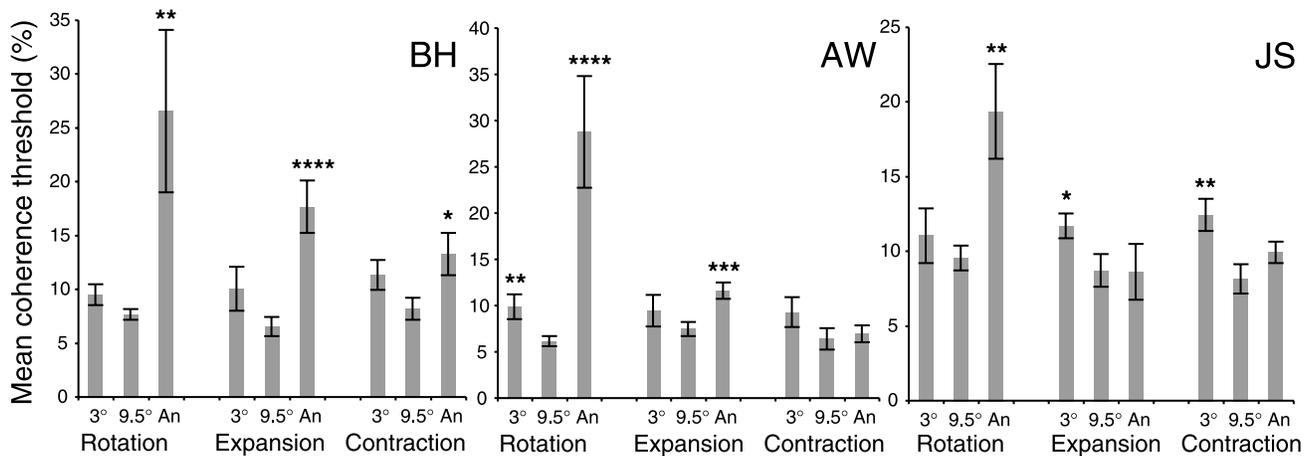
Figure 8. Mean coherence thresholds for position discrimination of rotating, expanding and contracting motion patterns when presented in circular windows with 3° or 9.5° diameter or in an annulus (An). Possible center of motion positions were 1.5° apart. *P*-values for differences compared to 9.5° window condition. *Note*: *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$, ****$p < 0.0001$.

dynamic noise (Figure 8). For subject BH, performance for all motion types was reduced by replacing the center, but not by reducing the circle size. This is also true for rotation for subject JS and expansion for AW. However, reducing the area of the pattern to three degrees in diameter also increased the position discrimination coherence threshold for rotation for AW and expansion and contraction for JS. In summary, neither restriction on the stimulus area was always effective, and sometimes both were.

As in Experiment 1, in the full stimulus condition both coarse and fine position discriminations had far higher coherence thresholds than analogous pattern detection tasks for BH and JS, though AW had similar coarse position discrimination and pattern detection thresholds. As the results of Experiment 1 show, AW was particularly good at position discrimination tasks.

When we repeated the pattern detection and fine position discrimination tasks with BH at 15°/s, qualitatively similar results were seen to those at 1.9°/s. Again, for all motion types coherence thresholds for detection were statistically significantly increased by reducing the size of the partially coherent stimulus presentation area to 3° (Figure 9). Mean coherence thresholds of 5.58–6.21% were increased to 12.20–19.51%, with ratios of the two results ranging from 2.19 to 3.45. However, when the stimulus was presented in an annulus with no change in area, performance was unaffected.

Again, fine position discrimination was unaffected by reducing the size of the stimulus presentation area (Figure 10). Again, when the stimulus was presented in an annulus with the central 24 min of visual angle replaced with dynamic noise, coherence thresholds were
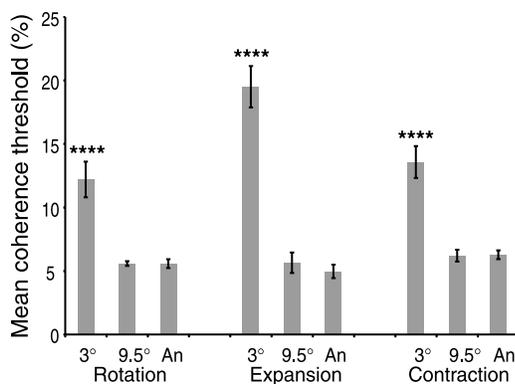

Figure 9. Mean coherence thresholds for detecting rotating, expanding and contracting motion patterns, moving at 15°/s, when presented in circular windows with 3° or 9.5° diameter or in an annulus (An). *P*-values for differences compared to 9.5° window condition. *Note*: ****$p < 0.0001$.
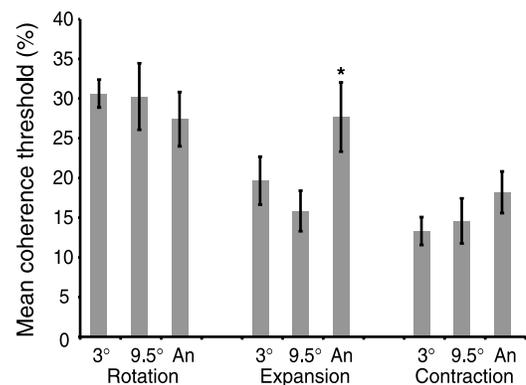

