The detection of multiple global directions: Capacity limits with spatially segregated and transparent-motion signals

John A. Greenwood

School of Psychology, The Australian National University, Canberra, ACT, Australia, & UCL Institute of Ophthalmology, University College London, London, UK   ✉

Mark Edwards

School of Psychology, The Australian National University, Canberra, ACT, Australia   🏠 ✉

An important constraint on motion processing is the maximum number of directions that can be perceived at the same time. When transparent-motion stimuli are constructed based solely on direction differences, prior studies demonstrate that no more than two directions are seen simultaneously. However, this limit has been extended to three when signal directions drive independent speed- or disparity-tuned global-motion systems. The present study sought to determine whether this three-direction capacity reflects the specific mechanisms of transparent-motion detection or a more general restriction on global-motion processing. Using both transparent and spatially segregated stimuli, observers indicated which of the two intervals contained the most directions, with simultaneous processing ensured through brief durations and n vs. $n + 1$ signal comparisons. When spatially segregated directions were interleaved in patches, no more than two were seen, as with direction-defined transparent motion. In contrast, separating these directions into distinct spatial regions allowed the detection of up to three. Signal-detection thresholds did not vary across these signal arrangements, suggesting that the two-direction capacity results from signal-to-noise pooling across the entire stimulus, with the higher capacity for spatially distinct directions arising from independent pooling within each region. Together, these results provide further evidence for an upper capacity of three directions within the global-motion stage.

Introduction

Our perception of motion relies upon a largely hierarchical process, with the initial extraction of motion performed by spatially restricted local-motion detectors, prior to extensive spatial integration within the global-motion stage (e.g., Braddick, 1997; Movshon, Adelson, Gizzi, & Newsome, 1986; Welch, 1989). Though much is known about the global-motion stage, relatively little attention has been directed toward the number of global directions that can be detected simultaneously. This capacity sets an important upper limit for the integration and segmentation operations that characterize global-motion processing (Braddick, 1993), as well as the read-out algorithms used to interpret population activity within this stage (Pouget, Dayan, & Zemel, 2000). Recently, a strict capacity limit has been found for the detection of transparent motion, which occurs when multiple objects move simultaneously through the same spatial region. When simulated with random-dot stimuli, where multiple interspersed dot groups move in distinct directions (e.g., Clarke, 1977), no more than two directions can be detected simultaneously (Edwards & Greenwood, 2005), with the addition of speed or disparity differences able to extend this to three (Greenwood & Edwards, 2006a, 2006b). However, though the representation of transparency depends heavily on the signal-to-noise operations of the global-motion stage (e.g., Edwards & Greenwood, 2005; Snowden & Verstraten, 1999), signal intensities within these stimuli should have allowed the detection of up to four directions. The aim of the present study was thus to determine whether this three-signal limit reflects the specific mechanisms of transparent-motion detection, or a more general restriction on the detection of multiple global-motion signals.

The capacity limit for transparent-motion detection was first examined by Mulligan (1992), who required observers to discriminate between intervals containing n and $n + 1$ transparent-motion signal directions. Simultaneous detection of these signals was ensured using brief presentation times around 200 ms, as in many subsequent

studies of transparent-motion detection (Braddick, 1997; Braddick, Wishart, & Curran, 2002). With signals defined purely by direction differences, performance on this task reveals a perceptual limit of two—observers can reliably discriminate between two and three directions but fail to distinguish between three and four (Edwards & Greenwood, 2005; Mulligan, 1992). This limit is determined, at least in part, by high signal-detection thresholds for transparency, coupled with the decrease in signal intensity that occurs as the number of directions increases. If the signal intensity within transparent-motion stimuli is defined as the proportion of dots moving in one of the signal directions, two directions can at most be presented at intensities (or coherence values) of 50%, with the addition of a third reducing the maximum intensity to 33%. As the detection of two directions in a 2 vs. 3 comparison requires intensities above 40% for each (Edwards & Greenwood, 2005), well above thresholds for unidirectional detection (e.g., Braddick, 1995), the maximum number of transparent-motion directions that can be presented at suprathreshold intensities is two.

Consistent with the dependence of this capacity limit on high detection thresholds, an increase in signal intensity allows the detection of a greater number of transparent-motion directions. Though intensities in these initial examinations were at their physical maximum (Edwards & Greenwood, 2005; Mulligan, 1992), further elevation is possible by distributing processing among independent global-motion channels. Because the global-motion stage contains a continuum of speed-tuned detectors, speeds that drive detectors with non-overlapping sensitivities exhibit independent signal-to-noise processing (Edwards, Badcock, & Smith, 1998; van Boxtel & Erkelens, 2006). Global-motion signals on distinct depth planes show a similar independence, suggesting the existence of at least two systems selective for binocular disparity (Hibbard & Bradshaw, 1999; Snowden & Rossiter, 1999). The independence of these systems means that transparent-motion signals processed by one set of detectors will not reduce the intensity of signals processed by other detectors. Accordingly, when these directions are presented with sufficiently large differences in speed and binocular disparity, up to three directions can be detected simultaneously (Greenwood & Edwards, 2006a, 2006b). However, were signal intensity the sole constraint on transparent-motion detection, these stimuli should have allowed the detection of up to four directions. Yet, even with combined speed and disparity differences, observers were unable to detect signal numbers beyond three (Greenwood & Edwards, 2006b). These results point to a second capacity limit that restricts the maximum number of detectable transparent-motion directions to three, regardless of their signal intensity.

Given the dependence of transparent-motion detection on the global-motion stage (Braddick, 1997; Qian, Andersen, & Adelson, 1994; Snowden & Verstraten, 1999), this three-signal limit may reflect the maximum number of global-motion directions that can be detected simultaneously. However, much higher capacities have been found in tasks where observers are required to track discrete moving objects over an extended duration. In displays containing 12 moving objects, observers can track 4–5 target objects with an 85–90% success rate in indicating whether post-cued objects were targets or distractors (Pylyshyn & Storm, 1988). Though the long durations employed by these studies make it difficult to ensure that objects are tracked simultaneously (Oksama & Hyönä, 2004), multiple object tracking appears to share resources with visual attention and working memory (Fougnie & Marois, 2006), where similarly high capacity limits are found. For instance, the number of objects that can be simultaneously attended to without sequential counting (a process known as subitization) has been established at four, typically using static dots on a uniform background (Atkinson, Campbell, & Francis, 1976; Kaufman, Lord, Reese, & Volkmann, 1949). Similarly, change detection tasks reveal that up to four items can be stored simultaneously in visual working memory (Luck & Vogel, 1997). Indeed, when the many tasks designed to measure the capacity of attention and working memory are compared, a range of values between three to five is found, with an overall average of four (Cowan, 2001).

