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The perception of motion transparency: A signal-to-noise limit

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Abstract

A number of studies were conducted to determine how many transparent motion signals observers could simultaneously perceive. It was found that that the limit was two. However, observers required a signal intensity of about 42% in order to perceive a bi-directional transparent stimulus. This signal level was about three times that required to detect a uni-directional motion signal, and higher than was physically possible to achieve in a tri-directional stimulus (in a stimulus in which the different transparent signals are defined only by direction). These results indicate that signal intensity plays an important role in establishing the transparency limit and, as a consequence, implicates the global-motion area (V5/MT) in this process.
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1. Introduction

A great deal of work has been devoted to trying to determine how the visual system extracts motion signals (for a review, see Smith & Snowden, 1994). Relatively little work, however, has focused on how transparent motion signals are processed. Motion transparency occurs when multiple objects move over the same region of space. Examples of motion transparency are when an animal moves through tall grass or when rain runs down the window of a moving car. Typically, at least one of the objects is spatially sparse. In these conditions, there are a number of distinct motion signals within the same region that correspond to the different objects. If the visual system can correctly segment and group these motion signals, then the transparent motion of the different objects is perceived. There are three main aims to the present study. The primary aim is to establish the number of signals that can be processed and represented by the visual system. The secondary aims are to determine the nature of the processing limit and hence where in the visual system this limit is imposed.

In addressing the question of a transparency limit, it is important to consider the different ways that the signals can be perceived. Signals can be perceived either sequentially or simultaneously. That is, it is possible to perceive each signal one at a time, or they can all be perceived simultaneously. It is only when they are perceived simultaneously that transparent motion is actually being processed, so it is that condition that is of interest in the present study (see Braddick, Wishart, & Curran, 2002 for a discussion of this issue).

Two studies have sought to establish the motion-transparency limit. Mulligan (1992, abstract only) investigated the ability of observers to identify which of two temporal intervals contained the greater number of signal directions (n versus $n + 1$ signal directions). He found that only two signals could be perceived simultaneously. Mulligan ensured simultaneous perception by using the discrimination task combined with a short

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presentation time of 250 ms. A study by Andersen (1989) found that observers could reliably indicate the presence of up to three signal directions. However, that study presented stimuli for 2 s, so it is possible that observers could perceive the different signals sequentially.

An additional factor that is useful to consider when investigating motion transparency is the extent to which the different cortical motion areas are involved in representing motion transparency. Such a consideration can offer clues to the factors that contribute to the formation of the limit. It is possible that a number of processing areas impose limitations on the processing of transparent signals and that the nature of these limitations differ from area to area. Given that local-motion (V1) cells can only represent a single motion direction at a given location in space, it is clear that while these cells are obviously important in the extraction of motion signals, they cannot represent motion transparency. The first area where motion transparency could, theoretically, be represented is at the global-motion level (V5/MT). This area combines the output of many local-motion units across both space and direction and has been convincingly linked to the processing of motion transparency (e.g. Qian & Andersen, 1994; Qian, Andersen, & Adelson, 1994).

A stimulus that has been extensively used to investigate the properties of the global-motion stage is the one developed by Newsome and Pare (1988). This stimulus consists of a sequence of moving dots in which the dots are broken down into two groups: a signal group in which the dots move in the same (global-motion) direction and a noise group in which the dots move in random directions that cover the full 360°. The signal intensity is varied by altering the percentage of the dots that are signal dots. Cells in area V5 of macaques have been shown to be highly tuned to global-motion signal intensity. The response of most V5 cells increase in a linear manner with increasing signal intensity (Britten, Shadlen, Newsome, & Movshon, 1993). The performance of human observers in a signal-intensity discrimination task has been found to mirror this tuning (Edwards & Badcock, 1998). The global-motion area can be considered as performing a signal-to-noise analysis, with the signal being motion vectors in the preferred direction of the cell and the noise being motion vectors in all other directions (Edwards & Nishida, 1999). Given the involvement of the global-motion area in processing motion transparency, it is highly likely that signal intensity will play a role in determining transparency limits.