Figure 10. Mean coherence thresholds for position discrimination of rotating, expanding and contracting motion patterns, moving at 15°/s, when presented in circular windows with 3° or 9.5° diameter or in an annulus (An). Possible center of motion positions were 12 min of visual angle apart. *P*-values for differences compared to 9.5° window condition. *Note*: *$p < 0.05$.
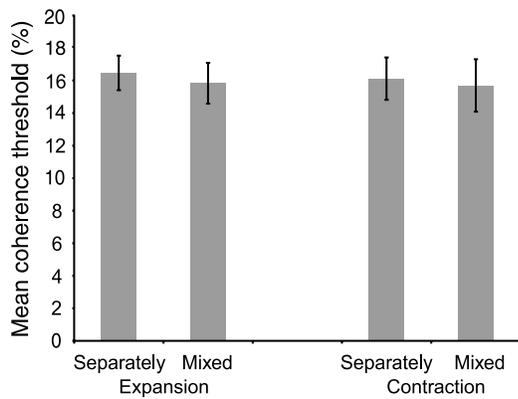
Figure 11. Mean coherence thresholds for position discrimination of expanding and contracting motion patterns when presented separately, or in randomly mixed blocks. Patterns were presented in circular windows 9.5° diameter. Possible center of motion positions were 12 min of visual angle apart. No significant differences were seen.

statistically significantly increased with expanding motion patterns. The mean coherence threshold of 15.84 was increased to 27.68, an increase by a factor of 1.75. Again, performance was not statistically significantly affected by replacing the center of contracting motion patterns with noise. At this speed, the coherence threshold was not significantly affected by replacing the center of rotating motion patterns with noise. However, we expected this change, and it was one of the main reasons we used a lower dot speed, as discussed below.

When we repeated the fine position discrimination task with BH for expanding and contracting patterns and compared coherence thresholds when the two directions of motion were presented separately or in randomly mixed blocks, we found no difference between the coherence thresholds obtained in the two conditions (Figure 11).

Discussion

Both the increased detection threshold when the stimulus area is reduced and the identical performance for full stimulus and annulus conditions show that the detection task integrates global motion information over a wide area. These results fit well with Burr et al.'s (1998) similar experiment for pattern direction discrimination, where performance was determined by the total area displayed, and not by how that area was distributed within the overall display, suggesting that the entire display area contributes equally to the processing underlying detection. While we do not intend to test the limits of spatial summation, in this task we see spatial summation at least beyond three degrees of visual angle. Burr et al. (1998) show spatial summation up to 70°.

In contrast, the region immediately around the center of motion is very important for fine position discrimination

of the center of expansion or rotation, which cannot easily be performed from dot motions outside this central region. When peripheral dot motions are incoherent, performance is unaffected, while making only a very small area around the center of motion incoherent in the annulus condition greatly increases the coherence threshold.

The effect of removing the area near the center is smaller or non-existent for fine discrimination of contracting patterns. A possible basis for this result is that the dots are moving toward the center of motion, and subjects appear to recover its position by extrapolating these paths. Subjects seem to predict the path of slightly peripheral dots moving toward the center of motion, and thus recover its position.

The mixed result for coarse position discrimination suggests many similarities with fine position discrimination, but also some differences. Performance for BH was affected by making the center of motion incoherent, but not by making the surrounding area incoherent, as was seen for fine discrimination. This suggests that the center of motion needs to be present, and cannot be easily recovered from nearby dot paths. The same was seen for both other subjects in some motion patterns. However, for both AW and JS, position discrimination coherence thresholds for certain motion patterns were increased by making the surround area incoherent. In some cases, neither manipulation was affected coherence thresholds, while in others both did. Small increases in coherence threshold were normally seen for either manipulation, though these often did not reach significance. It seems that both central and peripheral information could be used to perform this discrimination, and the strategy used varied between subjects and motion patterns.

When the dot speeds were increased to 15°/s for pattern detection and fine position discrimination tasks, qualitatively similar results were seen to those at 1.9°/s. However, at this speed, the fine position discrimination coherence threshold was not significantly affected by replacing the center of rotating motion patterns with noise. We would expect this change when increasing the dot speed to 15°/s, because the distance between two dot positions on consecutive frames is 0.25° at 60 Hz. This leaves a large space between consecutive dot positions. With such a spatial interval, successive positions of dots near the center may well be on opposite sides of the center, meaning that the rotational optic flow is poorly represented in this region and the motion here is essentially useless for position discrimination of the center. In support of this view, fine position discrimination coherence thresholds for rotating patterns were statistically significantly higher than for expanding ($p = 0.0034$) or contracting ($p = 0.0020$) patterns 15°/s, but not at 1.9°/s ($p > 0.05$ in both cases).

