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Attention modulates perception of transparent motion

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Abstract

Human observers can extract a given motion direction from sets of random dots moving simultaneously in two or more directions in the same region of the visual field, a phenomenon referred to as motion transparency. As a necessary condition for separating transparent motion directions, low level encoding of local motion signals must generate frequency distributions of local directions with separable peaks corresponding to these directions—this process would be constrained by local stimulus attributes and the properties of local motion detectors. Furthermore, a representation of multiple directions is needed for simultaneous retrieval of several directions in a psychophysical task—this operation would be limited by higher level processes, such as attention selecting a particular direction to rise into awareness. Preliminary observations suggest that the number of directions that can be seen simultaneously is rather limited and the question arises whether this could be related to limitations of low-level encoding or higher level representations. To study specifically the effect of attention on transparent motion perception, observers were presented with sets of dots moving coherently in a variable number of directions, and were asked after the presentation whether one particular direction was present in the set. When the direction of motion was not known before stimulus onset (uncued condition), observers detected a particular motion direction among no more than 3 other directions. When direction of motion was indicated prior to stimulus onset (precued condition), however, this limit increased up to 6 directions. This attentional effect showed some inter-individual variability and appeared to benefit from spatiotemporal integration of the motion signals. A corresponding effect became apparent when observers were tested in the same paradigm whether they could separate two motion directions with variable angular difference between them. In the precued condition a typical minimum direction difference was about 60°, whereas in the uncued condition this was about 120°, suggesting that the performance in detecting one direction in a multiple direction stimulus might be limited by the ability to separate adjacent motion directions. This pattern of results suggests that attention can reliably improve transparent motion processing by affecting the separability of directional signals in low level encoding mechanisms.
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1. Introduction

In everyday life we can experience situations in which motion is perceived as either interleaved such as raindrops falling against a background of moving pedestrians and cars, or superimposed, such as cast shadows on moving surfaces. The phenomenon of perceiving different motion signals in the same region of the visual field at the same time is referred to as motion transparency. It has attracted considerable experimental and theoretical interest, because at first sight it is a computational challenge to perceive two different directions in the same spatio-temporal slice of the world (Qian & Andersen, 1994; Snowden & Verstraten, 1999; van Doorn & Koenderink, 1982; Zanker, 2001). Motion transparency is often investigated using Random Dot Kinematograms (RDKs), which contain two or more

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sets of random dots moving smoothly and independently across one another. The perception of transparent motion surfaces can be accompanied by the perception of relative depth: with continued viewing of such displays, some observers may see directions flipping in front of or behind each other (Grunewald, 2000). However introspective reports of many of observers indicate that multiple directions can be perceived in a single depth plane, which corresponds to the physical stimulus in the laboratory and is the starting point for cortical processing.

Observers pick up the motion of individual dots with the help of local motion detectors that encode a range of preferred directions and speeds at any location in the visual field. With as little as 10% of dots moving in a single coherent direction it is possible to perceptually group all these dots into a unified moving surface (Raymond, 2000), which usually is interpreted as a global integration process. Conversely, it has been shown that our visual system detects motion transparency only when motions in different directions are locally unbalanced, and that the coherent motion percept is abolished when dots are moving in different directions in close proximity (Qian, Andersen, & Adelson, 1994). This makes sense because two dots moving in opposite directions within the receptive field of a local motion detector, such as the opponent Reichardt detector model (Borst, 2000; Borst & Egelhaaf, 1989), would cancel each other's signal—any standard motion detector model would necessarily lead to the same result. When the output of local motion detectors is globally integrated (Braddick, 1997; Braddick, Wishart, & Curran, 2002; Cropper, 2001), one or more motion surfaces can only become visible if there are detectable and separable peaks in the frequency distributions of local directions. Computational modelling indeed suggests that local pooling mechanisms may be responsible for the transition from spatial segmentation of motion defined regions to transparency and from transparency to the perception of uncorrelated noise (Zanker, 2001).

A puzzling question about motion transparency refers to the number of directions that can be perceived simultaneously in the same region of the visual space: if we can encode and retrieve two directions, why not three, or six? There are sparse and not fully coherent reports about such limitations that are hampered by technical difficulties to find the appropriate experimental methods, because identifying any one particular motion direction in a set of a given number (n) of simultaneously presented motion directions could be similar to the detection of coherent motion in noise (Braddick et al., 2002). It has been shown that only with a small number of transparent directions is it possible to discriminate n simultaneous directions from a larger number of directions (Mulligan, 1993b). Furthermore, humans are only able to identify a small number of directions (2–3) from noise when other cues to discriminate the groups of dots (e.g. depth, colour, brightness) are excluded (Zanker, 2000). From a computational point of view this is surprising, because a simple model of a motion detector network is able to separate a considerable number of motion directions in the same field (Zanker, 2005). Such a pattern of similarities and discrepancies between computer simulations and psychophysical results suggests that at some stage the human capacity of processing of visual motion information is substantially limited. What could be the reason for such capacity limitation? Firstly, low level encoding of local motion signals must generate frequency distributions of local directions with separable peaks corresponding to these directions as a necessary condition for separating transparent motion directions after appropriate global integration. Secondly, a representation of multiple directions is needed for simultaneous retrieval of several directions in a psychophysical task. Both operation s could be modulated by higher level processes, such as attention mechanisms selecting a particular direction to reach awareness (the ultimate stage of representation). In a more ecological perspective, because it is not very likely to encounter a large number of transparent surfaces in the real world, it might be possible that human observers selectively attend to only parts of the information that is initially available in the stimulus. Indeed, attention is an efficient and common mechanism of data reduction in visual information processing.