The primary aim of this study is to establish the transparency limit, and to determine whether this is a fixed limit. The approach used was similar to that used by Mulligan (1992). Observers were required to discriminate which of two temporal intervals contained the larger number of motion directions. A maximum number of five directions were used. In the stimuli, all dots moved in a signal direction. This meant that a consequence of increasing the number of directions was to reduce the signal intensity of those directions. For example, in an interval that contained a single motion direction, the signal intensity was 100%, while in an interval that contained five directions, the signal intensity was only 20%. Thus the starting point for this study was to establish that the minimum signal intensity used in the transparent conditions was greater than that required to see a single motion direction, i.e. to ensure that thresholds for the detection of a uni-directional signal, using a two temporal-interval procedure, are lower than 20%. This control assumes that signal intensities required to see transparent signals are similar to that required to see uni-directional signals. This assumption was explicitly tested in Experiment 3.

2. Experiment 1: uni-directional thresholds

Increasing the number of transparent directions results in a decrease in the signal intensity in each direction. It was therefore necessary to first establish the thresholds for the detection of a uni-directional signal to ensure that they are above the minimum signal intensity used in the transparent conditions in Experiment 2 (20%).

2.1. Method

2.1.1. Observers

Three observers were used in all experiments reported here, one of the authors (JAG) and two who were naïve with respect to the aims of the study. All observers had normal or corrected-to-normal acuity and no history of any visual disorders.

2.1.2. Apparatus

Stimuli were displayed a on Clinton Monoray monitor which was driven by a Cambridge Research Systems VSG 2/5 in a host Pentium computer. Observers' responses were recorded via a button box. The monitor had a refresh rate of 120 Hz.

2.1.3. Stimuli and procedure

Global-motion stimuli were presented within a circular aperture of 13° diameter. 120 dots were presented, giving a dot density of 0.9 dots/deg^2. The spatial step of each dot was 0.3° (eight pixels), which resulted in a speed of 6°/s. This combination of dot density and step size resulted in a low probability of false motion signals occurring (Willaims & Sekuler, 1984). The dots had a diameter of 0.2° and a Michelson contrast of 20%. The mean luminance of the display was 82 cd/m^2. A black fixation cross was presented at the centre of the viewing aperture. The duration of each frame was 50 ms and four different sequence lengths were used: 2, 4, 8 and 16 motion frames. This resulted in stimulus durations of 100, 200, 400 and 800 ms, respectively. A range of durations was used in order to directly examine the effect that duration has on the transparency limit (Andersen, 1989; Mulligan, 1992). Each dot moved in the same direction for the entire number of frames, i.e. a fixed-walk stimulus was used (Scase, Braddick, & Raymond, 1996).

A temporal, two-alternative forced-choice procedure was used. The two intervals were separated by a 1 s delay. This delay was used to minimise any hysteresis effects (Williams, Phillips, & Sekuler, 1986). One of the intervals contained purely random motion (0% signal intensity) and the other contained the signal. For each trial, the signal direction was chosen randomly from the full 360°. The observer's task was to indicate the interval that contained the signal. Based upon the results of pilot studies, eight signal intensities were used, ranging from 5% to 40% in 5% step sizes. A method of constant stimuli was used and each block of trials consisted of 40 stimulus presentations, i.e. each signal intensity was presented five times. Each performance measure represents the mean of 10 blocks of trials. Observers sat in a dark room 0.5 m from the monitor with their heads supported by a chin rest.

2.1.4. Results and discussion

The results for the three observers are shown in Fig. 1. A psychometric curve plotting performance, percentage of correct responses, against signal intensity is shown for each observer. Note that each curve is the average of the 10 obtained for each observer in the four separate conditions. From each observer's individual psychometric curves, threshold values (75% performance level) were calculated (see Fig. 2). As can be seen from Fig. 2, threshold levels for all observers at all stimulus durations were less than 20% (the lowest transparent signal level used in Experiment 2) and thresholds were consistent across all four durations. Note that the thresholds obtained in this study are somewhat higher than those obtained in some previous studies (e.g. Edwards, Badcock, & Smith, 1998). This is most likely due to the directional uncertainty of the signal direction (Felisberti & Zanker, 2004).

3. Experiment 2: transparency limit

The aim of the present experiment was to establish the motion-transparency limit. Based upon the results of Experiment 1, we know that the signal intensities used in all of the transparent conditions are above the threshold values to detect uni-directional signals.