As we found no change in coherence threshold when radial motion patterns were presented separately or when their directions of motion were randomly mixed, we consider it unlikely that subjects discriminated the position of the centers of pattern motion by looking at the direction of unidirectional dot motion in a small area.

Experiment 3: Spatial summation in form detection and position discrimination tasks

The tasks required for motion patterns in Experiments 1 and 2 have analogues with static form patterns, in which the elements are short line or arc segment rather than motion trajectories. Coherence detection for form and motion patterns has been used to compare global visual integration in different extrastriate systems (Atkinson et al., 1997; Braddick, O'Brien, Wattam-Bell, Atkinson, & Turner, 2000; Gunn et al., 2002). In Experiment 3 we extended the method of Experiment 2 to analogous concentric and radial form stimuli. These stimuli contained very similar information to the motion stimuli except that the elements carried no directional information, and the dynamic noise of the motion stimuli was replaced by static random orientation noise. The various different stimulus area conditions were identical to those used for motion in Experiment 2 (Figure 5).

This allowed us to examine how far the differences in spatial integration for the different tasks were specific properties of motion processing systems, and how far they might represent informational constraints that are common to the processing of geometrically analogous information by different cortical systems. In addition, since the form stimuli had no direction information, the unidirectional motion confound was eliminated.

Methods

Stimuli

Instead of using moving dots, we integrated the positions of the dots over their lifetimes to make a streak following the dot's path. Each dot was drawn on the same frame, with five consecutive positions, and this frame, including all five dot positions, was shown for the entire 3-s presentation.

This produced static stimuli, containing no motion. Instead of expanding, contracting and rotating motions, stimuli were either concentric or radial form patterns. The dynamic noise of the motion stimuli was replaced by static random orientation noise.

Except for the static patterns replacing moving ones, all stimuli were identical to their moving counterparts (Figures 1, 2, and 5), for detection and coarse and fine position discrimination tasks.

Results

Different patterns of statistically significant differences between stimulus area conditions were seen for detection and coarse and fine discrimination tasks. For all subjects and both form patterns, coherence thresholds for detection were statistically significantly increased by reducing the size of the stimulus presentation area to 3° (Figure 12). Mean coherence thresholds of 4.77–7.29% were increased to 9.85–17.45%, with ratios of the two results ranging from 1.69–2.82. However, when the stimulus was presented in an annulus with no change in area, performance was unaffected.

In contrast, fine position discrimination was unaffected by reducing the size of the stimulus presentation area (Figure 13). When the stimulus was presented in an annulus with the central 24 min of visual angle replaced with orientation noise, coherence thresholds were statistically significantly increased for all subjects with concentric, but not radial, patterns. For concentric patterns, mean coherence thresholds of 15.07–24.39% were increased to 27.20–37.37%, with ratios of the two results ranging from 1.53–1.81.

Coarse position discrimination results varied between subjects. For all subjects, coherence thresholds increased
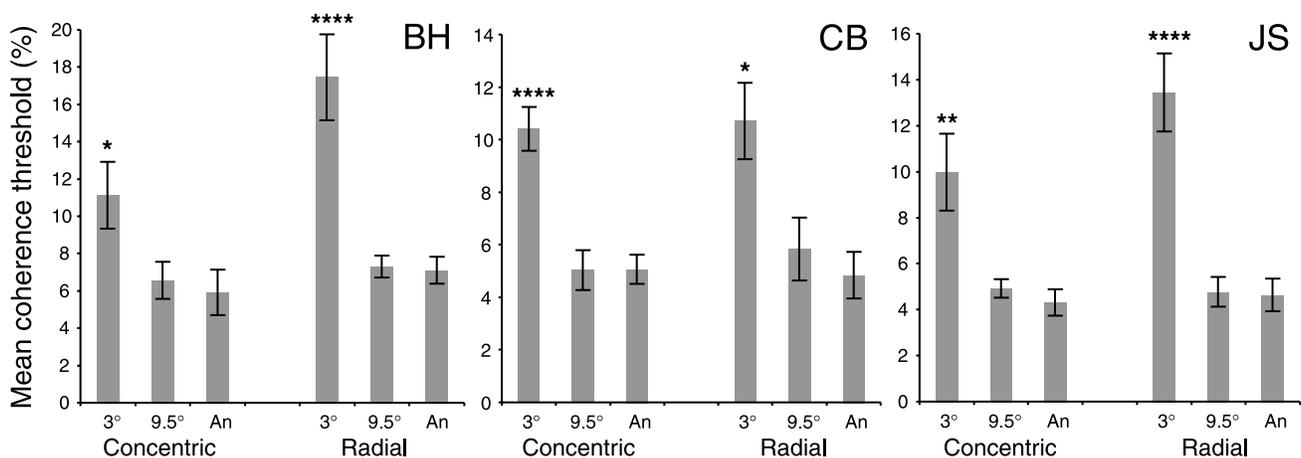

