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An extension of the transparent-motion detection limit using speed-tuned global-motion systems

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Abstract

When transparent motion is defined purely by direction differences, no more than two signal directions can be detected simultaneously. This limit appears to occur because higher signal intensities are required to detect transparent motion compared with uni-directional motion (Edwards, M., & Greenwood, J. A. (2005). The perception of motion transparency: A signal-to-noise limit. *Vision Research, 45,* 1877–1884). Increasing the effective signal intensities should therefore increase the number of signals that can be detected. We achieved this by adding speed differences, dividing transparent-motion signals between two speed-tuned global-motion systems. When some signals moved at appropriate low speeds and others at high speeds, up to three signals were detected. This is consistent, at least in part, with the signal-to-noise processing basis of the transparency limit. Differences in contrast polarity were also used to assess whether the limit could be extended using stimulus features without independent global-motion systems. A modest improvement in performance was obtained, suggesting that there may be multiple routes to extending the transparent-motion limit.

Keywords: Motion perception; Transparency; Global motion; Speed processing

1. Introduction

Transparent motion occurs when multiple objects move through the same region of the visual field without total occlusion. Naturally occurring examples can be seen when an animal moves behind foliage blown by wind, or when rain streams down the window of a moving vehicle. These conditions can be simulated with random-dot stimuli where two or more groups of dots move in different directions within the same aperture (e.g., Clarke, 1977). When transparency is defined purely by direction, observers are unable to detect more than two transparent-motion signal directions simultaneously (Mulligan, 1992; Edwards & Greenwood, 2005). In the present study, we investigate whether this limit can be extended to allow the detection of a higher number of transparent-motion signals.

1.1. The transparent-motion limit

To examine the perception of transparent motion, it is important to distinguish between simultaneous and sequential detection of the signal directions. Previous experiments have ensured simultaneous detection through the use of brief presentation times and tasks that require detection of all signals present. In contrast, the signals could be detected in sequence, which may be more comparable to uni-directional detection for each signal (Braddick, Wishart, & Curran, 2002). To examine the limitations of transparent-motion detection, it is therefore important to ensure simultaneous detection of the signals.

When simultaneous detection is required, observers are unable to detect more than two transparent-motion

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signals with direction differences as the sole cue to transparency (Mulligan, 1992). We have recently linked this limitation with signal-to-noise detection thresholds for transparent motion, which are three times higher than uni-directional thresholds in a comparable task (Edwards & Greenwood, 2005). This provides a basis for the transparency limit because increasing the number of transparent-motion signals decreases the maximum signal intensities. Throughout this paper, we will use *signal intensity* to refer to the proportion of dots in random-dot stimuli moving in one signal direction. For the detection of this signal, dots moving in other directions (either randomly or within other signals) will act as noise. So, when direction is the sole basis for transparency, two signals can at most be presented at intensities of 50% each. The addition of a third direction reduces signal intensities to 33%. To detect bi-directional transparency, observers in our previous study required signal intensities of 40% for each of the two signals. If detection thresholds for three signals are at least as high as those for two, it would therefore be impossible to present three signals at the required intensities within these stimuli.

1.2. Extending the transparent-motion limit

This dependence on the signal-to-noise ratio in transparent-motion stimuli is consistent with the notion that the global-motion stage is involved in setting the transparency limit (Britten, Shadlen, Newsome, & Movshon, 1993; Rees, Friston, & Koch, 2000). Within the visual system, this is the first point at which transparent motion can be represented (e.g., Snowden, Treue, Erickson, & Andersen, 1991; Qian, Andersen, & Adelson, 1994).

If the transparent-motion limit of two is the result of global-motion signal-to-noise processing, increasing the signal intensities within our stimuli should allow an extension of the limit. One means to increasing signal intensity is to distribute the transparent-motion signals between independent speed-tuned systems (Edwards, Badcock, & Smith, 1998; Snowden, 1990; Verstraten, van der Smagt, & van de Grind, 1998). In particular, Edwards et al. (1998) found that thresholds for the detection of a low-speed signal were elevated when additional low-speed noise dots were added to the stimulus, but not when additional high-speed noise dots were added. The inverse was found for high-speed detection thresholds. This suggests the existence of at least two global-motion systems: one tuned to low speeds, the other to higher speeds. Signal-to-noise processing in one system is independent of the other.

It follows that transparent-motion signals detected by one of these global-motion systems would have no effect on signal-to-noise processing in the other system. By presenting transparent-motion signals at speeds specific to either of the two speed-tuned systems, we can thus increase the effective signal intensities in our stimuli. For instance, three low-speed signals would each have a signal intensity of 33%. If one of these signals moved at a high speed beyond the sensitivity of the low-speed system, its intensity would be at 100% within the high-speed system. The intensity of the two low-speed signals would then be increased to 50% each. If the transparency limit arises due to high signal-to-noise detection thresholds at the global-motion stage, this manipulation should allow the detection of more than two signals.

Three experiments were conducted to determine whether the transparent-motion limit can be extended. Experiment 1 established the appropriate speeds to be used for each participant. In Experiment 2, we then used these speeds in transparent-motion stimuli to assess whether the speed-tuned systems could allow the detection of more than two signals. Finally, in Experiment 3 we examined whether an extension of the transparent-motion limit could occur in the absence of independent global-motion systems, using differences in contrast polarity (Edwards & Badcock, 1994).