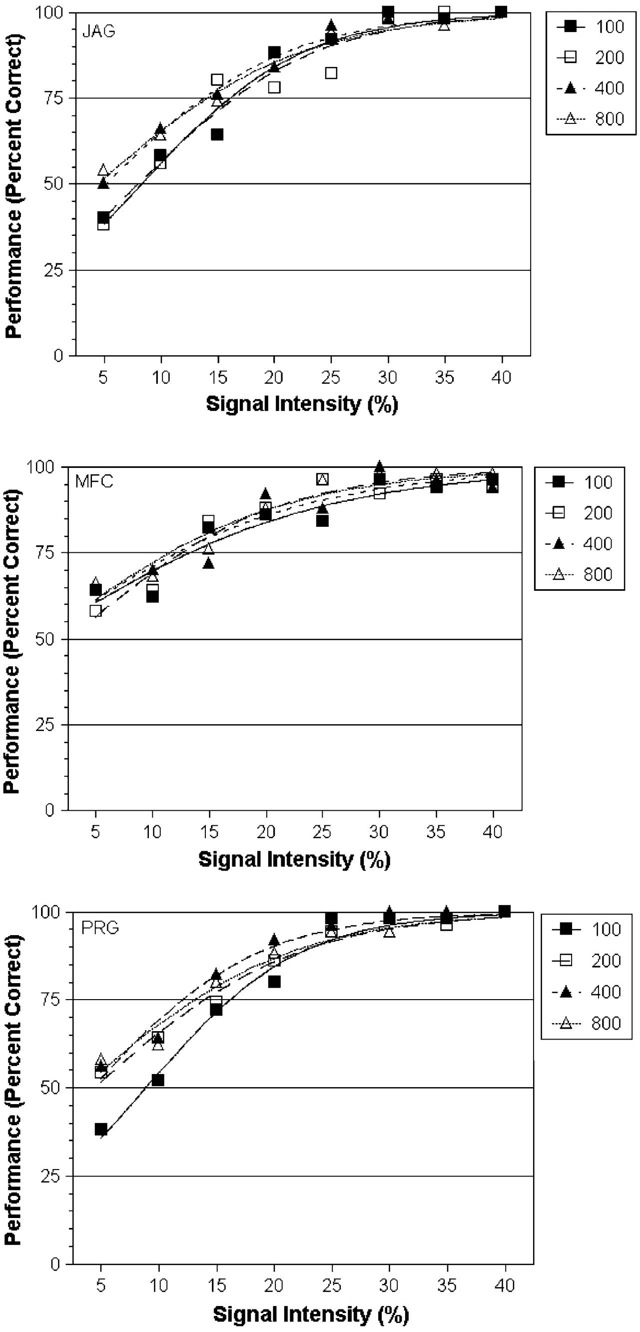

Fig. 1. Results for Experiment 1. Average psychometric curves for each observer for the detection of uni-directional motion. Four durations were tested: 100 ms (filled squares), 200 ms (open squares), 400 ms (filled triangles), and 800 ms (open triangles). Each data point represents 50 trials.

3.1. Method

3.1.1. Stimuli and procedure

A temporal, two-alternative forced-choice procedure was used. The two intervals were separated by 1 s. One interval contained *n* signal directions, and the other *n* + 1 directions. *N* varied from 1 (1 versus 2) to 4 (4 versus 5). All dots moved in a signal direction which

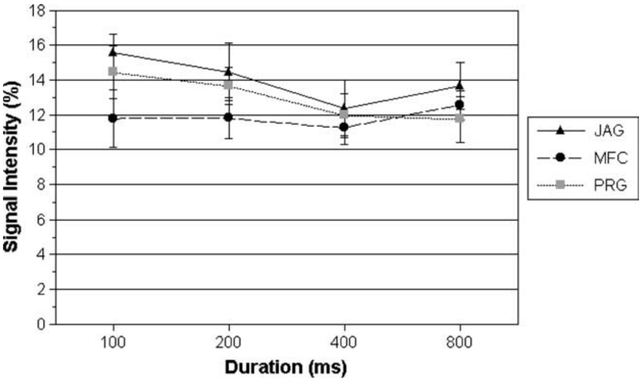

Fig. 2. Results for Experiment 1. Threshold values (75% performance level) for the detection of uni-directional motion across the four durations. Each data point represents 10 threshold estimates; error bars represent 1 SEM.