Figure 12. Mean coherence thresholds for detecting concentric and radial form patterns when presented in circular windows with 3° or 9.5° diameter or in an annulus (An). *P*-values for differences compared to 9.5° window condition. *Note*: $*p < 0.05$, $**p < 0.01$, $****p < 0.0001$.
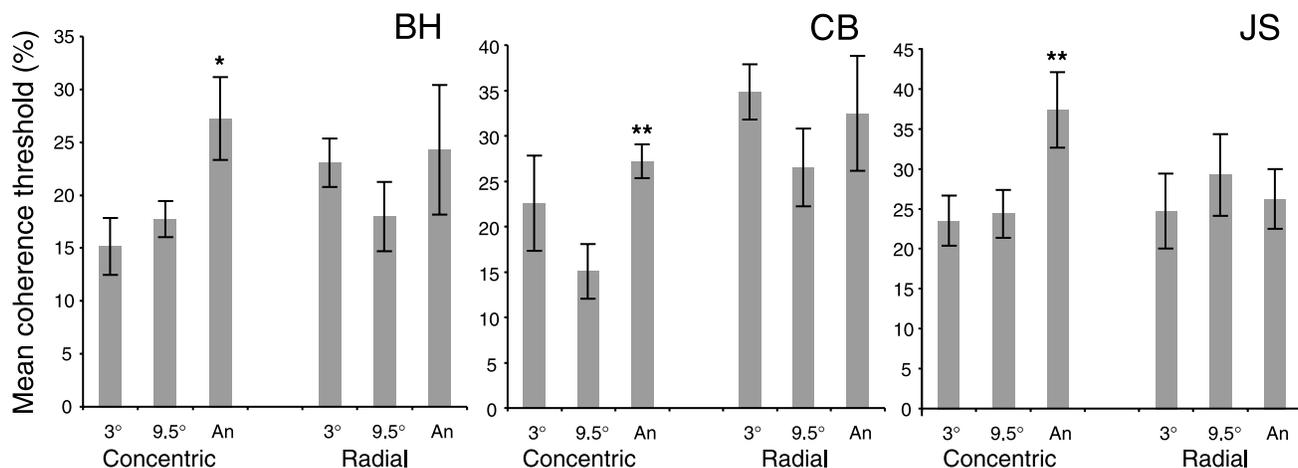
Figure 13. Mean coherence thresholds for position discrimination of concentric and radial form patterns when presented in circular windows with 3° or 9.5° diameter or in an annulus (An). Possible pattern center positions were 12 min of visual angle apart. P-values for differences compared to 9.5° window condition. Note: *$p < 0.05$, **$p < 0.01$.

when the stimulus area was reduced for radial form patterns and also for concentric patterns for CB (Figure 14). Presenting the stimulus in an annulus affected coarse position discrimination only in radial patterns for BH, and not at all for any other subject.

Discussion

As with the analogous motion tasks in Experiment 2, the increased detection threshold with a reduced stimulus area and the identical performance for full stimulus and annulus conditions show that the form detection task relies heavily on global processing. The size of the pattern, rather than which part is displayed, determines performance, suggesting that detection processing uses the entire display area.

For fine position discrimination of the center of concentric patterns, the central region is again very important to performance, and cannot easily be derived from line segments in the surrounding area. When the latter are incoherent, performance is unaffected, while making only a very small area around the center incoherent, in the annulus condition, greatly increases the coherence threshold for concentric patterns.

The lack of effect of removing the central area for the fine discrimination task with radial patterns is similar to that for contracting motion in Experiment 2. We suggest the same probable explanation: the line segments point toward the center of the pattern and subjects may be able to recover the location of the center by extrapolating these oriented segments.

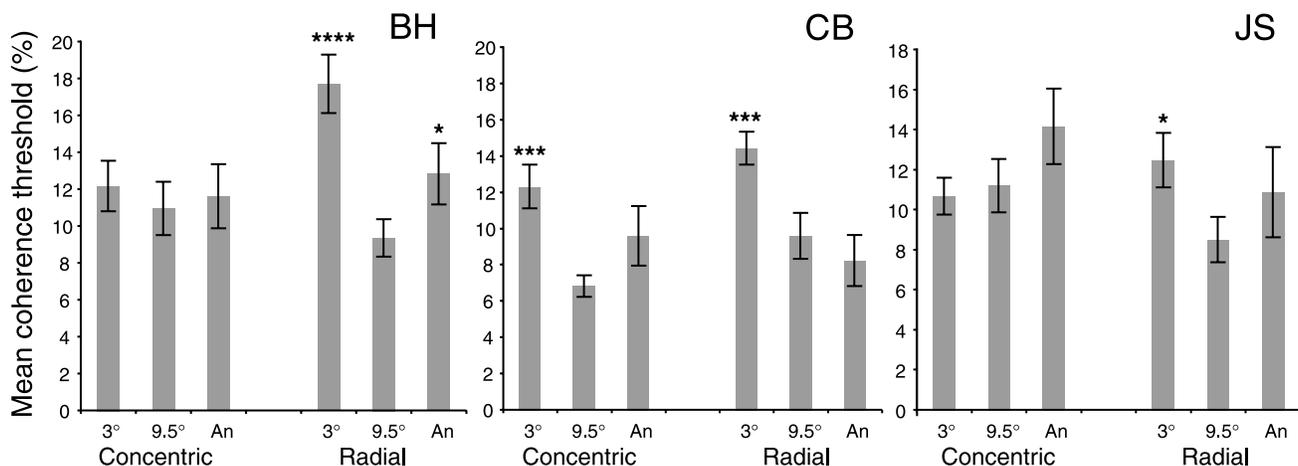A similar ability to recover the center location appeared in the coarse position discrimination task. When the