2. Experiment 1: Sensitivity of the speed-tuned systems

We first sought to find two speeds that would be processed independently by distinct speed-tuned global-motion systems. Because there is individual variation in the sensitivity ranges of these systems (Edwards et al., 1998), it was expected that the speeds required to obtain independent processing might vary between observers. A series of global-motion tasks was performed to select the appropriate speeds, using stimuli designed to be as similar as possible to the transparent-motion stimuli of Experiment 2.

2.1. Method

2.1.1. Observers

Three observers took part in the first two experiments: one of the authors (J.A.G.) and two naïve observers. All had normal or corrected-to-normal vision, with no history of any visual disorders.

2.1.2. Apparatus

Stimuli were displayed on a Clinton Monoray monitor with a refresh rate of 120 Hz, driven by a Cambridge Research Systems VSG 2/5 in a host Pentium computer. Stimuli were viewed from a distance of 1 m, with head movements restricted by a chin rest. Observers initiated each block of trials and responded to the trials via mouse buttons. The same apparatus was used for all three experiments.

2.1.3. Stimuli

Global-motion stimuli were presented within a circular aperture of 11.5° diameter. Either 60 or 120 circular dots were presented, each with a diameter of 0.14°. This gave a dot density of approximately 0.6 dots/deg^2 with 60 dots, or 1.2 dots/deg^2 with 120 dots. Both these values minimise the occurrence of motion correspondence errors (Williams & Sekuler, 1984). The luminance of the background was 82 cd/m^2. Dots were defined by a luminance increment, with a Michelson contrast of 20%. A $0.4 \times 0.4°$ black fixation cross was used to minimise eye movements.

The dots within each aperture were assigned as signal or noise at the beginning of each stimulus interval and moved in a continuous trajectory for the entire duration (*fixed-walk* motion). Dots that moved beyond the aperture boundary were re-plotted in the opposite half of the aperture, based on the direction of motion.

2.1.4. Procedure

A temporal two-alternative forced-choice (2AFC) procedure was used. The stimulus intervals within each trial were both present for 200 ms and consisted of four frames of motion, each present for 50 ms. One interval consisted solely of noise dots. The other contained a global-motion signal of varying intensity, with the remainder of the dots set as noise. Stimulus intervals were separated by a 1 s blank interval to minimise the effects of hysteresis (Williams, Phillips, & Sekuler, 1986). Observers were required to indicate which interval contained the global-motion signal. This is analogous to the n vs. $n+1$ comparisons used in our transparent-motion tasks, amounting to a 0 vs. 1 comparison.

Prior to each trial, the signal direction was chosen randomly from a rectangular distribution from 0 to 360°. Noise directions were selected randomly from the same distribution without replacement. Dots could move at one of two speeds, though the exact values varied between observers. The low speed was 0.9°/s for all observers, with a step size of 0.05° (2 pixels) per motion frame. For J.A.G., the high speed was 8.6°/s, a step size of 0.44° (19 pixels) per frame, while a high speed of 9.5°/s was required for M.F.C. and R.C.W., at a step size of 0.48° (21 pixels) per frame. These values were chosen during pilot testing as the minimum high speed that would be processed by the high-speed system independently of the low-speed system. This ensured the clarity of motion signals whilst still driving the two speed-tuned systems independently.

Six conditions were conducted. Three low-speed conditions assessed signal-to-noise detection thresholds with 60 low-speed dots, 120 low-speed dots, and a mixed-speed condition with 60 low-speed and 60 additional high-speed noise dots. In the latter, signal dots were drawn solely from the low-speed population. Likewise, thresholds were estimated with 60 high-speed dots, 120 high-speed dots, and a mixed-speed condition with 60 high-speed and 60 additional low-speed noise dots. Signal dots in the latter condition were always drawn from the high-speed population. If the selected speeds were processed independently, thresholds in mixed-speed conditions should be equivalent to thresholds with 60 dots in isolation, both of which should be lower than thresholds with 120 same-speed dots.

Thresholds were obtained with a modified staircase procedure, with each of the six conditions tested within distinct staircases. For each staircase, signal intensity began at 60 dots (out of 60 or 120 dots total, depending on condition) and was varied with a 3 down/1 up staircase converging on 79% correct performance. Eight reversal points were collected, with thresholds taken as the mean of the last six. Ten staircases were completed for each condition, interleaved randomly. Stimuli were viewed binocularly in a dark room, following approximately 5 min of dark adaptation. No feedback was given regarding performance during trials.

2.2. Results and discussion

All scores throughout this series of experiments were screened for outliers. If scores were outside 2.5 standard deviations from the mean, additional staircases were conducted. Fig. 1 displays the mean and standard error for the six conditions, separately for each observer. Low-speed (LS) conditions are shown left of the dividing line, with high-speed (HS) conditions on the right.