Table 1
Signal intensities for the different transparent motion conditions

Number of directions	Signal intensity (%)
1	100
2	50
3	33
4	25
5	20

resulted in the signal intensity in each direction decreasing as the signal number increased. See Table 1. Signal directions were randomised but when there were multiple directions present, there was at least 45° between each direction. A separation of 45° ensured that a given motion signal had the same effect on a neighbouring signal as the same number of noise dots (Braddick et al., 2002; Edwards & Nishida, 1999). Observers were required to indicate the interval that had the highest number of signal directions. As in Experiment 1, four stimulus durations were used: 100, 200, 400 and 800 ms. Each block of trials consisted of 10 trials for each signal number and duration combination, resulting in a total of 160 trials. Each performance measure represents the mean of 10 blocks of trials.

3.1.2. Results and discussion

The results for the three observers are shown in Fig. 3. Each graph shows the percent-correct values as a function of the signal-discrimination number for all observers at a given stimulus duration. Error bars indicate plus and minus one standard error of the mean. The basic pattern of results is the same for all observers. For the short stimulus durations (100 and 200 ms, Fig. 3a and b) performance was about 100% for the 1 versus 2 discrimination, reduced to about 75% for the 2 versus 3 discrimination and reached chance level (50%) for the 3 versus 4 signal discrimination. Chance level performance was maintained for the 4 versus 5 discrimination task. Once the transparency limit was exceeded, observers reported perceiving random motion. These results indicate that observers were able to perform the 2 versus 3 discrimination by noting that one interval contained two directions, and the other appeared to contain noise. For the 3 versus 4 discrimination, both intervals were above

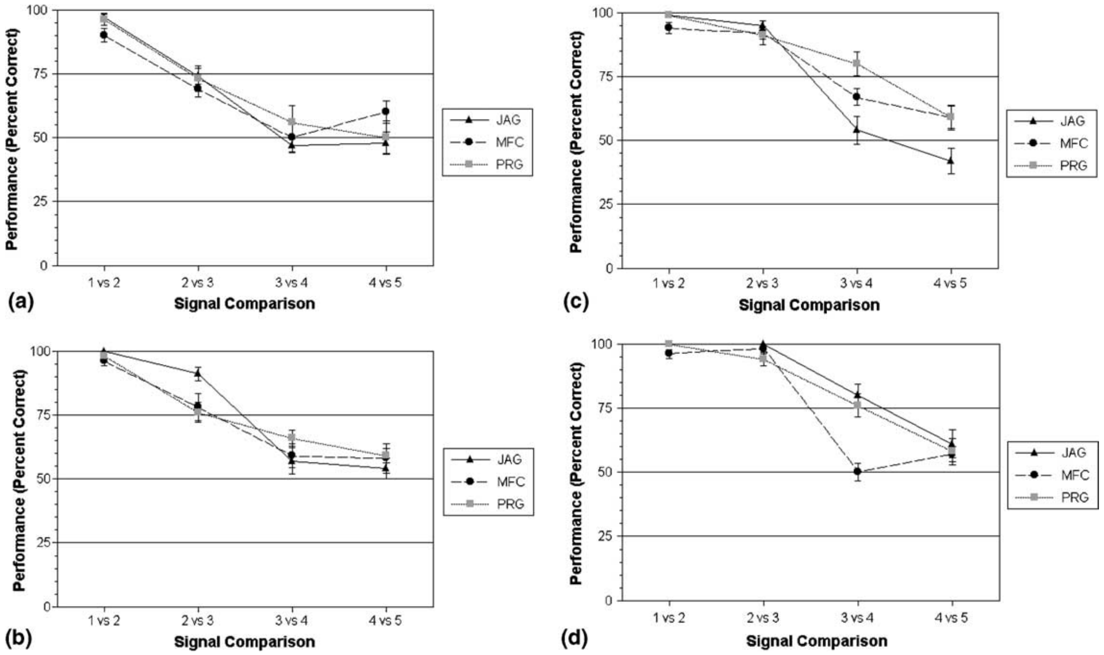

Fig. 3. Results for Experiment 2. Percent-correct values are plotted against the signal-discrimination number for all observers. Each graph shows a different stimulus duration: (a) 100 ms, (b) 200 ms, (c) 400 ms, and (d) 800 ms. Data points represent the average of 10 blocks of trials; error bars represent 1 SEM.

the transparency limit, and so noise was perceived in both intervals, resulting in the observers being unable to perform the discrimination. This finding of a two signal limit is consistent with that of the study by Mulligan (1992).