Figure 14. Mean coherence thresholds for position discrimination of concentric and radial form patterns when presented in circular windows with 3° or 9.5° diameter or in an annulus (An). Possible pattern center positions were 1.5° apart. P-values for differences compared to 9.5° window condition. Note: *$p < 0.05$, ***$p < 0.001$, ****$p < 0.0001$.

central 3°, a considerable area, was removed to make an annulus, performance was not affected for either radial or concentric patterns. Clearly subjects easily recover the position of the center from peripheral form information in this task. Conversely, reducing the presentation area by removing peripheral lines increased the coherence threshold for coarse position discrimination of radial patterns, and concentric patterns for CB.

The similarities in the contrast between coarse and fine tasks, and detection, in Experiments 2 and 3 suggest that the factors determining this contrast are not unique to the motion system, but have their analogues for static form. It appears that similar constraints apply to the extraction and integration of spatial information in the two types of display, even through they are presumed to depend on quite different cortical systems (MT+/MSTd and perhaps V3a for motion; V4 for form).

However, there seems to be considerable interaction between the processing of analogous form and motion patterns at various levels of cortical processing. In macaques, V1 cells respond to motion streaks, neural representations of form produced by fast-moving motion stimuli (Geisler, Albrecht, Crane, & Stern, 2001). Furthermore, fMRI data suggest that motion-selective neurons in human MT+ are also activated by implied motion in static Glass patterns (Krekelberg, Vatakis, & Kourtzi, 2005).

Experiment 4: Stimulus information content

One critical factor when interpreting the spatial summation results is where the information to differentiate between the subjects' choices in these tasks is found in the stimuli. If a subject only uses a restricted part of the stimulus to perform the task (as for position discrimination tasks in Experiments 2 and 3), perhaps this is because this is where the useful information is.

In the case of pattern detection, information is evenly distributed. The subject has to discriminate between a partially coherent pattern and random dot motion or line orientation. Any coherent motion or orientation could be used to do this. The entire partially coherent part of the stimulus contains the same coherence level, and all dots move at the same speed, or all lines are the same length. As their direction of motion (or orientation of lines) is not important to perform the task, all points in the stimulus contain the same information. Thus to best perform the task, the subject should pool all of this information, leading to extensive spatial summation.

This is not the case for center of motion or form position discrimination. To discriminate between the two possible positions, the subject uses direction or orientation differences between pattern elements whose pattern center

can be in one of two possible positions. This will vary considerably across the stimulus.

Consider, for example, a contracting motion pattern whose center can be in one of two positions, one to the left and one to the right. If a dot lies between the two possible positions, it will move toward whichever is the center of motion. If this is on the left, the dot will move left. If on the right, it will move right. The direction of motion varies by 180° between the two possibilities, so will be the most informative dot possible. A dot lying directly left of both positions, on the other hand, will move to the right, whichever position is the center, and will move at the same speed (as all dots do in these stimuli). As such, this provides no useful information to the observer.

Furthermore, the further the dot is away from the possible position of the center, the smaller the difference between the angles at which the dot could move. Thus, the peripheral part of the stimulus may only be of little use because it contains little information.

Methods

Using MATLAB, we plotted the angular difference between motions or orientations of coherent dots produced by the two possible positions of the center of motion or orientation. The angular difference at each point in the stimulus is shown as a grayscale shade on the output image. For motion, the maximum possible angular difference is 180°. For orientations there is no directional information, so the maximum difference is only 90°.

We examined two measurements in the stimuli which could predict performance. First was the sum of the angular differences at all points in the stimulus. This models a linear global integration of the discriminatory information over the whole visual field, and we would expect this figure to predict performance if global integration was occurring, limited only by the information present. While linear global integration is unlikely to actually occur, any global integration might produce a result along these lines. The second measure was the maximum angular difference at any one point in the stimulus. This models a local analysis of only the most useful information. While this strictly models a situation where the subject was only looking at one point between the two possible center of motion positions, and we do not believe subjects use this strategy, this measure is likely to predict performance if subjects use a small region containing the most useful information, i.e. near the possible center of motion positions.