The nature of selective visual attention has attracted a lot of interest in psychology and vision science, generating a number of prominent but sometimes conflicting concepts about its function for human perception and behaviour (Shipp, 2004). Some cognitive models of attention use the 'spotlight' or 'searchlight' metaphors to liken the attentional focus to a beam of light which moves smoothly across the visual field, with size and processing efficiency of the focus being adjusted by 'zooming in or out' (Crick, 1984; Eriksen & St. James, 1986; Posner, 1980). Searching for a target within a set of distracters that are equally salient would require serial processing, like a 'spotlight' scanning across the display being in one place at one time, thus reflecting limited-capacity processing mechanisms. The notion of a unitary attentional focus, however, is debated (Driver & Baylis, 1989; Juola, Crouch, & Cocklin, 1987) because there is evidence that attention can be assigned to non-contiguous regions of the visual field (Castiello & Umiltà, 1992). It is possible that there are some conditions requiring unimodal and others requiring multimodal distributed attention, which suggest differential spatial or temporal cognitive load in different spatial positions (McCormick, Klein, & Johnston, 1998). On the other hand, Broadbent's filter theory (1958) proposes that the perceptual processing of attended and unattended information differs at early stages. In other words, an attentional bottleneck would filter out parts of the information available at the first steps of sensory processing. Later studies showed that in many circumstances unattended information is more likely to be 'attenuated' rather than blocked entirely (Raymond, 2000; Treisman, 1964). It also has become clear that attention does not need to be focused on a restricted part of space, but can be attached to objects instead (Braun, 2000; Intriligator & Cavanagh, 2001). In particular, it has been shown to be possible to track several independently moving targets in parallel (Pylyshyn & Storm, 1988).

Taken together, these findings clearly indicate that attention does affect visual perception in manifold ways—in the context of motion transparency it could influence the early stages of encoding local motion signals by changing local filter properties, as well as on higher levels of representation, selecting a limited number of directions from a set of encoded directions by dividing attention between separate surfaces. In this study we therefore made an initial step to investigate the effect of attention on the early steps of transparent motion perception by asking whether focusing attention can improve the detection of a particular motion direction in set of several transparent motion directions. Whereas motion transparency can also be used as an experimental tool to study the potential and limitations of human observers to split attention to multiple surfaces, similar to multiple objects or locations, we first need to know about early limitations of transparent motion processing, which is the topic of the present study. Some of the preliminary work leading up the experiments described here have been published as conference abstract (Felisberti & Zanker, 2004; Zanker & Taylor, 2003).

2. Methods

One of the authors and five volunteers from the Department of Psychology participated in this study. The four women and two men had normal vision and gave informed consent to participate in this study. All but one observer (FF) were unaware of the purpose of the experiments.

Stimuli were generated on a digital stimulus generator (VSG 2/5, Cambridge Research Systems) hosted by a standard PC (Pentium IV). The experimental programs were written in Visual C++. Stimuli were displayed on a high-resolution monitor (EIZO T662) at a frame rate of 80 Hz. Observers were sitting at 50 cm viewing distance from the monitor in a dimly illuminated room and were asked to fixate a central fixation point on the screen. Random Dot Kinematograms (RDKs) consisted of 256 bright dots, each covering 2×2 pixels (0.1°), which were displayed within a circular aperture with 256 pixels diameter (13°). The dots were plotted as bright, white dots against a grey background. Each dot in the RDK was displaced by 2 pixels between two consecutive frames along a linear path (leading to a velocity of 8.2°/s) and was warped around the stimulus field when leaving the frame boundaries such as to keep dot density constant at 2%. The luminance of the dots was 58.5 cd/m^2 and that of the background was 13.8 cd/m^2, leading to a local contrast of 62%.