These high capacities suggest that the previously observed limit of three directions may be specific to transparent-motion stimuli. This would be consistent with the many processing costs observed for transparent-motion detection when compared with unidirectional motion (e.g., Braddick et al., 2002; Curran, Hibbard, & Johnston, 2007; Edwards & Greenwood, 2005; Wallace & Mamassian, 2003). If so, it should be possible for observers to detect a higher number of global directions when these signals are spatially separated across non-overlapping regions. Alternately, the three-signal capacity may reflect limitations placed upon global-motion detection that are distinct from the mechanisms utilized in both multiple object tracking and subitization. In this case, no more than three directions should be seen, regardless of their spatial arrangement. The aim of the present study was thus to examine the capacity of the global-motion stage by comparing the number of global directions that can be detected simultaneously with both spatially segregated and transparent-motion signal arrangements.

Experiment 1: Capacity limits for the detection of multiple global directions

To examine the detection of multiple global directions, three types of stimuli were utilized (as depicted in Figure 1). In each case, capacity limits were assessed using n vs. $n + 1$ comparisons with brief presentation
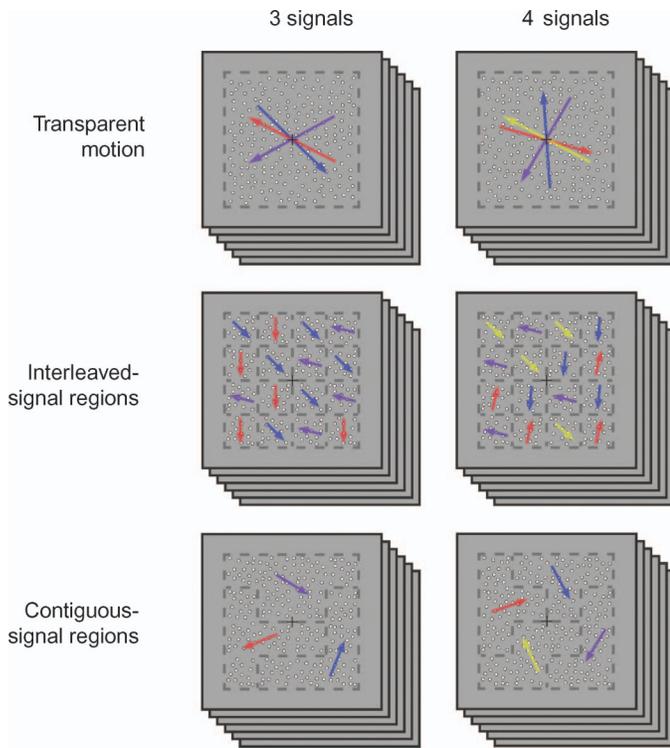
Figure 1. A depiction of stimuli used in Experiment 1. Two examples are presented for each stimulus type, one with three signal directions (left) and the other with four (right). Transparent-motion stimuli (top row) contained multiple signal groups interspersed throughout the entire aperture, while the two spatially segregated conditions were constructed by dividing this aperture into 16 smaller patches. For the interleaved-signals condition (middle row), adjacent patches moved in distinct directions, while the contiguous-signal regions (bottom row) were constructed by arranging patches with common directions together.

times to ensure the simultaneous detection of all directions present (Edwards & Greenwood, 2005; Mulligan, 1992). As before, *transparent-motion* stimuli were created with multiple interspersed dot groups moving in distinct directions within the same aperture. Given our prior results, observers should fail to detect any more than two of these direction-defined signals (Edwards & Greenwood, 2005; Mulligan, 1992) in the absence of additional differences in speed and binocular disparity (Greenwood & Edwards, 2006a, 2006b). To examine both the local and global factors underlying this limit and determine whether the previously observed three-signal capacity applies to global-motion processing in general, performance was also examined with two types of spatially segregated stimuli. These stimuli were constructed by dividing the aperture into a number of smaller patches, each containing dots moving with a single direction.

In the *interleaved-signals* condition, each signal direction was distributed across the stimulus, with adjacent patches moving in distinct directions. That is, while global

directions were spatially interleaved in a similar manner to transparent-motion stimuli, each local region contained only a single direction, giving the appearance of a patchwork quilt defined by direction. This differs from transparent motion, where each local region will contain a mixture of dot directions over time, thus allowing examination of the influence of local-motion pooling on multiple signal detection. In the extreme, local pooling can be observed when moving elements with distinct directions overlap within a given local region, reducing multiple locally paired directions to the vector average (Curran & Braddick, 2000; Qian et al., 1994). Though our stimuli were constructed with continuous dot trajectories and low dot densities in order to minimize this averaging, temporal integration within the local pooling stage could still impair transparent-motion detection, given the temporal alternations in direction within each local region (Durant, Donoso-Barrera, Tan, & Johnston, 2006; Vidnyánszky, Blaser, & Papathomas, 2002). If local pooling is a significant problem in transparent-motion detection, higher signal numbers should thus be detected with the interleaved-signals configuration. In comparison, the *contiguous-signals* condition was constructed with patches containing the same direction arranged together to create larger regions of common motion. In this case, both local and global directions were spatially segregated to give the appearance of distinct, non-overlapping islands defined by direction. If the restricted capacity of transparent-motion detection arises from the superimposition of multiple global directions, this signal arrangement should allow an increased capacity. Importantly, these spatially segregated conditions also allow determination of the capacity of the global-motion stage to represent multiple non-overlapping directions. If the previously observed three-direction limit reflects a global-motion restriction, no more than three directions should be detected, regardless of the stimulus specifications.

Methods

Observers

Three observers took part in the first two experiments: one of the authors (JG) and two naive observers (CA and NB). All had normal or corrected-to-normal vision.

Apparatus

Stimuli were generated using a Cambridge Research Systems VSG 2/5 in a host PC and displayed on a Sony Trinitron 19″ monitor with a resolution of 1024 × 768 pixels and a refresh rate of 100 Hz (though stimuli were updated at 25 Hz, as described below). From a viewing distance of 1 m, the physical extent of the monitor subtended 21.3 × 16.2°. Stimuli were viewed binocularly in a dark room, with head movements restricted by a chin rest. Observers initiated each block of trials and responded

via the mouse buttons. The same apparatus was used for all three experiments.

Stimuli

Random-dot stimuli were presented within a square aperture, 12.8° to a side, with invisible boundaries. The background was set to mean luminance (47 cd/m^2), with a $0.5 \times 0.5°$ black fixation cross provided to minimize eye movements. The total aperture always contained 720 dots, each defined by a luminance increment of 30% Weber contrast with a diameter of 0.06°. This gave a dot density of 4.3 dots/deg^2, which has a low probability of local pooling (Qian et al., 1994). Each frame was presented for 40 ms, with dots displaced by 0.25° between frames. In conjunction with the low dot density, this step size gave a low probability of false correspondence matches (Williams & Sekuler, 1984) and is below d_{max} thresholds for transparent motion (Snowden, 1989). This also allowed the accurate displacement of dots in a large range of directions and produced a dot speed of 6.25°/s, close to the median speed preference for MT/V5 cells (Lagae, Raiguel, & Orban, 1993).