Results

The plots of angular difference between motions of coherent dots for motion patterns (Figure 15) and
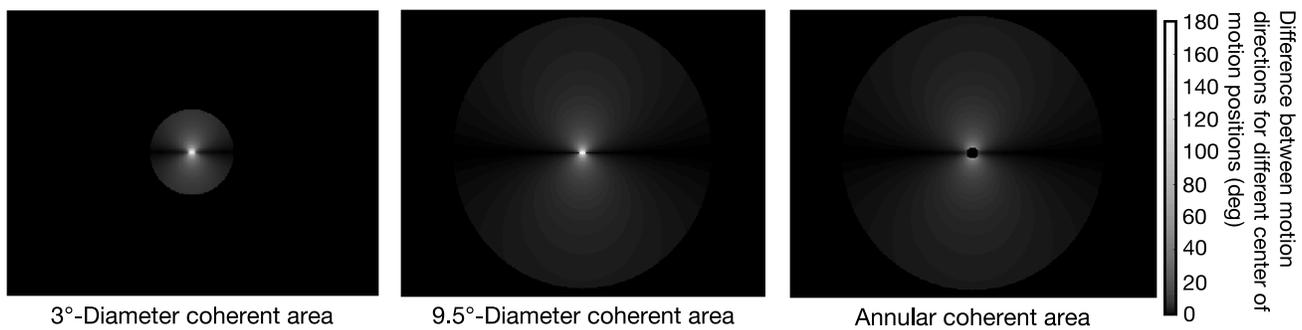
Figure 15. Plot of angular differences between motion directions of dots at each point in the display, with two possible center of motion positions 12 min of visual angle apart, when presented in circular windows with 3° or 9.5° diameter or in an annulus.

orientations of coherent lines for form patterns (Figure 16) can be seen below.

The sum of the angular differences at each point in the display (Figure 17) shows that in the annular condition, the amount of information is very similar to the 9.5° diameter full display for both form and motion displays. On the other hand, the information in the 3° display is very much less than either of these.

In contrast, the maximum angular difference in the display is much less in the annular condition than in the 9.5° diameter display for both form and motion (Figure 18). On the other hand, the maximum angle in the 3° diameter display is identical to that in the 9.5° diameter display.

Discussion

For both form and motion stimuli, while the angular differences seen in the peripheral parts of the stimulus are much smaller than those seen in the center, because of the large area removed when only the central 3° of the stimulus contained coherent motion or orientation, the total discriminatory information present was greatly reduced in this condition (Figures 15, 16, and 17), while the maximum angular difference at any one point was unaffected (Figures 15, 16, and 18). When the central 0.4° of the stimulus was replaced by random motion or

orientation, on the other hand, there was only a small reduction in the total discriminatory information (Figures 15, 16, and 17), but a large reduction in the maximum angular difference (Figures 15, 16, and 18). As such, this result suggests that the difference in performance with annular presentation, and the similar performance in the full stimulus and reduced area conditions, are not due to changes in the total information available, but rather changes in the information available in a restricted central area.

As radial and concentric form patterns produce different results for position discrimination, when the amount of information contained in the stimuli is identical (though orientations are perpendicular), this also argues against a purely informational explanation for the results.

Discussion

These results show considerable differences between detection and position discrimination tasks. First, even coarse position discriminations usually have much higher coherence thresholds than detection tasks, showing that position discriminations are more sensitive to noise.

Furthermore, in contrast to detection tasks, fine position discriminations rely heavily on the presence of the center
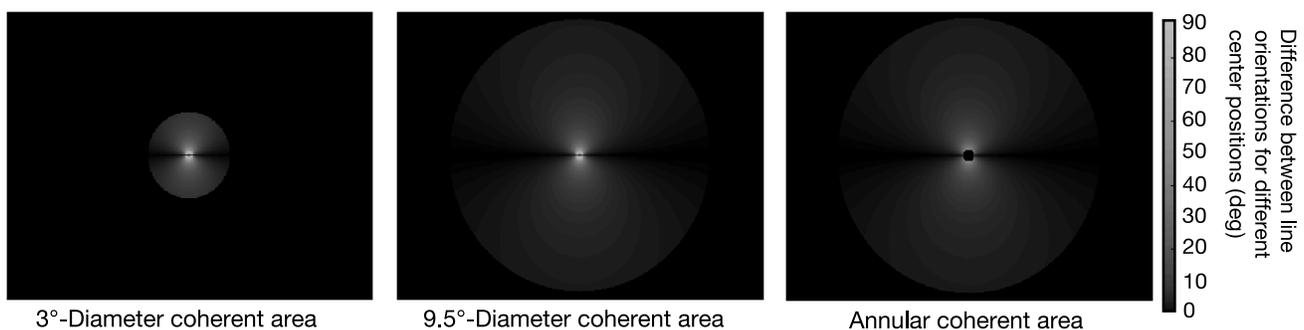