The motion direction was set to a random value for the first set of dots for each trial. An equal number of dots were randomly allocated to each of a given number of directions of motion with the overall number of directions present in the transparent motion display being treated as a stimulus variable (N_D). The angular separation (AS) between different directions in the initial experiments varied together with the number of directions and it was determined by dividing the total circumference by the number of directions (AS = $360/N_D$). In other words, a RDK with $N_D = 2$ will have 128 dots moving in one direction and 128 dots moving in a direction 180° apart. If $N_D = 8$, 8 sets of 32 dots would be moving at 45° from each other. In experiment 4 we used a different configuration, fixing the number of directions ($N_D = 2$) while varying AS between 45° and 180°.

In order to study temporal integration the duration of each RDK was varied between 100 and 600 ms. Dot lifetime, i.e. the path length on which each dot moved before disappearing and re-emerging at a completely new, random location in the display, was varied in a range from 4 consecutive frames to infinite (i.e. continuous motion of all dots). In the case of limited lifetime, the same number of dots was relocated for each frame and for each of the directions contained in a given stimulus.

To test a possible effect of attention on motion transparency, two conditions were randomly interleaved. In the *precued condition* a specific direction of motion was indicated to the observer prior to the RDK presentation, so that attention could be focused on that direction of motion. In the *uncued condition*, however, no such information about motion direction was given and the observer could allocate their attention to any of the directions present in the RDK. The observer's task was to decide on basis of a post-stimulus cue whether a particular motion direction was present or not in the RDK. The task remained the same when the effect of a range of stimulus parameters was investigated.

The method of constant stimuli was used to determine the threshold for the maximum number of directions that is present in a set of moving dots, from which a particular direction can be detected with and without attending to this direction. After each stimulus presentation the observer was asked in a yes–no task whether they had seen a particular direction contained in the stimulus. In half of the trials the asked motion direction was present but it was absent in the other half.

This task of detecting a particular direction of motion in a transparent stimulus differed critically from the standard design of transparency experiments as described in the introduction (Mulligan, 1993b). In those experiments the observers were just asked to notice any difference between two direction distributions, which did not require them to detect the presence of any one particular direction because the task could be solved purely on the basis of discriminating overall shapes of direction distributions (Treue, Hol, & Rauber, 2000). In contrast, in our experiments the observers needed to base their decisions about seeing a particular direction on an explicit representation of a set of motion directions.

Each trial consisted of four consecutive intervals (see Fig. 1). Trials were separated by a screen showing instructions which lasted about 500 ms. The presentation order was as follows: (i) a static, green arrow was displayed behind the red fixation point, indicating a direction of motion to be attended (*precued condition*), or a white circle surrounding the fixation point (*uncued condition*); (ii) the screen was grey, apart from the static red fixation point in the centre; (iii) the Random Dot Kinematogram appeared behind the static red fixation point; (iv) another static arrow was displayed together with the question whether this direction was part of the transparent motion stimulus. Two response buttons were shown on the screen for the observer to enter their decision by means of the computer mouse. The same number of precued and uncued trials was used, and the same number of trials in which the cued motion direction was present and in which it was absent; their order was randomized within each block of trials, together with the number of directions present in the transparent motion stimulus. A typical experimental run contained 5 blocks of 20 trials for one particular parameter setting (stimulus duration, dot lifetime), taking about 25 min. At least 40 trials were completed for each of the directions tested, by testing a given parameter setting twice or more for a given observer.

In each trial the subject's task was to indicate whether the direction indicated by the last arrow was present in the RDK or not, by clicking with the mouse the 'yes' or 'no' on the graphic user interface. In the standard experiments, no feedback was given as to whether the decision was correct or false. The computer program recorded the number of times a subject correctly identify the presence or absence of a direction for a given stimulus configuration, and the data were pooled for each of the two attention conditions and each number of motion directions separately. The psychometric functions were fitted to two-parameter cumulative Gaussian function using the gradient descent method in MATLAB (examples shown in Fig. 2). The 95% confidence intervals were estimated by a bootstrap procedure (Efron, 1979; Efron, 1982). The two parameters of the Gaussian function fitted to a given experimental data set were used to simulate new data sets by adding to the expected values a random number that was drawn from a normal distribution. The thresholds were calculated for 40 such simulations and the resulting variance was used to calculate the confidence interval.

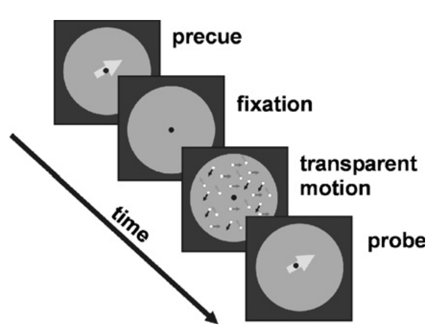

Fig. 1. Schematic representation of the sequence of events in a stimulus trial, as used in the precued condition. (i) *Precue*: static arrow indicating a direction of motion to be attended (in the uncued condition, the fixation spot would be centered on a small white disk); (ii) *Fixation screen*: central fixation point only; (iii) *Transparent motion*: RDK with up to 8 motion directions; (iv) *Probe*: another static arrow to ask whether a particular was present in the stimulus (in this example was the same as the precue, but the answer should be 'no' because this direction was not part of the transparent motion stimulus).