For transparent-motion stimuli, dots with each signal direction were dispersed throughout the entire stimulus, with an equal proportion of the total dots moving in each direction. Dots moved continuously for the entire stimulus duration to avoid the interference that occurs with rapid changes in direction (Watamaniuk, Flinn, & Stohr, 2003), with dots that exceeded the aperture boundary wrapped to the opposite side. For the two spatially segregated conditions, the total stimulus region was divided into 16 square patches in a 4×4 arrangement, each 3.2° to a side and without gaps. Each patch contained 45 dots moving in the same direction, with dots that moved beyond patch

boundaries wrapped within the same patch. Dot wrapping within patches was maintained in the contiguous-signals condition to ensure that the trajectory length of individual dots was not a cue to the signal number (due to the decreased size of signal regions with an increase in the number of directions). This dot wrapping is unlikely to have added significant noise to the contiguous-signals condition, as the low dot density and brief presentation times meant that the boundaries between patches sharing a common direction were not highly visible.

With only a single direction, all of the patches in these spatially segregated conditions moved with the same direction. For higher signal numbers in the interleaved-signals condition, each signal was dispersed throughout the entire aperture by requiring that adjacent patches contained distinct directions. With two signals, this gave the appearance of a checkerboard defined by motion. For each signal number above two, 16 patch configurations were possible, making it difficult to perform the task based on recognition of a given pattern. In the contiguous-signals condition, patches with the same direction were adjacent to one another, forming large regions of common motion. Patches with shared directions were grouped into irregular shapes to avoid the entire display being divisible into simple geometric patterns (such as alternating rows of common motion). Sixteen signal configurations were constructed for each signal number, with four examples depicted for each in Figure 2. The full sixteen configurations were produced using four rotations of those depicted. In both spatially segregated conditions, the total number of signals determined the number of patches moving in a given direction. With either two or four directions, an equal proportion of patches moved in each direction. Other signal numbers required an uneven distribution—for instance, three directions required that
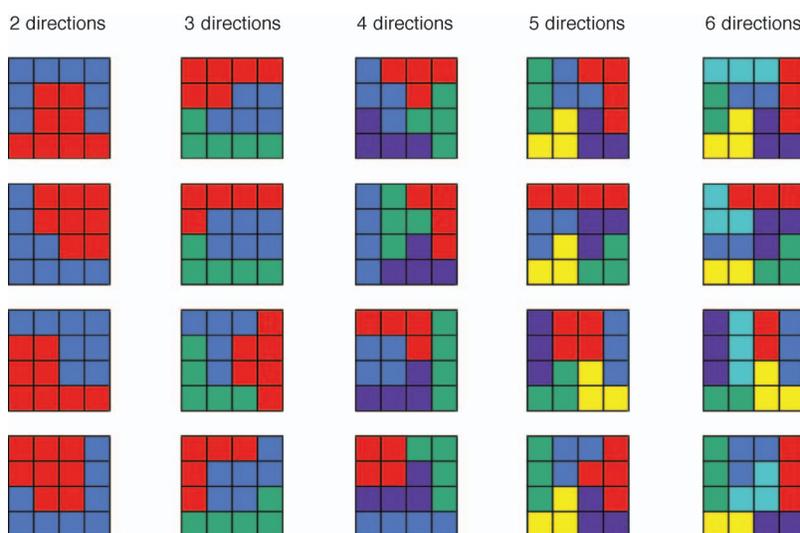
Figure 2. A depiction of the contiguous-signal regions stimuli with more than one direction. Four arrangements are shown for each number of directions, with the full 16 configurations produced using four rotations of each pattern. Each color represents a distinct direction that was randomly determined on each trial, as described in the text.

two were distributed across five patches each with the remaining direction covering six patches. No noise dots were present in this experiment.

Procedure

As in our previous studies (Edwards & Greenwood, 2005; Greenwood & Edwards, 2006a, 2006b), a 2AFC procedure was used. Each trial contained two stimulus intervals presented sequentially for 200 ms each (five frames) and separated by a 500-ms inter-stimulus interval. Comparisons were always between n and $n + 1$ signal directions, with five possible comparisons: 1 vs. 2, 2 vs. 3, 3 vs. 4, 4 vs. 5, and 5 vs. 6. The presentation order of stimulus intervals was randomized, with observers required to indicate the interval containing the greater number of signals. For each trial, directions were chosen randomly from a rectangular distribution covering 0–360°, with the constraint that each be separated by a minimum of 45° to ensure suprathreshold angular separations (Edwards & Nishida, 1999; Greenwood & Edwards, 2007a; Smith, Curran, & Braddick, 1999). Randomized directions ensured that observers could not perform the task by detecting the presence or absence of a single direction. This also minimized the occurrence of patterns such as motion parallax (with opposing directions creating a sense of depth), as well as the buildup of direction-specific adaptation (e.g., Raymond, 1993). Thus, when paired with the brief stimulus duration, this task ensures simultaneous detection of all signals within at least one of the intervals (Braddick et al., 2002; Edwards & Greenwood, 2005). Patch configurations for the spatially segregated trials were also selected randomly for each trial. A block of trials contained ten of each n vs. $n + 1$ comparison presented in a random order to make fifty trials per block. Ten blocks were run for each condition in a random order, with the final responses converted to percent-correct scores.