The expected pattern of results is present for each observer. Thresholds for conditions with 60 dots (LS 60 and HS 60) were between 15 and 20 dots. Adding 60 noise dots of the same speed (LS 120 and HS 120) raised thresholds to between 25 and 35 dots. In contrast, additional noise dots of a markedly different speed (LS mix and HS mix) had no effect on thresholds, which were the same as those with 60 dots in isolation. Because thresholds were equivalent for both speeds in isolation, and independence in the mixed-speed conditions could be demonstrated with either the low-speed or the high-speed as the target, these results cannot be accounted for by a single system with differential sensitivity to the two speeds. Rather, our results indicate that the speeds selected for each observer were processed independently by distinct global-motion systems.

It should be noted that thresholds were slightly higher than those typically seen in global-motion tasks (Braddick, 1995). This is most likely due to direction uncertainty arising from the randomised signal direction,

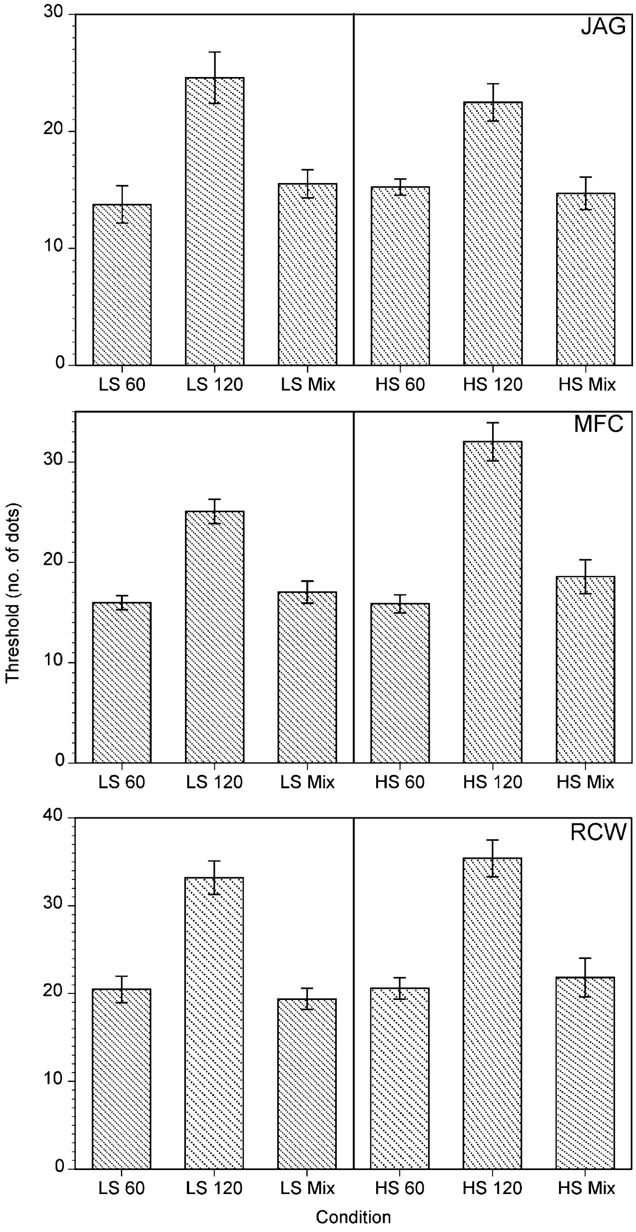

Fig. 1. Mean thresholds for global-motion signal detection, assessing the independence of the speed-tuned systems. Low-speed (LS) conditions are left of the dividing line, high-speed (HS) conditions are on the right. For each speed, thresholds were obtained with 60 and 120 dots. Mixed conditions had 60 dots of each speed, with target dots drawn from one speed only. Error bars represent 1 SEM.

which leads to an elevation in thresholds compared to conditions where the signal direction is known in advance (Ball & Sekuler, 1980).

3. Experiment 2: Transparent-motion detection with speed differences

We next sought to increase the signal intensities within transparent-motion stimuli by presenting signal directions at the speeds selected in Experiment 1. If the transparent-motion limit of two occurs primarily as a result of global-motion signal-to-noise processing, this increase in signal intensity should allow an extension of the limit. If the limit of two is applicable to each speed-tuned system, it may even be possible for observers to detect up to four transparent-motion signals.

3.1. Method

3.1.1. Procedure

The aperture configuration was the same as in Experiment 1, with 120 dots present. A temporal 2AFC procedure was used, as in our previous study (Edwards & Greenwood, 2005). In each trial, one stimulus interval contained n transparent-motion signals, with $n+1$ signals in the other. Presentation order was randomised. Between one and five signals were presented, making four potential comparisons: 1 vs. 2, 2 vs. 3, 3 vs. 4, or 4 vs. 5. Both intervals were presented for 200 ms, separated by a 1 s blank interval. Observers were required to indicate which contained the greater number of signals. Brief presentation times such as this restrict performance to that based on simultaneous detection of transparent-motion signals, particularly when coupled with tasks that require detection of all signals present (Braddick et al., 2002; Edwards & Greenwood, 2005).

The direction of each signal group was determined randomly, with the constraint that signal directions had an angular difference of at least 45°. This constraint ensured maximum visibility of each signal, as observers have difficulty in detecting separations lower than this when direction is the sole basis for transparency (Edwards & Nishida, 1999; Smith, Curran, & Braddick, 1999). The minimum 45° separation was kept in the mixed-speed conditions for consistency, though observers can detect speed-based transparency with uni-directional stimuli (e.g., Masson, Mestre, & Stone, 1999).