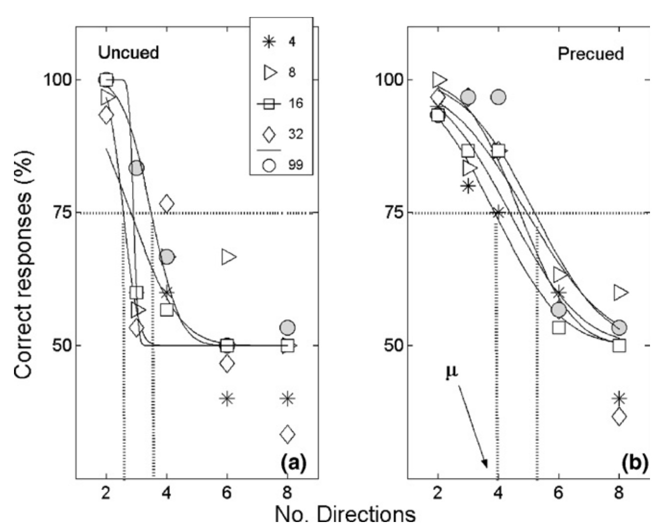

Fig. 2. Psychometric curves from one observer (raw data for Fig. 4a). The five points in each graph show the proportion with which the observer NM identified correctly the direction of motion in RDKs containing 2, 3, 4, 6, and 8 transparent motion directions; the five graphs represent data for five different dot lifetimes (see different symbols in the legend). Sigmoidal curves were fitted to the data points and the threshold for each curve was considered to be the number of directions at which the psychometric curve reached 75% correct decisions (indicated by vertical dotted lines and 'μ'). (a) '*Uncued*' condition and (b) '*Precued*' conditions. The stimulus duration in this example was 400 ms.

3. Results

3.1. Effect of attention and stimulus duration

The first objective was to identify the upper limit of number of transparent stimulus directions that still allows an observer to recover a direction, which therefore needs to be explicitly represented in the visual system, and whether this limit depends on attention. Because we did not know whether and how attention mechanisms might benefit from temporal integration of motion information, we varied stimulus duration in our first experiment and measured performance for precued and uncued motion directions. Previous studies have shown that attentional modulation involves later levels in the motion processing stream (Büchel et al., 1998; Chawla, Rees, & Friston, 1999) and therefore might benefit from additional processing time which is available when stimulus duration increases. We varied the duration of the stimulus presentation from 100 to 600 ms and the number of directions (N_D) from 2 to 8. We did not use longer stimulus duration because we wanted to minimise the chance that individual dots are tracked overtly or covertly, which could enable the observer to convert the transparency problem into a strategy to sequentially track different directions. Although it is clear that tracking can be initiated with shorter latencies (Findlay & Walker, 1999), switching between different directions would only become a substantial issue for stimulus durations much longer than a few hundred milliseconds. For all durations dot lifetime was kept constant at 32 steps, such that each dot was moving along a given trajectory for up to 32 frames and that each frame contained 256/36 = 8 dots 'reborn' in random locations.

Fig. 3 shows the effect of stimulus duration on thresholds for detecting a given direction in a number of transparent motion directions for the four observers participating in this experiment. Thresholds appear not to be systematically affected by inspection time in the absence of directional cues ('uncued' condition), remaining between 2 and 3 directions for all but one observer (RA reaching 4 under some conditions, Fig. 3b). A different picture emerges when observers were given a direction cue prior stimulus presentation. Attending to a precued direction helped to improve the performance of NM and RA considerably (Fig. 3a–b), who reliably identify a direction of motion amongst 4–6 directions. This improvement is small for short stimulus durations, suggesting that attentional mechanisms benefit from temporal integration. The performance of FF and MF (Fig. 3c–d) improved only slightly to 4 directions and only with long inspection durations ($\geqslant$400 ms). These results show that attention can play an important role in direction identification during motion transparency in some observers, but has much less effect in others.