Results and discussion

For each condition, the mean percent-correct scores and standard error are plotted in Figure 3, as a function of the n vs. $n + 1$ signal comparisons. Chance-level performance corresponds to 50% correct. With transparent-motion stimuli, 1 vs. 2 and 2 vs. 3 comparisons were both performed with a high level of accuracy, while 3 vs. 4 and higher comparisons dropped to chance. Consistent with our prior studies, this shows that two directions could be detected and discriminated from three, though the poor performance in 3 vs. 4 comparisons demonstrates that three directions were not detected (Edwards & Greenwood, 2005; Greenwood & Edwards, 2006a, 2006b). This response pattern was also found in the interleaved-signals condition, despite each local patch containing only a single direction. In contrast, when spatially segregated signals were arranged in the
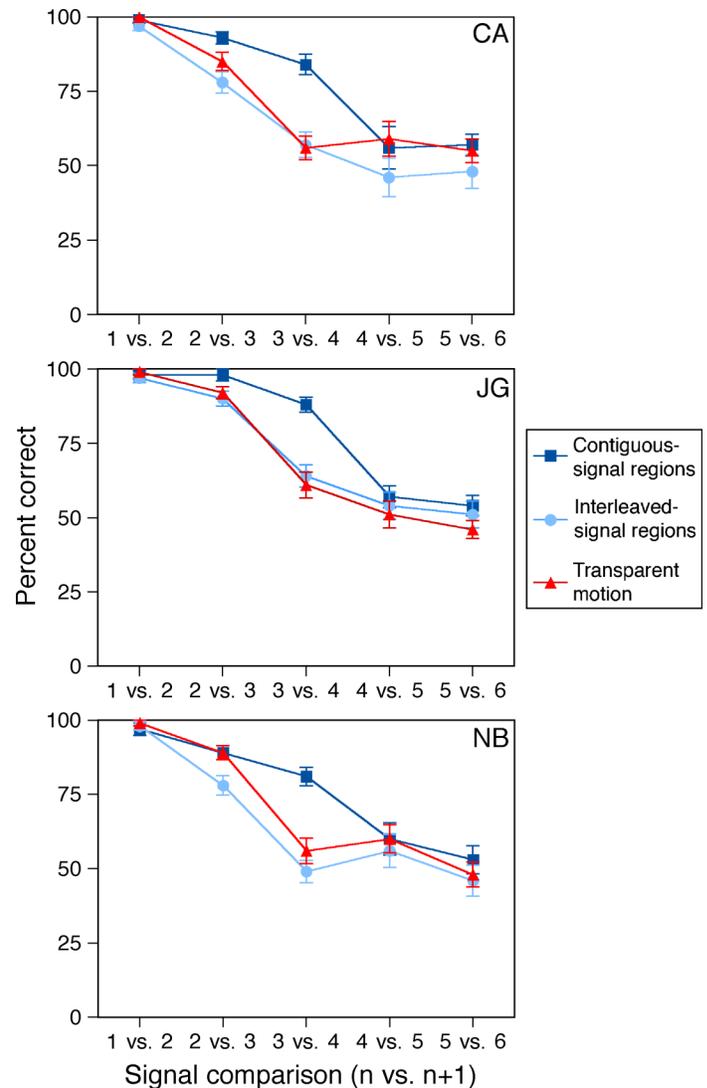
Figure 3. Mean percent-correct scores as a function of the n vs. $n + 1$ signal comparisons. Each data point is the mean of 100 trials; error bars represent 1 *SEM*. Results with transparent-motion stimuli are presented as red triangles, interleaved-signal conditions as light blue circles, and contiguous-signal regions as dark blue squares.

contiguous-signals condition, performance on 3 vs. 4 comparisons rose from chance to between 80% and 90% correct. Thus, observers were able to detect three directions and discriminate them from four, though the chance-level performance with 4 vs. 5 comparisons indicates that four directions were not detected.

One problem with increasing the number of signals in the spatially segregated conditions is the resulting decrease in the number of patches carrying each signal. The failure of observers to detect four directions may thus relate more to either the spatial region devoted to each direction, or the number of dots carrying each direction, than the number of global directions *per se*. To investigate the role of signal-region size and dot number, a control condition was run with each signal restricted to three patches. Thus, two-signal

intervals contained six signal apertures, with nine signal apertures for three-signal intervals, and so on. Remaining apertures contained random-noise dots moving in continuous trajectories, with directions selected from a 360° rectangular distribution. The size of these signal regions was equivalent to those in the five-direction stimuli above, with identical signal arrangements used. Noise apertures were selected at random, as required for each signal number. If the inability to detect five signals resulted from the reduction in signal-region size (or the number of signal dots), a similar reduction should impair all signal comparisons to some degree. Only observer JG completed this condition, with 2 vs. 3 and 3 vs. 4 comparisons both performed at 83% correct, before performance again dropped to chance levels for the 4 vs. 5 comparisons. This demonstrates that the failure to detect more than three directions in this condition related more to the number of directions present than to the size of each signal region or the number of signal dots. There is, of course, likely to be a lower limit on this required signal-region size. We simply demonstrate here that this is not a significant constraint on the three-direction capacity observed with these stimuli.

The pattern of performance obtained with contiguous-signal regions mirrors the extended capacity obtained when transparent-motion signals are separated in either speed or depth (Greenwood & Edwards, 2006a, 2006b), suggesting that the capacity limit of three directions applies to the global-motion stage as a whole. This extended capacity did not result from the reduction of local-pooling operations, as indicated by the lower capacity with interleaved-signal regions. Rather, performance in the contiguous-signals condition suggests that global pooling could operate independently within each signal region. Because all dots within a given region moved in the same direction, independent signal-to-noise processing could elevate the intensity of each signal to as much as 100%, depending on the efficiency with which these pooling areas were fit to each region of common motion. As with our prior extensions of the transparent-motion capacity limit (Greenwood & Edwards, 2006a, 2006b), an intensity elevation would allow the detection of higher signal numbers. In contrast, the similarity between the transparent-motion and interleaved-signal conditions suggests that global signals were pooled across the entire stimulus display in both conditions. Thus, signal intensities in the interleaved-signals condition would be identical to those within transparent-motion stimuli, leading to a capacity limit of two (Edwards & Greenwood, 2005).

To examine whether these results could have arisen from variation in global pooling operations, signal-detection thresholds were examined with each stimulus configuration. If the interleaved-signal regions forced global pooling to occur across the entire stimulus, signal-detection thresholds in this condition should be similar to those observed with transparent-motion stimuli (Edwards & Greenwood, 2005), when calculated across the stimulus as a whole. An examination of signal-detection

thresholds with contiguous-signal regions also allows insight into the basis of these high thresholds. In particular, though transparent-motion stimuli have been shown to require intensities of 40% for each signal, thresholds for the detection of one direction within bidirectional transparent-motion displays are between 5% and 15% (Edwards & Nishida, 1999; Hibbard & Bradshaw, 1999). This suggests that the high thresholds found using our n vs. $n + 1$ task result from the requirement to detect two directions simultaneously. Were this the case, similarly high thresholds should be found for the contiguous-signals condition, though the relevant intensities are likely to be determined within each signal region, rather than across the stimulus as a whole. Costs associated with dividing attention across multiple signal directions should also produce further threshold elevation for the detection of three signal directions within contiguous-signal displays.

Experiment 2: Signal-detection thresholds for multiple directions

Signal-detection thresholds were determined using a modification of the 2AFC procedure employed in Experiment 1. For each condition, comparisons were fixed such that one interval in each trial contained a detectable signal number, while the other contained a number exceeding the capacity limit for that condition. Noise dots were added to each interval with a staircase procedure to determine the global-motion signal intensities required to perform each comparison.