For the two higher stimulus durations, 400 and 800 ms (Fig. 3c and d) above chance performance was obtained for the 3 versus 4 discrimination. This above chance performance was most likely due to the longer duration allowing observers to sequentially detect the multiple signal directions. Refer to Section 5 for a more detailed analysis of this issue.

4. Experiment 3: effect of signal intensity on transparency

The results of Experiment 2 indicate that the transparency limit is two. While observers could detect the presence of more signal directions if the stimulus duration was increased, they could only perceive two directions simultaneously. Given that all dots moved in one of the signal directions, a consequence of increasing the number of directions was to decrease the signal intensity in those directions. For example, in the two-direction condition, each direction had a signal intensity of 50% (60 dots) while in the three-direction condition this was reduced to 33% (40 dots). Both of these intensities are above that required to detect a uni-directional signal (Experiment 1) and so it could be argued that the fact that observers can perceive two signals but not perceive three is not the result of different signal intensities in the two conditions. However, this assumes that higher signal intensities are not required for the perception of transparent signals, i.e. that there is not an additional processing load for motion transparency that manifests itself as an increase in required signal level.

Such a notion could seem reasonable in light of the study by Edwards and Nishida (1999). This study investigated the ability of observers to detect the presence of a global-motion signal when the non-signal dots either all moved in random directions or when some of the noise dots moved in different direction at highly supra-threshold signal intensities. It was found that thresholds were the same for all conditions, i.e. that a secondary signal direction had the same effect as an equal number of noise dots on the ability to detect a threshold signal level (as long as the directions differed by at least 45°). However, the task in that study did not require the perception of transparency. A temporal, two-alternative procedure was used and observers knew the direction of the signal they had to detect. It is still possible, therefore, that the perception of transparency required a higher signal level than that required for detection of a uni-directional signal.

The aim of this experiment was to investigate the effect that signal intensity has on the ability to perceive motion transparency. Specifically, it was to determine whether the ability to perceive a stimulus containing two directions of motion would be impaired by decreasing the intensity of the signals below their maximum level (50%) but still maintaining them well above uni-directional threshold signal levels (15%).

4.1. Method

4.1.1. Observers

Two of the observers took part in this experiment.

4.1.2. Stimuli and procedure

A temporal two-interval procedure was used to establish the ability of observers to discriminate two signal directions from three as a function of the signal intensity in the two-direction condition. The signal intensity in the two-signal condition was varied between 50% (maximum possible) and 30% in 5% steps. The intensity of the three-direction condition was kept constant at 33%, which was the maximum signal level possible and a level at which observers performed at chance levels in Experiment 2. To ensure simultaneous processing of the transparent signals, a stimulus duration of 200 ms was used. Each block consisted of 10 trials for each condition, and 10 blocks were run.

4.1.3. Results and discussion

The results for the two observers are shown in Fig. 4. Performance (percent correct discrimination) is shown as a function of the signal intensity in the two-direction interval. The results for both observers are the same. Performance declines with decreasing signal intensity such that by signal levels of around 35% performance had reached chance level. Note that this signal level is about the maximum level possible in the three-direction condition (33%). Fig. 5 shows the signal level required

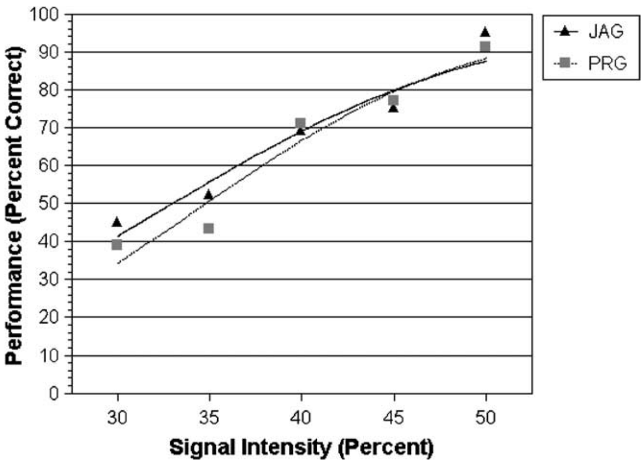

Fig. 4. Results for Experiment 3. Performance (percent correct discrimination) is plotted against the signal intensity in the two-direction interval. Intensities in the three-direction interval were fixed at 33%. Each data point represents 100 trials.