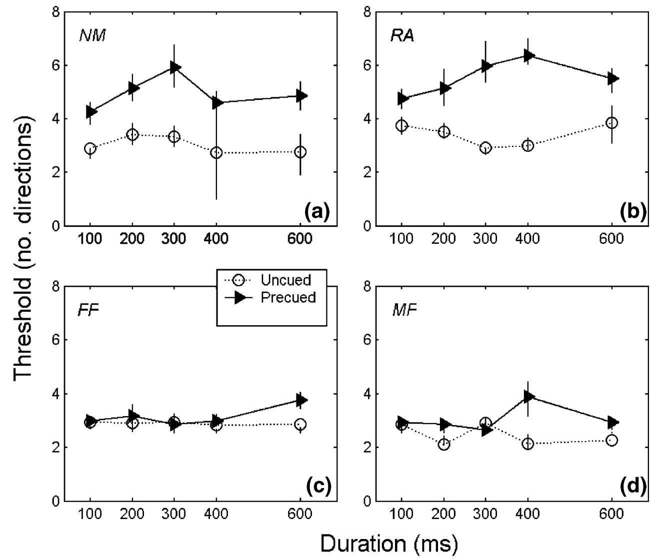

Fig. 3. Effect of stimulus duration on thresholds for detecting a particular direction in a variable number of transparent motion directions for 4 different observers. In the '*Precued*' condition (closed triangles) the direction of to be detected was indicated prior to stimulus presentation, while in the '*Uncued*' condition (open circles) no prior information was provided. Dot lifetime was 32 steps. Error bars reflect 95% confidence intervals. (a,b) The presence of a directional cue helped the two experienced observers NM and RA to improve performance all durations tested. (c,d) The effect of precueing was small or absent in the two other observers, FF and MF.

Temporal integration mechanisms that can take advantage of extended stimulus durations could operate on various levels of the visual processing stream. While the allocation of attention itself could be a time-limited process, it is equally possible that the accumulation of directional information over time could improve the decision-making on a higher level, or that the integration of local information along the trajectory of individual dots could improve the quality of the early sensory signals on a lower level. For instance, additional time might allow observers to track individual dots and use sequential tracking episodes to identify a growing number of directions. Tracking a particular dot direction would also change the retinal stimulus information considerably, for instance with respect to perceived contrast of dots moving at different speeds. One might suspect that attentional cues could be exploited to prepare tracking eye movements, and that the differences in performance observed for different participants could be due to developing such strategies. Taking advantage of tracking the precued direction would not directly explain the strong influence of the number of transparent motion directions, whereas tracking performance might also depend on the number of dots in the stimulus (i.e. the density of distracter signals), which is shown in section 4.4 not to be the case. To clarify this situation, we compared fixation stability for different stimulus conditions in a control experiment using an infrared eye

Table 1
Average fixation errors (in degrees) for two observers (FF and RA) for transparent motion stimuli containing $n = 2$, 4, or 8 directions, for uncued and precued stimulus conditions

	Uncued			Precued		
	$n = 2$	$n = 4$	$n = 8$	$n = 2$	$n = 4$	$n = 8$
FF	0.163+/−0.029 95%	0.174+/−0.045 70%	0.166+/−0.036 40%	0.168+/−0.033 100%	0.166+/−0.040 80%	0.155+/−0.022 65%
RA	0.147+/−0.048 100%	0.136+/−0.033 95%	0.143+/−0.033 60%	0.142+/−0.026 95%	0.140+/−0.039 95%	0.156+/−0.064 70%

Stimuli in these control measurements had 400 ms duration and infinite dot lifetime. The table lists the mean values and standard deviations for 20 stimulus episodes in the top row, and the percentage of correct responses for the same stimuli in this control experiment in the bottom row for each observer.

tracker (CRS Video Eyetracker Toolbox) to monitor eye position during the motion stimulation in our multiple direction experiment. Table 1 shows for two observers the mean two-dimensional distance of the eye position from the average position during the motion stimulus interval for 2, 4, and 8 transparent motion directions with and without presenting a direction cue prior to the stimulus. The fact that these fixation errors are very small, generally below 0.2° of visual angle suggests that stability was excellent indeed, and if anything was better for the trained participant who achieved higher performance levels. Furthermore, fixation stability did not depend on the number of directions in the stimulus and the presence of attentional cues. Together, these observations make it highly unlikely that our participants are making use of eye movement strategies.

Furthermore, in the simplest case of temporal integration mechanisms, individual moving dots could lead to motion streaks by means of temporal integration in the sensor arrays at the earliest processing stages which could be used as orientation cues to tell motion directions apart (Geisler, 1999). Therefore in our second experiment we investigated the role of local, and thus spatial, integration mechanisms by manipulating the trajectory length of individual dots while keeping the global motion information approximately constant.

3.2. *Effect of motion path length—spatial and temporal integration*

With the first experiment we showed that some observers are able to reliably identify a particular direction of motion in a set containing 4–6 directions, if they attended to it for at least 100 ms. Performance improvements for precued directions with increasing stimulus duration could be due to local integration along motion paths or temporal integration of global motion information. Decreasing the average path length of dots by reducing their lifetime, while keeping stimulus duration constant, would affect local integration mechanisms but should have only a minor effect on temporal integration mechanisms because reducing dot lifetime does immediately restrict local integration but marginally reduces the overall number of coherent displacement steps. We set up our second experiment to test the effect of dot lifetime on direction identification in the presence or absence of directional precues.