Methods

Stimuli and procedure

Timing, aperture, and dot parameters were identical to those of Experiment 1 for each of the three conditions. Each threshold estimate was determined using one signal comparison, fixed at either n vs. $n + 1$ or n vs. $n + 2$. To determine thresholds for the detection of two directions in the transparent-motion and interleaved-signals conditions, one interval always contained two directions, with three in the other. Because three directions were detected with contiguous-signal regions, 2 vs. 4 comparisons were used to determine bidirectional thresholds and 3 vs. 4 comparisons used to determine thresholds for three contiguous-signal regions. As before, observers indicated which interval contained the highest number of directions.

To determine signal-detection thresholds, signal intensities were manipulated equivalently within both intervals. With transparent-motion stimuli, signal intensity was defined as the percentage of dots moving in a given signal direction. Intensities of 25%, for instance, meant that 25% of the total dots moved in each of the directions in both intervals, with the remaining 50% moving in noise

directions. Accordingly, noise dots were only added to the three-signal interval when intensities in the two-signal interval dropped below 33%. For the spatially segregated conditions, signal intensities were defined as the percentage of dots moving in the signal direction within each patch. Equal levels of noise were added to all patches within both intervals. This was particularly important in the contiguous-signals condition, as signal numbers above the capacity limit had a visible spatial structure in the absence of noise. The addition of noise thus ensured performance was based on detection of the directions present, rather than extraneous spatial cues. In all conditions, noise directions were selected randomly without replacement from a 360° rectangular distribution. Signal intensities began at their maximum value for each condition and were varied with a modified 3-down 1-up staircase procedure converging on 79% correct performance (Levitt, 1971). The step size for intensity changes began at 8% and was reduced after each reversal to reach 1% for the final reversals. Eight reversal points were collected, with thresholds taken as the mean of the last six.

Results and discussion

Scores in both experiments were screened for outliers, with additional staircases run when scores exceeded 2.5 standard deviations from the mean. As above, signal intensities within transparent-motion stimuli were calculated in terms of the percentage of dots moving with a given signal direction, while spatially segregated intensities were calculated as the percentage of signal dots within each patch. The resulting signal-detection thresholds are presented in Figure 4.

Thresholds for the detection of two transparent-motion signals occurred when 40% of the total dots moved in each signal direction. This replicates our earlier results (Edwards & Greenwood, 2005) and accounts for the capacity limit of two in this condition—three signals cannot ordinarily be presented at intensities above this threshold. In the interleaved-signals condition, the detection of two directions required 80% of the dots within each patch as signal. However, as discussed above, performance in this condition suggests that signals were pooled across the stimulus as a whole, as in transparent-motion stimuli. When signal intensities are calculated in the same way as transparent motion, by determining the percentage of total dots moving in a given signal direction, intensities of 40% were required in each direction to reach threshold. Were the global-motion stage pooling across the entire stimulus in this way, three signals would not reach these intensity levels, producing the observed two-signal capacity.

In the contiguous-signals condition, two directions could be detected with intensities between 40% and 55% in each patch. Thus, if signal intensities were calculated independently within each spatial region, these thresholds are
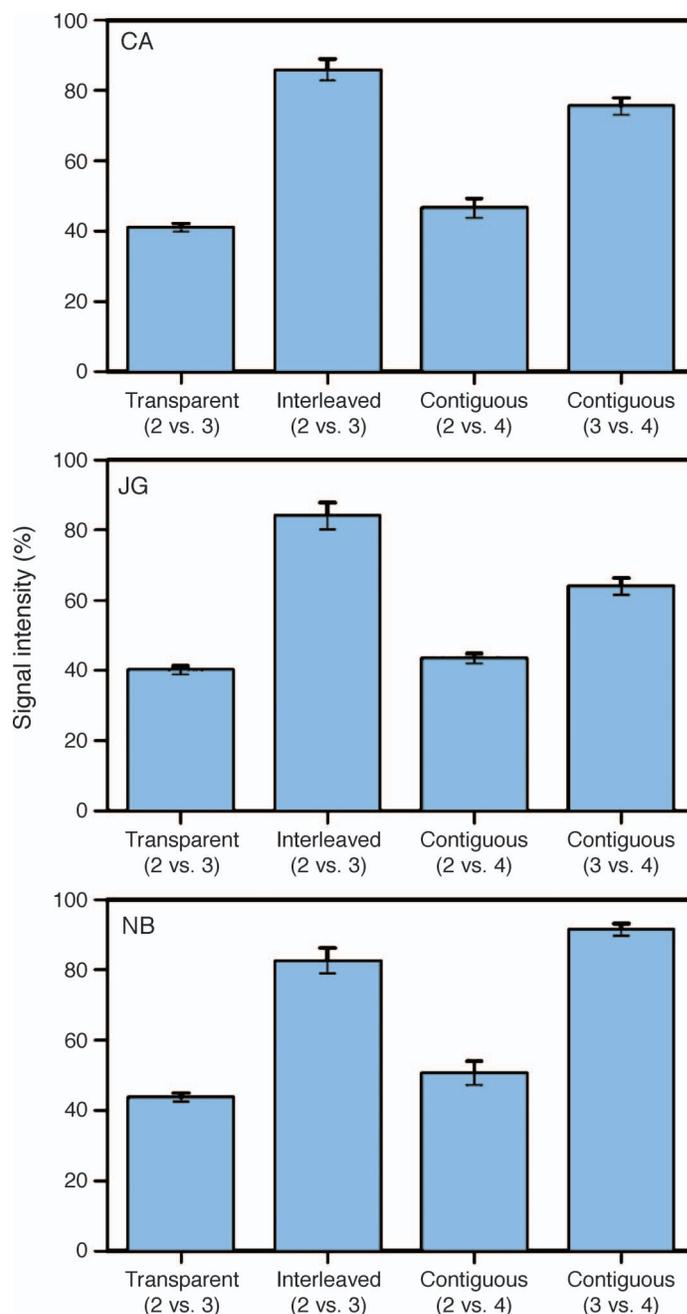
Figure 4. Thresholds for the detection of two directions in transparent, interleaved and contiguous signal arrangements, and for three directions with contiguous-signal regions. Transparent motion thresholds are expressed as the percentage of total dots moving in one of the signal directions. Interleaved and contiguous-signal thresholds are expressed as the percentage of dots within each patch that moved in the signal direction. Each data point represents the average of ten staircase estimates; error bars represent 1 *SEM*.

similar to those obtained with both transparent-motion and interleaved-signals stimuli. Thresholds rose for the detection of three signals, with intensities between 65% and 90% required to reach threshold. This suggests that the detection of higher signal numbers requires increasingly

high signal intensities. However, this elevation in three-direction thresholds could also have arisen from the decrease in signal-region size (or the total number of dots moving in each direction) that occurs with increasing signal number. To rule this out, thresholds for the detection of two contiguous-signal regions were obtained using 2 vs. 4 comparisons with each signal restricted to five apertures, as in the three-signal intervals. Remaining apertures were filled with noise dots. Only observer JG was tested, with thresholds of 40% again obtained when intensities were calculated within each patch. Thus, signal-region size had a negligible effect on performance in this condition.[1] Were the global-motion stage pooling across the entire stimulus region in this condition, the addition of pure noise patches should have produced a substantial elevation of thresholds. This result thus offers further evidence that the spatial extent of global pooling can be dynamically altered depending on stimulus properties.