Randomised directions ensured that observers had to detect each signal within the interval to perform the task, rather than simply responding to the presence or absence of a single direction, or attending to the general 'noisiness' of the stimuli. This also minimises the occurrence of any patterns of motion, particularly in the mixed-speed conditions where patterns such as motion parallax may otherwise have been used to perform the task. Finally, random directions minimise adaptation, which would hinder the detection of specific directions (e.g., Raymond, 1993). *Fixed-walk* dot motion was used to avoid any degradation of the signal arising from changes in direction (Watamaniuk, Flinn, & Stohr, 2003).

Four conditions were run: two same-speed and two mixed-speed. In the two same-speed conditions, all dots in the stimulus moved at either the low speed (0.9°/s) or the high speed (8.6°/s for J.A.G.; 9.5°/s for M.F.C. and R.C.W.), which gave a baseline performance for transparent-motion detection with these speeds. For these stimuli, each signal consisted of an equal proportion of the total dots.

With mixed-speed intervals, half the dots in each interval always moved at the low speed, the other half at the high speed. Were this not the case, a potential cue to the number of signals in each interval would be the difference in the proportion of dots moving at each speed. Signal directions were then assigned one of the two speeds, with signal intensities determined accordingly.

Given the previously established transparency limit of two, no more than two signals were assigned the same speed where possible. Thus, mixed-speed intervals with an even number of signals (two and four) contained an equal number of low-speed and high-speed signals. Intervals with an odd number of signals (three and five) had two versions, which differed only in the number of signal directions moving at each of the two speeds. *Majority-slow* intervals contained a greater number of low-speed than high-speed signal directions, while *majority-fast* intervals had the inverse arrangement. For instance, a majority-slow interval with three signals would contain two low-speed signals, each comprising 50% of the low-speed dots (25% each of the total dots), as well as a high-speed signal composed of all the high-speed dots in the display (50% of the total dots). Observers were thus presented with two versions of each n vs. $n + 1$ signal comparison.

For the same-speed conditions, a block of trials contained ten of each n vs. $n + 1$ signal comparison, making forty trials per block. The 1 vs. 2 comparisons were excluded from the mixed-speed conditions, leaving three comparisons for each of the majority-slow and majority-fast conditions. Mixed-speed trials were interleaved within the same block, making sixty trials. This meant that observers did not know in advance which of the speeds would contain the greater number of signals. Each block was presented separately, with signal comparisons presented according to the method of constant stimuli. Observers completed 10 blocks of trials for each condition, interleaved randomly, with responses converted into percent correct scores.

3.2. Results and discussion

The mean percent correct scores for the n vs. $n + 1$ signal comparisons within each of the four conditions are plotted in Fig. 2, where chance level performance corresponds to 50% correct. The crucial feature of this data is the point that performance shifts from a high level of accuracy to near-chance performance. For the same-speed conditions, the 1 vs. 2 and 2 vs. 3 comparisons were both performed with a high level of accuracy. With higher signal numbers, performance dropped to around chance level. This suggests that performance in the 2 vs. 3 comparisons was based solely on the detection of transparent motion in the two-signal interval. These signals could then be differentiated from the