Here we varied the dot lifetime from a short, flickering trajectory (4 stimulus frames) to a smooth, continuous one (infinite lifetime) in which dots persisted throughout all stimulus frames. Note that some dots would be wrapped around when leaving the aperture, so a small number of shorter trajectories are possible. The duration of the RDKs was fixed at 400 ms because most observers showed the strongest attentional effects at this presentation time (see Fig. 3). As before, the number of directions varied between 2 and 8. It is important to notice that when dot lifetime was 32, 8 dots were 'reborn' at each frame, while with infinite dot lifetime all dots moved along a continuous trajectory during all frames.

Fig. 4 shows the summary of the threshold measurements (maximum number of directions in which a given direction can be identified reliably) obtained from five observers. In some individuals thresholds depend on dot lifetime in the precued condition, while no consistent changes can be observed in the uncued condition. Similarly to results plotted in Fig. 3, observers in this experiment were able to identify one particular motion direction in no more than 3 others when precues were absent, suggesting that local integration mechanisms are not the limiting factor in pre-attentive perception of transparent motion, when the task is to identify a particular motion direction. The performance could change dramatically for some observes, however, when they were able to attend to a direction that was cued prior stimulus presentation.

Indeed, attending to a precued direction led to a clear effect of dot lifetime on observers NM, RA, and HG, who were able to identify one out of 4–6 transparent directions (Fig. 4a, b and d) showing a clear effect of path integration. Observers MF and FF do not show any significant improvement within the range of dot lifetime values used (Fig. 4c and e). Comparing Figs. 3 and

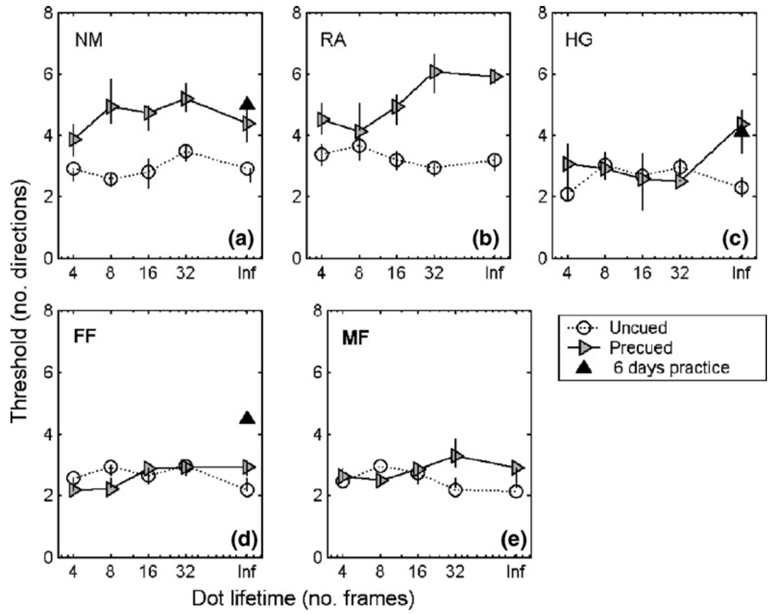

Fig. 4. Effect of dot trajectory length on thresholds for detecting a particular direction in a variable number of transparent motion directions for five observers. Dot lifetime is given as number of frames. Grey triangles: '*Precued*' condition. Circles: '*Uncued*' condition. Black triangles: thresholds after 6 days of practice with infinite lifetime and auditory feedback (tested in 3 participants). The stimulus duration was 400 ms. Error bars reflect 95% confidence intervals. (a, b) The motion direction cue helps to improve performance in observers NM and RA. The performance of NM did not change significantly with further practice. (c–e) Observers HG, FF and MF show a small effect of the cue at long dot lifetimes. The performance of FF improved further with practice, other than the performance of HG.

4, it appears that the patterns of performance changes resemble each other for increases of stimulus duration and increases of path length, respectively. This similarity could be interpreted as indication that the temporal integration effect observed in experiment 1 is not necessarily an effect of integrating local motion signals in time irrespective of their spatial relations, but could be due to mechanisms of local motion integration along the trajectories which grow longer with increased stimulus duration if they are not limited by dot lifetime. In general, the two figures show improvements of attentional effects with spatio-temporal integration. One might suspect that attention should have the biggest effect when a stimulus is most difficult to see, i.e. at shorter integration times or paths. However, it is not the case that the stimulus visibility as tested in our task is affected by integration as such, because the angular separation between different direction signals stays the same with time or along the path, but varies with the number of transparent directions presented. This suggests that the precue prompts attention mechanisms to select one particular direction, and that the extraction of this selected information then benefits from integration mechanism.