Our results indicate that the global-motion system was able to flexibly pool the signal directions based on their spatial arrangement within stimuli. As the interleaved-signals condition required integration across the entire stimulus, these stimuli were treated in the same fashion as transparent motion. In contrast, the global-motion system was able to selectively pool the directions within distinct spatial regions in the contiguous-signals condition. Though thresholds were similar to those of transparent-motion stimuli, selective pooling within each region would lead the intensity of each signal to be unaffected by signal directions in other regions. The resultant increase in signal intensities could allow the observed ability to see up to three directions. However, were pooling within one signal region to overlap slightly with other regions, the effective intensity within each would be lowered. This may have caused both the elevation in thresholds for three directions and the capacity limit of three for this condition. We thus sought to ensure that the failure to detect four directions was not the result of imperfect pooling within each region.

Experiment 3: Capacity limits for contiguous-signal regions with speed differences

If imperfect pooling was behind the restricted capacity of three in the contiguous-signals condition, an elevation of intensities should allow the detection of more than three directions. As with our prior extension of the transparent-motion capacity limit (Greenwood & Edwards, 2006a), one means to increasing the effective intensity of global-motion signals is by distributing processing among independent global-motion channels selective for distinct speeds (Edwards et al., 1998; van Boxtel & Erkelens, 2006). If global pooling within each signal region is ordinarily imperfect, the independence of these global-motion channels means that signal regions selectively processed within one channel will no longer reduce the intensity of signals detected within other channels. The resulting increase in signal intensities should then allow an increase in the capacity limit. Alternately, if the limit of three arises from a restriction on the number of global directions that can be detected simultaneously, performance should be unchanged by this manipulation.

Methods

Observers

Two observers participated in this experiment: one of the authors (JG) and a naive observer (BR). Both had normal or corrected-to-normal vision.

Stimuli and procedure

Observers were presented with four versions of the contiguous-signals stimuli: two with all dots moving at the same speed and two with mixed speeds. Same-speed stimuli were presented with an arrangement identical to that of Experiment 1, though all dots moved at either slow or fast speeds to examine performance with each in isolation. Consistent with the speeds used previously to drive independent global-motion channels (Edwards et al., 1998; Greenwood & Edwards, 2006a), slow dots took a step of 0.05° per frame to give a speed of 1.25°/s, while fast dots took steps of 0.39° to give 9.75°/s. These conditions were run in distinct blocks of trials, again with five signal comparisons each to make 50 trials per block.

Two mixed-speed conditions were also examined, where half the patches within each display moved at each of the two speeds. This ensured that the proportion of patches with a given speed was not a cue to the number of signal regions. With even signal numbers, an equal number of signal directions were presented at each speed. For odd signal numbers, some variation in signal-region size was required. For instance, with three directions, two would contain one speed, each consisting of four patches, while the remaining eight patches would contain a third direction at a distinct speed. As a result, two versions of each mixed-speed signal comparison were constructed: one with a majority of directions moving at the slow speed (*majority slow*) and one with a majority of fast-moving directions (*majority fast*). These conditions were kept separate for scoring but were interspersed within a given block to prevent observers attending to a single speed. To reduce the number of trials within blocks, 1 vs. 2 comparisons were omitted to leave eight possible signal comparisons and 80 trials per block. Remaining stimulus and procedural parameters were identical to those of

Experiment 1, with ten repetitions performed for each condition.

Results and discussion

For each of the four conditions, mean percent-correct scores are presented in Figure 5 as a function of the *n* vs. *n* + 1 comparisons. Both same-speed conditions show the same pattern of performance observed with contiguous-signal regions in Experiment 1. That is, a high level of performance was possible for comparisons up to and including 3 vs. 4, with performance dropping to chance thereafter. Though the high-speed condition was slightly more difficult than the low-speed condition, three directions were clearly detected in both cases. Performance in the mixed-speed conditions has a similar pattern—both observers could perform comparisons between three and four directions but failed to reliably discriminate between intervals containing four and five. Thus, speed differences did not elevate the number of contiguous-signal regions that can be detected simultaneously, demonstrating that imperfect global pooling is unlikely to have been a major factor in this capacity limit.
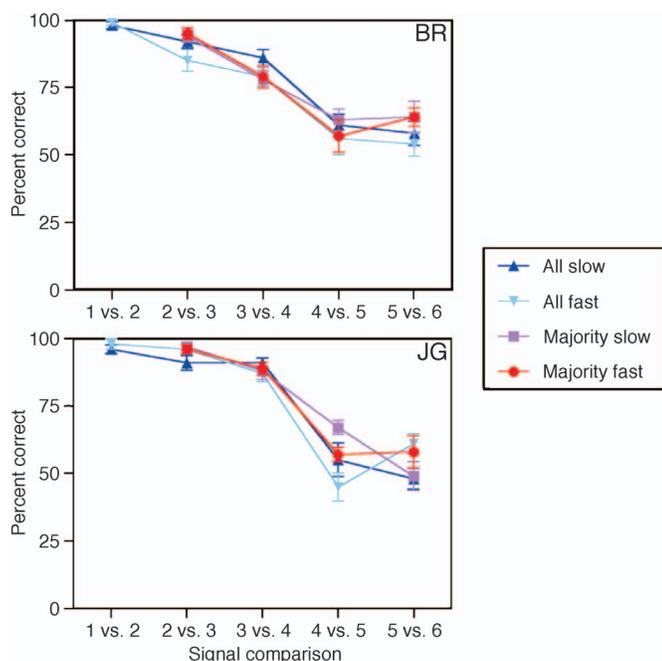
Figure 5. Mean percent-correct scores as a function of the *n* vs. *n* + 1 signal comparisons in four versions of the contiguous-signals stimuli. In the same speed conditions, dots moved with either the slow speed (*all slow,* dark blue triangles) or fast speed (*all fast,* light blue inverted triangles). Mixed-speed conditions consisted of either more slow than fast signal directions (*majority slow,* purple squares), or vice versa (*majority fast,* red circles). Each data point is the mean of 100 trials; error bars represent 1 *SEM.*

General discussion

Results from the present study provide further evidence for the existence of two capacity limits on the detection of multiple global directions. When all directions are present within the same spatial region, as with transparent motion (Edwards & Greenwood, 2005; Mulligan, 1992) and the interleaved-signals condition of the present study, no more than two global-motion signals defined by direction can be detected simultaneously. However, up to three directions can be detected when distributed between independent global-motion detectors. This extended capacity limit has been observed using transparent-motion signals with appropriately distinct values of speed and depth (Greenwood & Edwards, 2006a, 2006b), as well as in the present study with the separation of directions into spatially distinct contiguous-signal regions. The addition of speed differences to these regions did not allow the detection of more directions, suggesting that this three-signal capacity reflects a strict limit. Importantly, these results demonstrate that the capacity limit of three is not restricted to transparent-motion detection. Rather, it represents an upper limit for global-motion processing in general.