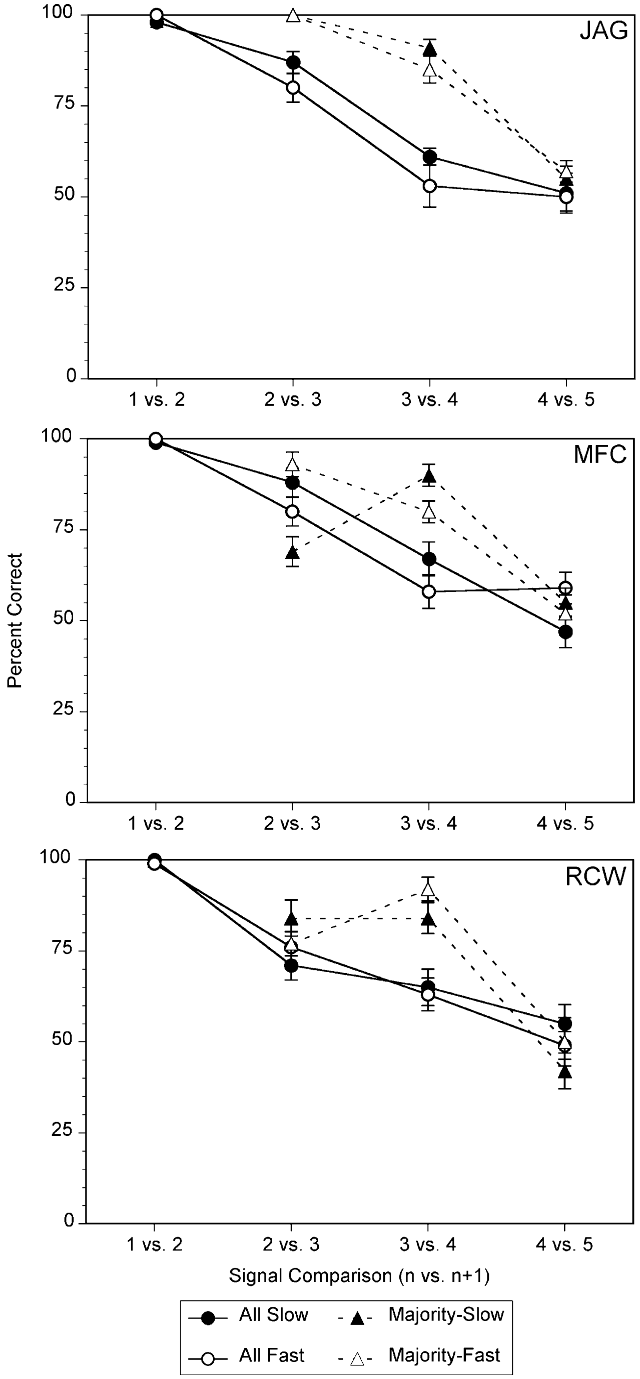

Fig. 2. Mean percent-correct scores as a function of the n vs. $n + 1$ transparent-motion signal comparisons. In the same-speed conditions, dots either moved at the slow speed (All Slow, filled circles) or the high speed (All Fast, open circles). Mixed-speed conditions contained both speeds, with either more slow signal directions than fast (Majority-Slow, filled triangles), or vice versa (Majority-Fast, open triangles). Error bars represent 1 SEM.

three-signal interval, where signals were not detected. The inability to detect three signals is suggested by the near-chance performance for the 3 vs. 4 comparisons. Indeed, observers reported that the three-signal interval was similar in appearance to random noise. This replicates our previous result (Edwards & Greenwood, 2005), where dots moved at 6°/s, and extends this to speeds of 0.9, 8.6 and 9.5°/s.

A different pattern of performance was obtained in the mixed-speed conditions. For all observers, speed differences pushed performance on the 3 vs. 4 comparisons from near-chance levels to between 80% and 90% correct. This indicates that observers were able to detect three signals and discriminate them from four. However, they were unable to detect four signals, as seen in the chance performance in 4 vs. 5 comparisons. This occurred regardless of the speed configuration used. Thus, the addition of speed differences allowed the detection of up to three transparent-motion signals—an extension of the transparent-motion limit. Nonetheless, observers were unable to detect four signals, which will be considered further in Section 5.

Rather than increasing the effective intensity of the signals, it is possible that this extension of the transparent-motion limit may relate to the additional segmentation cues in the stimulus more generally. If this were true, the addition of stimulus differences without independent global-motion systems should lead to a comparable extension of the transparency limit. We sought to examine this possibility in Experiment 3 by using differences in luminance contrast polarity.

4. Experiment 3: Transparent-motion detection with contrast polarity differences

At early stages in the visual processing hierarchy, motion signals with opposite luminance contrast polarities are processed independently by the ON and OFF channels (Schiller, 1992). However, the output of these channels is pooled prior to (or within) the global-motion stage (Edwards & Badcock, 1994). Motion signals with negative contrast polarity (e.g., dark dots) are therefore processed by the same global-motion system as those with positive polarity (e.g., light dots). Because there are no independent polarity-tuned systems for global-motion signals, any improvement in transparent-motion detection cannot be attributed to this manner of increasing signal intensity.

4.1. Method

4.1.1. Observers

J.A.G. and R.C.W. again served as observers. An additional naïve observer, ALB, had corrected-to-normal vision and no history of visual disorders.

4.1.2. Stimuli

Stimuli differed from those of Experiment 2 in two respects. Firstly, all dots moved at the same speed of 4.1°/s, with a step size of 0.21° (9 pixels) per frame. This was selected because it is close to the median preferred speed of V5 neurons (Lagae, Raiguel, & Orban, 1993). Secondly, two luminance contrast polarities were used. All dots had a Michelson contrast of 20%, with light dots defined by a luminance increment and dark dots by a luminance decrement.

4.1.3. Procedure

The procedure was the same as that of Experiment 2, with contrast polarity manipulated instead of speed. Four contrast polarity conditions were presented: two in which all of the dots had the same polarity (either All Light or All Dark), and two with mixed polarities (Majority-Dark or Majority-Light). For the mixed-polarity conditions, there were two forms of each signal comparison: with an odd number of signal directions, majority-dark stimuli had more dark signal directions than light while majority-light stimuli had the opposite configuration.

4.2. Results and discussion

For all observers, the mean percent-correct scores for each condition are shown in Fig. 3. The same-polarity conditions produced the same pattern of results as the same-speed conditions of Experiment 2. Observers could not detect more than two transparent-motion signals reliably in these displays. The mixed-polarity conditions produced a modest improvement in the 3 vs. 4 comparisons, though the magnitude differed between observers. For J.A.G. and R.C.W., scores improved from around 65% correct to between 70% and 80% correct. ALB did not improve in the majority-dark condition, but performed at 88% correct for the majority-light 3 vs. 4 comparisons. The 4 vs. 5 comparisons were again near chance. Thus, polarity differences did facilitate the detection of three signals to some extent.