The attentional effect on motion transparency varied substantially among our observers in the first two experiments. The observers showing a larger attentional modulation were seasoned observers (NM and RA), having taken part in a wide range of previous psychophysics experiments involving visual motion stimuli (but not similar to any of our stimuli). The other observers did not have any previous experience with motion detection experiments. The most obvious question was whether previous practice with motion stimuli could explain the differences observed so far. To test the possibility that practice would influence the motion transparency task three observers run through 6 consecutive sessions with a standard stimulus configuration (400 ms duration, infinite dot lifetime), providing auditory feedback to boost perceptual learning. Whereas the two observers who already had reached better thresholds in the precued condition of experiment 2 did not show further improvement, one observer who only made marginal use of the precue in experiment 2 was indeed able to improve thresholds under this training regime (data are shown in Fig. 4 as black triangles).

3.3. The effect of attention on minimum angular separation between directions of motion

In the previous experiments the angle between transparent directions varied together with the total number of directions in the RDKs, because all directions were spaced equally. It follows that the stimulus with 8 directions of motion and 45° angular separation between neighbouring directions would pose a harder task of separating two neighbouring directions than the stimulus, for instance with 4 directions and 90° separation. With our third experiment we intended to find out to what extent the limits for extracting transparent motion signals are determined by the angular difference between directions present in the RDKs, and how these limits may be influenced by attending to a precued direction. The angular differences between two transparent directions were: 45, 60, 90, 120, and 180°. We used RDKs with dot lifetimes fixed at 32 steps, and each angular separation was tested at 4 stimulus durations ranging between 100–400 ms. The task was the same as in the previous experiments, i.e. to identify whether a particular motion direction was present in the motion stimulus, with and without a precue given prior to the motion sequence.

Fig. 5 shows how thresholds for the angular separation between two transparent directions depend on stimulus duration and cueing condition in four observers. In general, thresholds for the uncued condition were not affected by stimulus duration, but showed some inter-individual differences. The minimum angle between two directions that can be separated was generally larger for the uncued than for the precued condition. It appears that observer RA has reached peak performance in both precued and uncued conditions, being able to identify the direction of motion even when the angular difference between two motions was ~60° and the stimulus duration was as short as 100 ms (Fig. 5a). This could be partially related to the experimental design, which did not include separations smaller than 45°, thus allowing for the possibility of ceiling effects at these performance levels. With a directional cue prior stimulus onset the thresholds of the remaining observers (NM, HG, FF) decreased as stimulus duration went from 100 to 400 ms (Fig. 5b–d).

The minimum angle between two directions that can be separated is consistent with the performance of the subjects in our previous experiments. Most observers had thresholds around 120° in the uncued condition, which corresponds to the angular separation between 3 directions of motion in the first two experiments. Thresholds for the precued condition at long durations also agree with previous results. Observer NM had a precued threshold at around 60° (Fig. 5b), which corresponds to the angular separation in a set of 6 directions and is the best multiple directions threshold this observer achieved in the first two experiments. For observers HG and FF the lowest thresholds were at around 90° (Fig. 5c–d), which corresponds to an optimal performance with sets of 4 directions achieved in the first two experiments. This could suggest that the performance limits for detecting a particular direction in multiple direction transparent stimuli depends on the angular separation between neighbouring directions.

3.4. Influence of number of dots

In previous experiments, the total number of dots was kept constant in any given stimulus, but since the 256 dots were divided by the number of directions, *n*, the number of dots assigned to each individual direction varied accordingly (256/*n*). To study whether the number of dots assigned to a given direction of motion would affect the observer's performance, we carried a control experiment with a constant number of dots allocated to each direction while varying the number of