Figure 16. Plot of angular differences between line orientations at each point in the display, with two possible pattern center positions 12 min of visual angle apart, when presented in circular windows with 3° or 9.5° diameter or in an annulus.
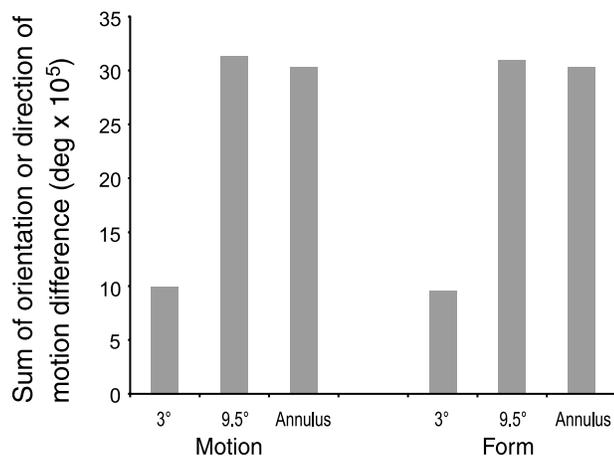
Figure 17. Linear sum of angular differences between line orientations or direction of dot motion at each point in the display, when presented in circular windows with 3° or 9.5° diameter or in an annulus, in form and motion displays. The two possible pattern center positions were 12 min of visual angle apart.

of motion, and are unaffected by replacing peripheral dots with random motions. This suggests that position discrimination relies on local information around the center of motion to accurately localize it, and does not use information from the entire pattern.

Many studies have examined the derivation of heading from optic flow, and so several models of optic flow analysis have tackled the question of localization or position discrimination (Lappe & Rauschcker, 1993; Page & Duffy, 2003; Perrone & Stone, 1998). However, all these models examine heading discrimination using stimuli with modified flow field geometry, of the type that would occur when heading and center of expansion are not identical. This situation occurs when the animal is looking away from the direction of heading, and the complex population codes used discriminate heading fairly crudely (perhaps only because of the limited numbers of neurons used in the simulations). Doubtless a similar model could be used for our displays, but our results suggest such a model would need to be more accurate and probably use less information from the peripheral visual field than has previously been proposed.

Population encoding in MT+ is supported by macaque neurophysiology, in which MSTd contains many neurons with position-dependant responses depending on the position of the center of motion (Lappe, Bremmer, Pekel, Thiele, & Hoffmann, 1996). Furthermore, macaque MSTd neurons show responses selective to the position of the center of optic flow (where this is manipulated by distorting rather than simply shifting the flow pattern) (Duffy & Wurtz, 1995). These responses contribute to neuronal population responses that represent heading direction (Page & Duffy, 1999). As most studies of macaque MT and MST neurons involve neurons with eccentricities of at least 5°, receptive fields of neurons

representing foveal vision may be much smaller than the 10–100° (Duffy & Wurtz, 1991a) described in macaque MSTd. The accuracy with which localization may be achieved by population encoding in MT+ when the pattern is foveated is likely to depend on the size of the receptive fields of the neurons involved. Not much is known about these, but they may well have small receptive fields, allowing accurate position discrimination.

It is also possible that accurate localization of the center of a form or motion pattern may rely on local analysis of variations in direction (motion patterns), orientation (form patterns), or form or motion contour curvature (concentric form and rotational motion respectively). The maxima in spatial differentials of these properties correspond to the centers of form and motion patterns in these stimuli.

This latter mechanism might involve extrastriate areas outside of MT+ representing position information. Beardsley and Vaina (2005) report a motion-impaired stroke patient, GZ, who cannot discriminate the direction of radial motion patterns, but can accurately localize their centers of motion, suggesting different areas may be involved in the two tasks. Indeed fMRI results implicate V3A in the analysis of form contour curvature (Caplovitz & Tse, 2007) and center of motion location (Koyama et al., 2005), making this a good candidate for a separate localization area. However, which areas are involved in this position discrimination requires further investigation.

While fine position discriminations have higher coherence thresholds with the center of motion replaced by noise, they are not impossible. Clearly, when the center of motion is missing, other information can be used to derive its position. Whether the information used is that closest to the center of motion (analyzing the trajectories of local nearby dots) or relies on the whole stimulus is an open question.
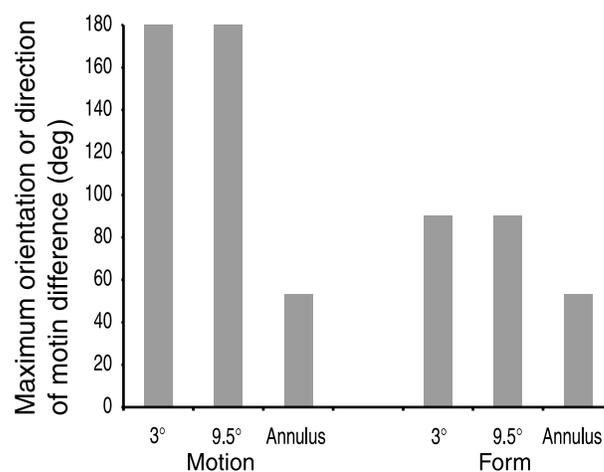

Figure 18. Maximum angular differences between line orientations or direction of dot motion at each point in the display, when presented in circular windows with 3° or 9.5° diameter or in an annulus, in form and motion displays. The two possible pattern center positions were 12 min of visual angle apart.