To compare the improvement in 3 vs. 4 discrimination produced by the polarity and speed manipulations, percent improvement scores were calculated. Because there were no differences between the All Slow and All Fast conditions, these scores were averaged to give a baseline 3 vs. 4 discrimination for each observer. The difference between this baseline and each of the mixed-speed scores was then taken and divided by the baseline. The same procedure was also carried out for the mixed-polarity conditions.

Fig. 4 displays the improvement in 3 vs. 4 comparisons in each of the four conditions, averaged across the three observers in each experiment. The addition of speed differences improved performance by

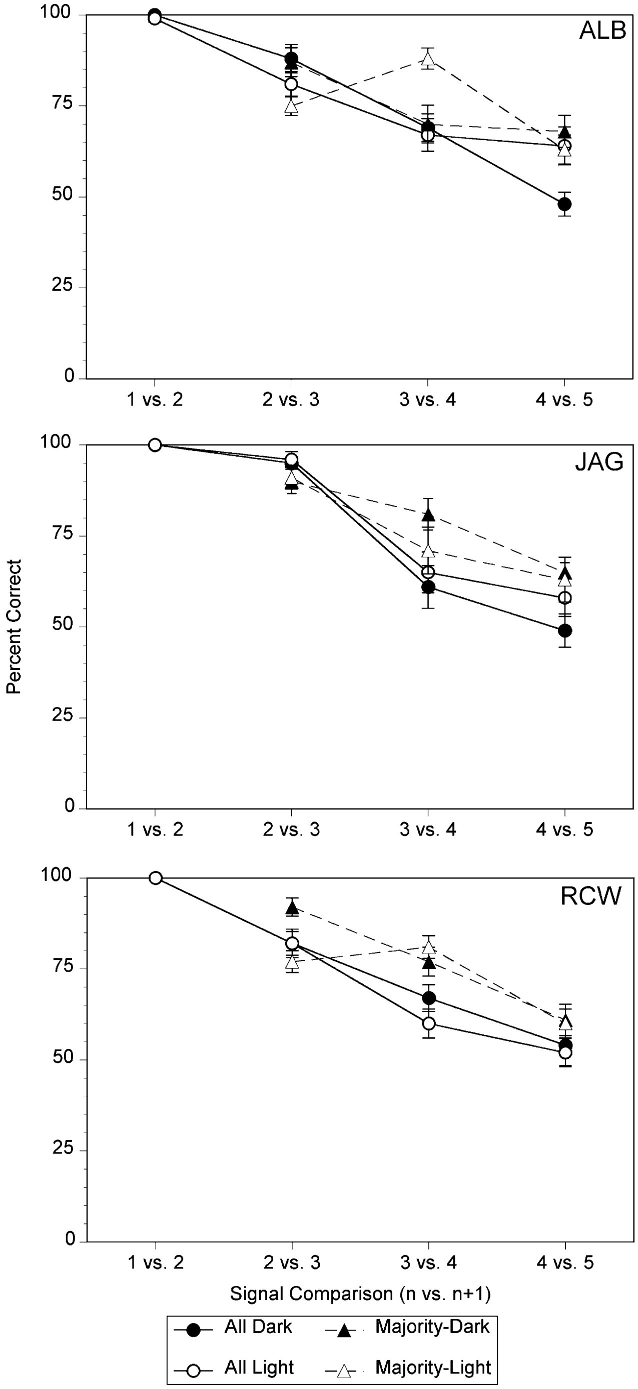

Fig. 3. Mean percent-correct scores as a function of the n vs. $n+1$ transparent-motion signal comparisons. Same-polarity conditions involved all dots being dark (All Dark, filled circles), or light (All Light, open circles). Mixed-polarity either had more dark than light signals (Majority-Dark, filled triangles), or vice versa (Majority-Light, open triangles). Error bars are 1 SEM.

40–45%, while polarity differences improved performance by around 20%. Clearly, speed differences facilitated the detection of three transparent-motion signals to a much greater extent than contrast polarity differences.

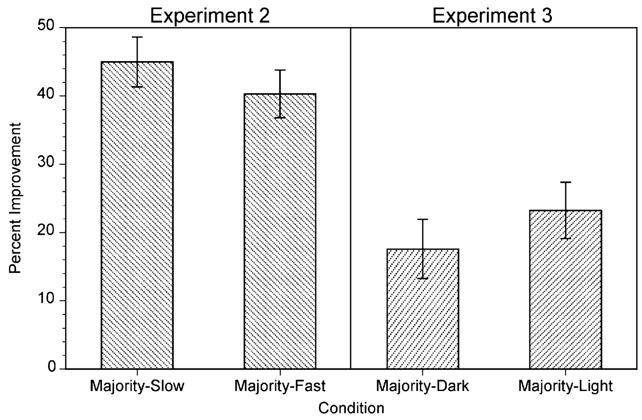

Fig. 4. Mean percent-improvement scores for the 3 vs. 4 signal comparisons, obtained by subtracting baseline 3 vs. 4 scores from those of the mixed conditions and dividing by the baseline. The mixed-speed conditions of Experiment 2 are presented on the left, with mixed-polarity conditions of Experiment 3 on the right. Scores are averaged across observers. Error bars represent 1 SEM.