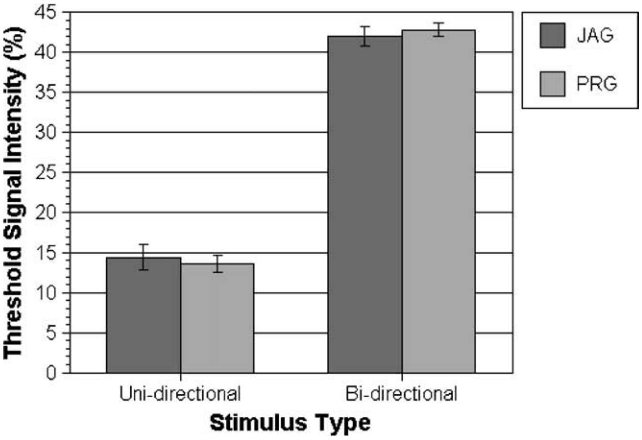

Fig. 5. Results for Experiment 3. Threshold signal level required to discriminate intervals containing two directions from those containing three (bi-directional). For comparison, uni-directional thresholds from Experiment 1 (uni-directional) are also shown.

for threshold (75%) performance levels. For comparison, threshold levels for the uni-directional condition (Experiment 1) are also shown. Both observers required signal levels of about 42% in order to detect the bi-directional transparent condition, compared to thresholds of slightly under 15% for the uni-directional condition. That is, compared to uni-directional motion, observers needed, on average, a three-fold increase in signal levels in order to perceive bi-directional transparent motion (2.9 for JAG and 3.1 for PRG). These results indicate that signal intensity has a substantial role in establishing transparency limits and that the signal intensity to detect a transparent signal is far greater than that required to detect a uni-directional signal.

5. General discussion

The results of Experiment 2 show that for short stimulus durations (200 ms or less), observers can simultaneously detect only two transparent motion signals. This finding is consistent with that of Mulligan (1992). This limit occurred even though the signal intensities in all conditions were above uni-directional thresholds (Experiment 1). The results of Experiment 3 show that when, in the bi-directional condition, signal levels were reduced from 50% (the maximum possible signal level) the ability of observers to perceive the transparent motion was severely impaired. Performance was at chance level at signal intensities of about 35% and threshold levels were about 42% (in each signal). These levels were about three times higher than uni-directional thresholds and higher than was physically possible to obtain, in the present study, for any transparent condition that contained more than two signal directions.

With the long stimulus durations used in Experiment 1 (400 and 800 ms) three transparent signals could be detected (though this ability varied across observers). We argue that it is likely that these signals were being perceived sequentially and so observers were not really perceiving transparent motion (Braddick et al., 2002). However, another interpretation is possible. Uni-directional thresholds decrease as the stimulus duration and/or number of frames is increased up to an integration limit (e.g. Festa & Welch, 1997). It is possible, therefore, that this greater sensitivity of the motion system at these long durations may have allowed the observer to simultaneously perceive three motion signals. If this hypothesis is true, it would not reject the finding that the perception of transparent signals requires higher signal levels than the perception of a uni-directional one, however, it would reject the notion of a transparency limit of two (when the different signals differ only in terms of their signal direction). In order to test this hypothesis, we increased the number of motion frames while keeping a stimulus duration of 200 ms. Festa and Welch (1997) found that the integration limit depended upon a combination of the temporal duration and the number of motion frames. Stable thresholds were obtained if the duration was 200 ms or more and the number of frames was greater than about 9. We used a duration of 200 ms and compared performance with 12 frames to that obtained with the four frames used in Experiments 2 and 3. The speed of the dots was kept constant at 6°/s, so in the 12 frame condition, the spatial displacement between each motion frame was reduced to 0.1° (three pixels). As can be seen in Fig. 6, performance for the 4 and 12 frame conditions are the same, meaning that sequential viewing is the most likely reason for the ability to perceive more than two signal directions in the long-duration conditions.