We have also replicated the high detection thresholds that underlie the two-signal transparent-motion capacity (Edwards & Greenwood, 2005) and extended this to the detection of spatially segregated directions. Though signal intensities were calculated differently in the two spatially segregated conditions, as dictated by performance, both required intensities around 40% for each direction, well above that required for the detection of a single direction within transparent-motion stimuli (Edwards & Nishida, 1999; Hibbard & Bradshaw, 1999). Thus, regardless of their spatial arrangement, higher thresholds are required for the simultaneous representation of two global directions than for unidirectional detection. This is consistent with the equivalent levels of error in angular separation judgements for spatially segregated and transparent-motion stimuli, compared with unidirectional judgements made with respect to a reference (Braddick et al., 2002). However, these stimuli do differ in some respects, with angular separation judgements for transparent-motion signals requiring longer presentation times than equivalent judgments for two spatially segregated directions (Curran et al., 2007). This discrepancy may reflect the presentation of spatially segregated signals at their maximum intensities within these studies. Independent global pooling within each signal region would produce higher intensities in the spatially segregated regions than in the transparent-motion comparison, which could alter the required temporal integration without an effect on the precision of direction judgements. An important implication of the present study is that the region of spatial pooling must be carefully considered for each stimulus type to determine whether equivalent levels of performance are possible.

The equivalence between thresholds for detection of two directions in both transparent and spatially segregated stimuli is likely to reflect the attentional demands imposed by the simultaneous representation of multiple directions. Accordingly, thresholds continued to rise for the detection of three contiguous-signal regions. This rising cost may reflect the inverse of the facilitation observed for selective attention: given the increased MT/V5 activity with selective attention to a specific direction (O'Craven, Rosen, Kwong, Treisman, & Savoy, 1997; Treue & Martínez Trujillo, 1999; Treue & Maunsell, 1996), and the resultant increase in the magnitude of adaptation (Alais & Blake, 1999; Lankheet & Verstraten, 1995), divided attention should produce a corresponding reduction in global-motion activity. If the detection of multiple directions relies on the presence of multiple activity peaks, as observed for transparent-motion detection (Greenwood & Edwards, 2007b), reduced peak height would impair the detection of these signal directions and produce the observed patterns of threshold elevation.[2] Alternately, rather than affecting the height of peak activity, divided attention could raise the level of peak activity that is required to detect each of the signal directions present. Were this the case, dependence upon a threshold level of peak activity should be evident in the read-out algorithms utilized to detect these signal directions. Given the increasing cost of divided attention, the maximum three-signal capacity could then result from a complete elevation of thresholds for signal numbers above three.

Though the equivalence of two-direction thresholds in spatially segregated and transparent-motion displays is consistent with the operation of divided attention, these thresholds are unlikely to be equivalent for three directions. While thresholds for the detection of three contiguous-signal regions exceeded 60%, these intensities could be reached through independent global pooling within each region. However, equivalent thresholds would not have allowed the previously observed detection of three directions using additional differences in speed and depth (Greenwood & Edwards, 2006a, 2006b). Though three directions were seen in these prior experiments, two signals would have been at 50% intensity within the same population of detectors, and thus below the contiguous-signals threshold. It is possible that the high thresholds for three directions might be the result of imperfect pooling within each region, particularly given the slight elevation of thresholds for two contiguous-signal regions over those in the transparent and interleaved conditions. However, the addition of noise patches had little effect on these thresholds, suggesting that inefficient pooling operations were not a major factor in determining performance. This may simply reflect differences in the difficulty of detecting these distinct stimulus types. Nonetheless, although results on the whole appear consistent with an attentional basis for these processing costs, we should be cautious in ascribing all of these costs to the difficulties associated with divided attention.

Given the equivalent thresholds for detection of two directions with each of the three signal arrangements, the distinct capacity limits must have arisen from variation in the intensity of component signals. This is likely to reflect variation in global pooling processes as a result of the distinct spatial arrangement of the global directions. Performance with interleaved-signal regions suggested that pooling occurred across the entire stimulus, as would be required to represent each direction in full. As with transparent-motion stimuli, higher signal numbers would then have increasingly lower intensities, yielding sub-threshold intensities for more than two directions. Similar pooling operations are apparent in a recent computational model, where bidirectional transparent motion and inter-leaved-signal regions both produced two peaks in global-motion population activity (Durant et al., 2006).[3] In contrast, the higher capacity obtained with contiguous-signal regions suggests that the directional information within each region was selectively pooled. As the selection of common regions of motion has been argued to produce effective signal-to-noise pooling within the global-motion stage (Nowlan & Sejnowski, 1994, 1995), this selection may represent the same process that gives rise to the independent pooling observed in the present study. As in our prior extensions of the transparent-motion capacity limit (Greenwood & Edwards, 2006a, 2006b), these pooling operations would elevate the effective intensity of three directions above the required thresholds. This flexibility is consistent with recent observations that distinct pooling algorithms are used by the global-motion stage based on the precise directional content of moving stimuli. That is, while locally ambiguous elements are pooled according to an intersection-of-constraints rule, vector averaging is applied to locally unambiguous signals (Nishida, Amano, Edwards, & Badcock, 2006, 2007). Our present results suggest that the spatial region of global pooling can also change in a stimulus-dependent manner.

Consistent with the potential role for divided attention, the observed three-signal capacity falls within the lower range of reported capacities for visual attention and working memory (Cowan, 2001). Of these two processes, attention is more likely to have restricted performance than working memory, as observers need only extract the number of directions in each interval, rather than retaining the precise directions. Though an attentional capacity of four is typically found for the simultaneous detection of spatially distinct objects such as static dots (Atkinson et al., 1976), the enumeration of multiple groups of dots defined by features such as color and orientation is significantly poorer. Reaction times for the enumeration of spatially intermingled dot groups defined by color were markedly increased with more than two groups, while up to three could be detected simultaneously if the colored dots were grouped into common regions. However, both conditions were less efficient than the detection of individual dots (Watson, Maylor, & Bruce, 2005). That is, while up to four distinct objects with precise locations

may be detected simultaneously, the distribution of attention across multiple feature-defined regions gives much lower capacities that are strongly affected by the distribution of local elements across space. This also suggests that flexible pooling operations are not restricted to the domain of motion.