It is possible that the polarity-based improvement may have arisen because aspects of our stimuli promoted independent processing of opposite-polarity signals. In particular, we used fixed-walk dot motion and a temporal 2AFC procedure compared with the random-walk motion and single-interval 2AFC procedure of Edwards and Badcock (1994). To address this concern, we conducted a uni-directional global-motion detection task using the sampling paradigm of Edwards and Badcock (1994). Stimulus parameters were the same as those of Experiment 1, substituting polarity differences for speed differences.

If opposite polarities are processed by the same global-motion system, thresholds with mixed-polarity dots

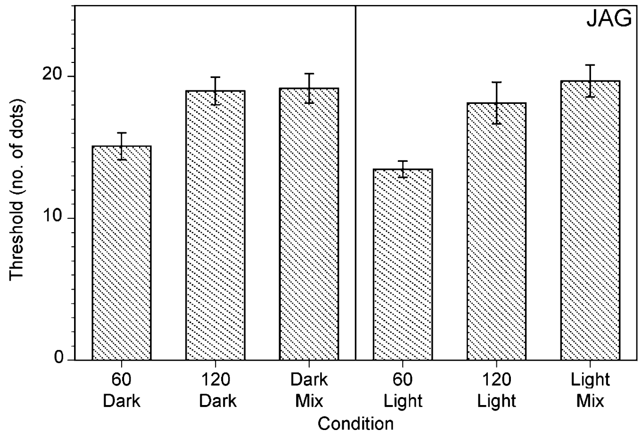

Fig. 5. Mean thresholds for global-motion signal detection, to assess the effect of contrast-polarity differences. Conditions where dark dots contained the signal are on the left; conditions with light signal dots are on the right. For each polarity condition, thresholds were obtained with both 60 and 120 dots. Mixed conditions had 60 dots of each polarity, with the signal drawn from one population only. Error bars are 1 SEM.

should be equivalent to those with 120 same-polarity dots. Only observer J.A.G. was tested, with results displayed in Fig. 5. Results demonstrate the expected pattern, which replicates the findings of Edwards and Badcock (1994) using our current stimulus parameters. The improvement in transparent-motion detection obtained using polarity differences cannot be attributed to distributed processing between independent global-motion systems.

5. General discussion

Our results demonstrate that the transparent-motion limit of two can be extended to three, when the appropriate speed differences are added to stimuli. A modest improvement in performance was also produced using differences in contrast polarity.

5.1. Extending the transparent-motion limit with speed differences

The speed-based extension of the transparent-motion limit gives further evidence that high signal-to-noise detection thresholds for transparency underlie the limit. In Experiment 1, noise dots processed exclusively by the high-speed global-motion system had no effect upon signal-to-noise processing within the low-speed system, and vice versa. Thus, when these speeds were added to transparent-motion stimuli, signals processed by one system would no longer reduce the intensity of signals processed by the other. With fewer signals processed by each system, the effective signal intensities would rise. This elevation in signal intensity allowed observers to detect up to three signal directions—an extension of the transparency limit. Were the limit based on a fixed numerical restriction, this would not have been possible.

The role of signal intensity in determining the transparency limit is consistent with the involvement of the global-motion stage, given the dependence of this stage on the signal-to-noise ratio of moving stimuli (Britten et al., 1993; Rees et al., 2000). This is compatible with a large body of work demonstrating the importance of the global-motion stage in transparent-motion detection more generally (e.g., Qian et al., 1994; Snowden et al., 1991). However, we cannot rule out the possibility that the limit of two is imposed within a higher-order stage receiving global-motion input. For instance, there are at least two distinct speed-tuned systems that operate independently in the detection of optic flow (Khuu & Badcock, 2002). It is plausible that these systems were responsible for the speed-based extension of the transparency limit, though the role of optic flow detectors in transparent-motion detection is unclear. The global-motion stage remains the logical starting point in these considerations.

Similar mechanisms could explain the results of Andersen (1989), who presented transparent-motion signals moving in the same direction at different speeds. With these stimuli, observers were able to detect three transparent-motion signals. However, given the small speed differences used, it is not clear that the signals were processed by independent global-motion systems. It is more likely that the 2 s presentation time allowed sequential detection of the signals, as we have discussed previously (Edwards & Greenwood, 2005).

5.2. Transparent-motion detection with contrast polarity differences

Differences in contrast polarity improved the detection of three transparent-motion signals by around 20%, compared with the 40–45% improvement elicited by speed differences. This effect cannot be attributed to the operation of independent global-motion systems (Edwards & Badcock, 1994), which suggests that transparent-motion detection could be facilitated by any additional segmentation cues, at least to some extent.

The mechanisms underlying the contrast polarity facilitation are not immediately clear. One possibility is that the polarity differences aided in the solution of the motion correspondence problem. This appears to occur in uni-directional stimuli, where polarity differences can increase thresholds for $d_{\max}$, the largest detectable displacement (Hibbard, Bradshaw, & Eagle, 2000). Because transparent-motion detection requires multiple solutions to the correspondence problem, facilitation of this process could increase the segregation of the signals. However, it is unclear why this would not have a similar effect on global-motion thresholds with mixed polarities (Edwards & Badcock, 1994). Alternatively, polarity differences may have facilitated the operation of selective attention, improving the sequential extraction of the motion signals. Though presentation times in this experiment were kept brief to minimise the use of selective attention, additional stimulus cues could increase the rate at which selective attention operates by improving image segmentation.