The finding that bi-directional coherence thresholds were about three times higher than uni-directional thresholds indicate that the perception of motion transparency has a high processing cost associated with it.

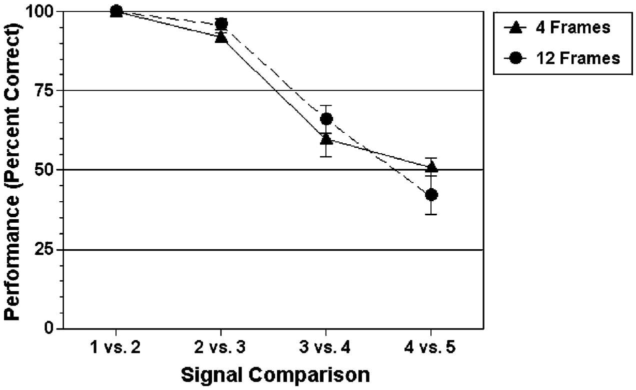

Fig. 6. Results for the control study in which the number of frames in the 200 ms duration sequence were increased to 12 frames. Observer JAG was tested. Each data point represents the average of 10 blocks of trials; error bars represent 1 SEM.

This result is consistent with other studies that have shown that uni-directional thresholds underestimate stimulus intensities required for the perception of transparent motion. For example, motion discrimination thresholds for speed (e.g. Masson, Mestre, & Stone, 1999) underestimate the speed differences required for the perception of transparency, contrast thresholds for transparent motion are higher than for uni-directional motion (Mather & Moulden, 1983) and direction discrimination is better for uni-directional signals than it is for transparent signals (e.g. Braddick et al., 2002). These findings have implications for neural models of transparency that are based upon cortical responses to uni-directional signals (e.g. Treue, Hol, & Rauber, 2000). Specifically, the neural activity levels that would be required to perceive both transparent motion signals would be far greater than that required to perceive a uni-directional signal.

A study whose findings are apparently at odds with the notion of a cost of transparency is the one by Edwards and Nishida (1999). This study showed that the ability of observers to detect a threshold-level signal was not affected by the presence of a secondary supra-threshold signal, when the secondary signal was generated by constraining a number of noise dots to move in a certain direction (i.e. when the total number of noise dots was kept constant). However, these results are compatible with the present study because the task of the observers in the previous study was only to indicate which interval contained the threshold signal. That is, observers did not have to perceive the transparent motion in order to perform the task, they merely had to detect the presence of one of the signals. It is interesting to note that the Edwards and Nishida study indicates that purely uni-directional motion processing can occur with a transparent motion stimulus, i.e. the visual system can attend purely to one of the uni-directional signals while the other is treated the same as noise dots. The same logic can account for the results of Hibbard and Bradshaw (1999).

While it is possible, and indeed likely, that multiple cortical areas play a role in determining whether transparent motion can be perceived, the finding that signal (coherence) level plays a major role in this process indicates that the transparency limit is at least partially set at the global-motion (V5) area. This finding is consistent with previous studies that have linked V5 activity to the perception of motion transparency (e.g. Castelo-Branco et al., 2002; Qian & Andersen, 1994; Stoner & Albright, 1992).

In dealing with the issue of a motion-transparency limit, it is worthwhile to consider ecological factors that may shape the visual system's processing characteristics. The present study has found that, when the transparent signals differ only in their direction, the maximum number that can be perceived is two. Additionally, if the coherence level of these signals decrease only slightly from the maximum possible (50%), then the perception of transparency is lost. Threshold signal levels required to perceive bi-directional transparency were 42% (in each signal), which is above maximum intensity of 33% that could be physically obtained in the tri-directional condition (using the present stimulus). However, from an ecological perspective, if there are more than two transparent signals, i.e. objects, in the same area, then it is likely these objects would differ not only in their direction of motion. They are also likely to differ in their depth and/or speed of motion. Studies have shown that we have independent global-motion systems that are tuned to stimulus speed (Edwards et al., 1998) and stereo depth (Snowden & Rossiter, 1999; also see Qian et al., 1994). These studies have shown the existence of independent global-motion systems by using a sampling paradigm (Edwards & Badcock, 1994). As would be expected, the number of signal dots required to perceive the global-motion direction increases as the number of noise dots increase. However, dots will only act as noise if they are processed by the same global-motion system that extracts the global-motion signal. If they are processed by a different system, then coherence thresholds are not affected. That is, in establishing the effective signal-to-noise ratio, those dots are ignored. Consequently, it may be possible to increase the transparency limit by using a stimulus in which different signals move at different speeds and/or depth. We are currently investigating this possibility.