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For contracting stimuli, replacing the center of motion with noise for fine position discriminations had no effect, or a smaller effect than when this was done for rotating or expanding patterns, suggesting that surrounding dot trajectories can be very useful for deriving the position of the center of motion in contracting patterns. Again, it is an open question whether these surrounding trajectories are analyzed as a flow pattern, or whether they are simply analyzed individually at a very local level to derive their future positions. That this only occurs for contracting motions supports the latter explanation.

For radial form patterns, replacing the center of the pattern with noise again does not affect performance. As with contracting motions, because this only happens for radial forms, it is likely that the orientations of surrounding lines are analyzed very locally to derive where they are pointing, as opposed to the alternative of using surrounding orientations as part of a global form analysis.

Finally, it is interesting that the results for analogous motion and form stimuli (in Experiments 2 and 3 respectively) are very similar. This suggests that, as the information in the two sets of stimuli is very similar, this information may be constraining subjects' performance. However, there are considerable similarities between the neural mechanisms of form and motion processing. Global motion, as analyzed in MT+, and global form, as analyzed in V4, are at the same intermediate level of processing, where directions/orientations of single texture elements are grouped together to derive an overall pattern in cells with large receptive fields (Desimone & Schein, 1987; Duffy & Wurtz, 1991a) and position-invariant responses (Duffy & Wurtz, 1991b; Gallant et al., 1996; Graziano et al., 1994). Furthermore, global motion and form perception tasks are both very tolerant of noisy stimuli (Burr et al., 1998; Wilson & Wilkinson, 1998).

There is also considerable interaction between the processing of analogous form and motion patterns at various levels of cortical processing. In macaques, V1 cells respond to motion streaks, neural representations of form produced by fast-moving motion stimuli (Geisler et al., 2001). Furthermore, fMRI data suggest that motion-selective neurons in human MT+ are also activated by implied motion in static Glass patterns (Krekelberg et al., 2005). With such interactions, the same neural populations might perform both form and motion tasks.

The results of Experiment 4 also suggest that performance in position discrimination tasks is not merely limited by the global amount of information present. While the angular differences seen in the peripheral parts of the stimulus are much smaller than those seen in the center, because of the large area removed when only the central 3° of the stimulus contained coherent motion or orientation, the total discriminatory information present was greatly reduced in this condition. When the central 0.4° of the stimulus was replaced by random motion or orientation, on the other hand, there was only a small reduction in the total discriminatory information, but a large effect on

performance. Instead, it seems that performance relies on the amount of information present in a restricted central area.

Also arguing against purely informational limitations is the fact that while form and motion results were similar, they were not identical. For example, coarse position discriminations were never affected by replacing the central area with noise for form patterns, but often were for motion patterns. Furthermore, some differences occur between the different form and motion patterns, when the information contained in each is essentially identical, the only differences being that trajectories were in perpendicular or opposite directions.

An interesting parallel of our results is seen in recent paper examining whether macaques use global or local information for a steering task with optic flow patterns (Page & Duffy, 2008). Macaques here used local motion cues at their fixation point to steer the centers of expanding optic flow patterns to the fixation point (i.e. they steered with the direction of motion at the fixation point). Again, this shows that local information is preferred to global information when certain tasks are performed with optic flow fields. This reduced neuronal responses in MSTd compared to passive viewing. When the direction of radial motion was randomized, preventing this strategy, the macaques initially failed to complete the task, and were then retrained to use global motion cues. This increased the neuronal responses of MST compared to passive viewing. Furthermore, when the experimenters masked peripheral areas of the stimulus, most MSTd neurons showed reduced activity, but some showed increased activity. Reduced activity was seen in neurons with large, peripheral receptive fields, while increased activity was seen in neurons with small, central receptive fields. It is therefore possible that the differences we see in spatial summation reflect changes in the activity of a human MST homologue depending on the type of task its neurons are attending to.

Clearly there are some differences in the position discrimination processing of radial and concentric form patterns and expanding, contracting and rotating motion patterns. These may arise from the differences in what characterizes the center of the pattern in each case. For rotating motion and concentric form patterns, this is the point of maximum contour curvature, while for expanding and contracting motion and radial form patterns, it is the point of the greatest difference between line orientations or dot motion directions.

Overall, these results show that position discrimination of the centers of expanding, contracting and rotating motion patterns, as well as radial and concentric form patterns, involves little spatial summation, in contrast to detection of these patterns, which involves considerable spatial summation. This dichotomy suggests that position discrimination of the patterns' centers may involve different mechanisms from pattern detection and direction discrimination. These results may have important implications for models of heading perception which rely on optic flow analysis.

Acknowledgments

Corresponding author: Benjamin M. Harvey.
Email: benjamin.harvey@psy.ox.ac.uk.
Address: Department of Experimental Psychology, Oxford University, South Parks Road, Oxford, UK, OX1 3UD.

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