Precise spatial localization is also important for multiple object tracking tasks, with tracking of spatially distinct objects again yielding a four-item capacity (Pylyshyn & Storm, 1988). However, this capacity drops when precise localization is impeded through an increase in dot density (Intriligator & Cavanagh, 2001). In addition, tracking fails completely when objects pour (like sand) or stretch (like rubber) between points, due to the ambiguity in their spatial location (VanMarle & Scholl, 2003). Even when spatially extended objects are tracked, attention appears focused on specific points such as the center of moving line elements, rather than being distributed across larger regions (Alvarez & Scholl, 2005). This reliance on precise positional information may relate to the increasing error in the perceived direction of these objects as the number of tracked objects increases (Tripathy & Barrett, 2004). Though this directional information may be sufficient to update the position of tracked objects, increasing error of the same magnitude may be insufficient to segment global regions defined by direction, leading to the global capacity of three observed in the present study.

Another important difference between the present study and multiple object tracking tasks is the use of distinct form elements. Tracking within multiple-object tasks relies on target and distractor items being easily segmented into distinct objects. Distinct parts of objects cannot be separately tracked, with a pairing of targets and distractors on opposite ends of a common line object producing a dramatic impairment in performance (Scholl, Pylyshyn, & Feldman, 2001). Similarly, though the enumeration of grouped items defined by color is poorer than that of spatially localized dots (Watson et al., 2005), clusters of dots that define form elements can be tracked within MOT tasks with an equal efficiency to that of discrete form elements (Trick & Enns, 1997). This may reflect an interaction between motion-selective cortical regions and form-selective areas within the ventral stream, given that thresholds for the detection of global-motion signals are also facilitated through the use of form-like configurations of signal dots (Edwards, 2007). Though our contiguous-signal regions produced irregular form arrays, organizing them into consistent geometric forms could give a further boost in performance, though it would be important to ensure that coherent patterns of geometric forms did not facilitate the sequential detection of these regions.

The sequential detection of moving objects is particularly difficult to rule out in multiple object tracking tasks, given the long tracking durations typically employed. Accordingly, tracking performance improves with increasing presentation times, particularly when 4 or more objects must be tracked, suggesting the involvement of a sequential mechanism (Oksama & Hyönä, 2004). Serial updating of these object positions may also explain some of the highest capacity limits reported, such as the tracking of 6–7 objects when distributed across distinct depth planes (Viswanathan & Mingolla, 2002). Though studies of subitization demonstrate that up to four static objects may be simultaneously detected, results from the present study question whether the direction of these four objects could also be detected simultaneously. Rather, it is possible that the smaller number of simultaneously available directions could be used to sequentially update the position of either individual targets or small subsets of the targets. Without careful examination of the simultaneity of this processing it is hard to rule out this sequential mechanism.

Finally, the capacity limits observed in the present study place several constraints on the mechanisms used to extract a small number of perceived directions from the broadly distributed population activity within MT/V5 (Pouget et al., 2000; Webb, Ledgeway, & McGraw, 2007). A range of read-out algorithms have been proposed for this purpose, including winner-take-all (Salzman & Newsome, 1994), vector averaging (Groh, Born, & Newsome, 1997; Nichols & Newsome, 2002), and maximum-likelihood estimation (Deneve, Latham, & Pouget, 1999; Seung & Sompolinsky, 1993). However, none of these algorithms can extract more than a single direction, making them unsuitable for the detection of bidirectional transparent motion. This has led many to propose that the entire shape of global-motion population activity may be utilized in these operations (Pouget et al., 2000; Treue, Hol, & Rauber, 2000; Zemel, Dayan, & Pouget, 1998), with multiple peaks in population activity likely to be an important requirement (Greenwood & Edwards, 2007b). The signal-to-noise basis of the transparent-motion limit suggests that three signals cannot ordinarily be presented with peaks of sufficient magnitude to allow their extraction. However, performance with transparent-motion signals separated by speed and depth (Greenwood & Edwards, 2006a, 2006b), as well as multiple spatially distinct regions defined by motion (in the present study) suggests that up to three peak directions can be determined from multiple independent global-motion populations. It may be the failure of these peak-detection operations with four signal directions that causes the capacity limits observed in the present study.

Conclusions

In contrast to the two-signal capacity for the detection of transparent motion defined by direction differences (Edwards & Greenwood, 2005; Mulligan, 1992), results from the present study demonstrate that up to three directions can be detected at the same time when

separated into distinct spatial regions. This extended capacity mirrors that obtained with transparent-motion signals differing in speed and depth (Greenwood & Edwards, 2006a, 2006b) and is likely to reflect independent global pooling within each spatial region, in comparison to the stimulus-wide pooling evident in both the capacity limits and signal-detection thresholds for transparent motion and interleaved-signal regions. As this capacity is insensitive to further signal intensity manipulations, it appears to represent a strict attentional limit on the detection of multiple directions and thus presents an important restriction on the read-out algorithms used to interpret global-motion activity. While this could reflect limitations specific to motion detection, similar 2–3 item capacities have been observed in subitizing tasks with interleaved or grouped arrays of colored dots (Watson et al., 2005). A capacity of three may thus reflect the maximum number of feature-defined peaks in activity that can be determined from a given population of neurons, in comparison to the higher capacities available with the use of precisely localized form elements (Atkinson et al., 1976). Similarly, the higher capacities observed in multiple object tracking may reflect a reliance on this positional information, or facilitation from cortical regions selective for form information, though it is important that the simultaneous detection of these directions be established, as in the present study.

Footnotes

[1]As in Experiment 1, there is likely to be a lower limit on the required signal-region size for this selective pooling to occur. In particular, the interleaved-signals region condition demonstrates that small patches of each signal direction may provide stronger cues to integration than to segmentation. This interplay between integration and segmentation is seen in many aspects of global-motion processing (Braddick, 1993).

[2]Though there was no evidence for this activity reduction in a recent study using adaptation, where threshold elevation for transparency was equivalent to that of 50% coherent unidirectional motion (Greenwood & Edwards, 2007b), the long durations required for adaptation would have minimized any difference between these conditions by allowing attention to be directed selectively to each of the transparent-motion signals over time.

[3]This strong equivalence is somewhat surprising given the patchwork appearance of the interleaved signals, compared with the multiple overlapping planes seen for transparent motion. The perceptual distinction between these stimuli must arise from processes other than global-motion pooling. In particular, temporal variation within each local region may play a key role, as each local region will be exposed to multiple directions over time in transparent-motion displays, compared with spatially segregated stimuli in which the local directions remain fixed (Durant et al., 2006), as in the interleaved-signals condition herein.

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