References

Andersen, G. J. (1989). Perception of three-dimensional structure from optic flow without locally smooth velocity. *Journal of Experimental Psychology: Human Perception and Performance, 15*, 363–371.

Braddick, O. J., Wishart, K. A., & Curran, W. (2002). Directional performance in motion transparency. *Vision Research, 42*, 1237–1248.

Britten, K. H., Shadlen, M. N., Newsome, W. T., & Movshon, J. A. (1993). Responses of neurons in macaque MT to stochastic motion signals. *Visual Neuroscience, 10*, 1157–1169.

Castelo-Branco, M., Formisano, E., Backes, W., Zanella, F., Neuenschwander, S., Singer, W., & Goebel, R. (2002). Activity patterns in human motion-sensitive areas depend on the interpretation of global motion. *Proceedings of the National Academy of Science USA, 99*(21), 13914–13919.

Edwards, M., & Badcock, D. R. (1994). Global motion perception: interaction of the ON and OFF pathways. *Vision Research, 34*, 2849–2858.

Edwards, M., & Badcock, D. R. (1998). Discrimination of global-motion signal strength. *Vision Research, 38*, 3051–3056.

Edwards, M., Badcock, D. R., & Smith, A. T. (1998). Independent speed-tuned global-motion systems. *Vision Research, 38*, 1573–1580.

Edwards, M., & Nishida, S. (1999). Global-motion detection with transparent-motion signals. *Vision Research, 39*, 2239–2249.

Felisberti, F., & Zanker, J. M. (2004). Does attention affect transparent motion perception?. *Perception*, 33:124.

Festa, E. K., & Welch, L. (1997). Recruitment mechanisms in speed and fine-direction discrimination tasks. *Vision Research, 37*, 3129–3143.

Hibbard, P., & Bradshaw, M. (1999). Does binocular disparity facilitate the detection of transparent motion? *Perception, 28*, 183–191.

Mather, G., & Moulden, B. (1983). Thresholds for movement detection: two directions are less detectable than one. *Quarterly Journal of Experimental Psychology, 35A*, 513–518.

Masson, G. S., Mestre, D. R., & Stone, L. S. (1999). Speed tuning of motion segmentation and discrimination. *Vision Research, 39*, 4297–4308.

Mulligan, J. B. (1992). Motion transparency is restricted to two planes. *IVOS Supplement, 33*(4), 1049.

Newsome, W., & Pare, E. (1988). A selective impairment of motion perception following lesions of the middle temporal visual area (MT). *The Journal of Neuroscience, 8*(6), 2201–2211.

Qian, N., & Andersen, R. (1994). Transparent motion perception as detection of unbalanced motion signals. II. Physiology. *The Journal of Neuroscience, 14*(12), 7367–7380.

Qian, N., Andersen, R., & Adelson, E. (1994). Transparent motion perception as detection of unbalanced motion signals. I. Psychophysics. *The Journal of Neuroscience, 14*(12), 7357–7366.

Scase, M., Braddick, O., & Raymond, J. (1996). What is noise for the motion system? *Vision Research, 36*(16), 2579–2586.

Smith, A. T. S., & Snowden, R. J. (1994). *Visual detection of motion*. Academic Press.

Snowden, R., & Rossiter, M. (1999). Stereoscopic depth cues can segment motion information. *Perception, 28*, 193–201.

Stoner, G., & Albright, T. (1992). Neural correlates of perceptual motion coherence. *Nature, 358*, 412–414.

Treue, S., Hol, K., & Rauber, H. J. (2000). Seeing multiple directions of motion-physiology and psychophysics. *Nature Neuroscience, 3*(3), 270–276.

Williams, D., Phillips, G., & Sekuler, R. (1986). Hysteresis in the perception of motion direction as evidence for neural cooperativity. *Nature, 324*, 253–255.

Willaims, D. W., & Sekuler., R. (1984). Coherent global motion percepts from stochastic local motions. *Vision Research, 64*, 275–286.