It is possible that a portion of the speed-based performance improvement could also be explained in this way. However, given the larger magnitude of the speed-based effect, it cannot be explained completely by the mechanisms underlying the polarity-based effect. The greater effectiveness of speed as a segmentation cue points to the involvement of the distinct speed-tuned global-motion systems. What this does suggest is that there are multiple routes to extending the transparent-motion limit.

5.3. The costs of transparent-motion perception

The high signal intensity thresholds underlying the transparent-motion limit are one of many costs associated with the detection of transparent motion. For instance, luminance detection thresholds for bi-directional transparency are higher than those for uni-directional detection (Mather & Moulden, 1983), as are thresholds for the discrimination of direction (Smith et al., 1999) and speed (Wallace & Mamassian, 2003) within transparent-motion displays. The speed differences required for uni-directional transparency are also well above speed discrimination thresholds (Masson et al., 1999). In addition, d_{max} thresholds are smaller for transparent motion than for stimuli with a single displacement direction (Snowden, 1989). These costs are perhaps reflected in the reduced response of V5 cells to transparent motion compared with uni-directional motion (Snowden et al., 1991).

At least part of the observed costs in these experiments may be due to differences in signal intensity between the transparent-motion and uni-directional stimuli used. That is, previous experiments have used uni-directional stimuli with 100% signal intensity, compared with transparent-motion stimuli, where each signal is at 50% signal intensity. Nonetheless, when signal intensity is directly examined, the costs associated with transparency remain. The results of the present study, as well as those of Edwards and Greenwood (2005), demonstrate that transparent-motion detection requires much higher signal intensities than uni-directional motion.

Previous authors have attributed these costs to competitive interactions between direction-selective units processing each of the transparent-motion signals (e.g., Snowden, 1989). That is, global-motion units selective for one of the transparent-motion directions would inhibit units selective for other directions and vice versa. This could raise signal detection thresholds for transparent-motion detection, leading to the transparency limit. In the present study, distributing transparent-motion signals across the speed-tuned global-motion systems would remove these competitive interactions, allowing an extension of the limit. A similar argument has been made by Snowden (1990). Thresholds for both the smallest ($d_{\min}$) and largest ($d_{\max}$) detectable displacements are impaired within transparent-motion displays when compared to uni-directional motion. Speed differences restore these thresholds to uni-directional levels, suggesting that the inhibition ordinarily incurred with transparency was removed.

This explanation is complicated by the fact that threshold elevations for transparency appear to be highly task dependent. Experiments requiring the detection of only a single transparent-motion signal within bi-directional displays yield thresholds of the same coherence level as uni-directional motion (Edwards & Nishida, 1999; Hibbard & Bradshaw, 1999). If competitive global-motion interactions were to underlie the elevated thresholds for transparency, they must only occur when both transparent-motion signals are detected simultaneously.

Alternatively, the task dependence of transparent-motion costs suggests that the demands placed upon attention may be an important factor. That is, threshold elevation for transparent-motion detection may relate to the division of attention across the detection of two signals. In agreement with this, Braddick et al. (2002) found that although the precision of direction judgements is much poorer for transparent motion than for uni-directional motion, similar costs are seen when the two signals are segregated into distinct areas. Furthermore, though the transparency limit occurs when detection of all signals is required, observers can detect a specific pre-cued direction in transparent-motion displays containing up to 6–8 signals (Felisberti & Zanker, 2005). If attentional demands were behind the raised thresholds for transparency, our present results suggest that these attentional demands can be overcome by elevating signal intensities. This could be tested by examining the influence of signal intensity on stimuli with multiple, spatially segregated, motion signals.

5.4. A higher-order transparent-motion limit?

Although speed differences enabled a clear extension of the transparent-motion limit, observers in our study were unable to detect more than three signals. The same-speed conditions of Experiment 2 demonstrate that each speed-tuned system in isolation is capable of detecting two signals simultaneously. However, regardless of the arrangement of the signal speeds, observers were unable to detect four signals when these speeds were combined. This suggests an additional limitation on transparent-motion detection.

The origins of this additional limitation are unclear. It may reflect a strict upper limit for the division of attention, allowing attention to be divided across no more than three signals simultaneously. Alternately, it could reflect motion processing in one of several higher-order areas known to be involved in transparent-motion detection, including the fusiform gyrus and MST (Muckli, Singer, Zanella, & Goebel, 2002; Roy, Komatsu, & Wurtz, 1992). Our present results do not allow us to differentiate between these possibilities.

One way to assess the existence of an additional limit would be to attempt to extend the transparent-motion limit using other stimulus features with independent global-motion systems. For instance, motion signals presented at crossed binocular disparities do not affect signal-to-noise processing for uncrossed disparities, and vice versa, suggesting the existence of independent global-motion systems tuned to binocular disparity (Snowden & Rossiter, 1999). Thresholds for the detection of transparent motion are also lowered by presenting signals on distinct depth planes (Hibbard &

Bradshaw, 1999). Differences in binocular disparity should therefore give an extension of the transparency limit of similar magnitude to that observed using speed. An additional limit would restrict any extensions of the transparency limit to three regardless of the stimulus features used. We are currently investigating these issues.

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