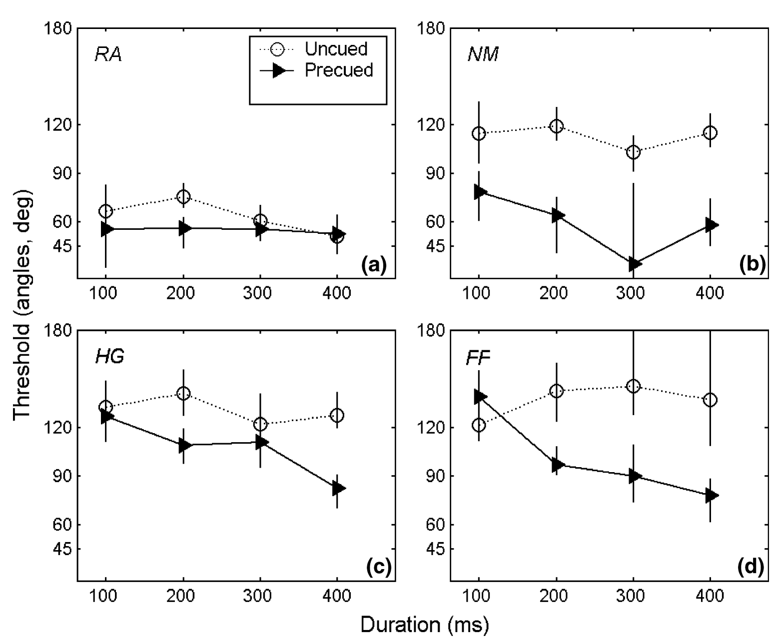

Fig. 5. Effect of stimulus duration on minimum angular separation thresholds at which a particular direction is detected in two transparent motion directions for five observers. Dot lifetime was 32 steps. '*Precued*' condition: triangles. '*Uncued*' condition: circles. Error bars reflect 95% confidence intervals. (a) Observer RA has a similar performance in both conditions and can consistently separate two directions down to small angles. (b–d) Angular separation thresholds for the precued condition are generally lower than for the uncued condition, decreasing for longer stimulus durations.

directions. It should be noted that this stimulus design led to a variation of the overall number of dots present in a RDK with the number of motion directions.

The stimuli in this experiment were similar to the ones in experiment 1. The main difference between the two experiments was that instead of a having a fixed number of dots *per stimulus* (256), here we had a fixed number of dots *per direction* and a fixed stimulus duration (always 600 ms). For example, in experiment 1 a stimulus with 8 directions of motion would contain 32 dots per direction. In experiment 5, each of the 8 directions contained a variable number of dots (1, 4, 8, 16, 24, 32, 48, 64, or 80) and therefore a given transparent motion stimulus could have between 2 and 640 dots.

The effect of varying the number of dots per direction for observer FF is shown in Fig. 6a and for RA in Fig. 6b. Thresholds for both observers were relatively stable in both precued and uncued conditions even though the number of dots per direction was increased from 1 to 80. Similar to the results obtained in experiment 1 (duration: 600 ms), precued thresholds were around 5–6 for observer RA for all numbers of dots per direction, while uncued thresholds were around 4 for all numbers of dots per direction above 1. However, if only a single dot was assigned to each direction, this observer was able to deal with more than 5 directions, suggesting a change of strategy for lower signal density, possibly making use of the tracking of multiple targets (cf. Pylyshyn & Storm, 1988). The thresholds for observer FF were similar, around 3, in the precued and the uncued condition

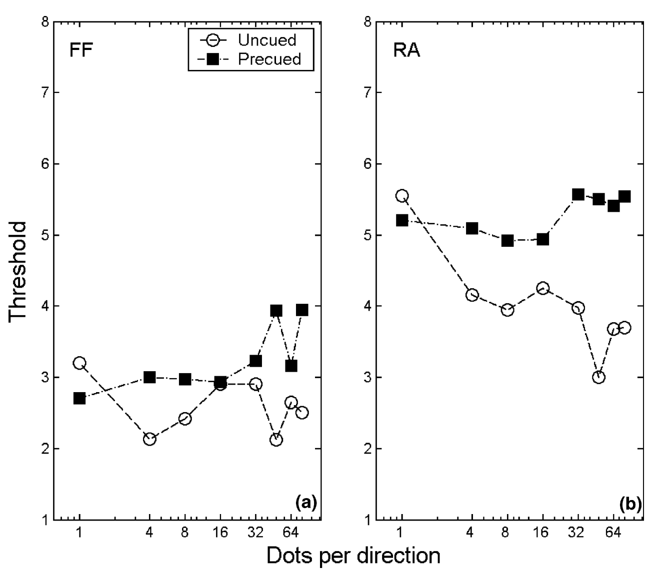

Fig. 6. Effect of number of dots per direction on direction thresholds for two observers. The stimulus duration was 600 ms, and dot lifetime was infinite. '*Precued*' condition: squares. '*Uncued*' condition: circles. (a) A directional cue helped to raise the threshold of FF only when 48 or more dots were presented per direction, while (b) the threshold for RA was visibly higher for the precued condition for all stimuli with more that a single dot per direction.

when the number of dots per direction was small, raising to near 4 dots/direction for the precued condition when the dot density was at its highest while remaining around 3 in the absence of directional cues. This pattern of results suggests that this observer could benefit slightly form higher signal density if attentional cues were available.

4. Discussion

Our results show that in general our observers, if they were given a cue about a motion direction to be attended, were more likely to detect the presence or absence of this direction in a display with multiple directions than without prior information about which direction to attend. The size and coherence of this effect varied considerably between our observers who had different amounts of previous experience with motion processing experiments. In transparent motion stimuli containing only two directions, detection performance decreased when the angular separation between the two directions was reduced. Most observers could reduce the minimum angular separation that still led to reliable identification of one of the directions in the precued condition. It is relevant to point out that in our experiments observers were not only asked to notice some unspecified difference between two transparent direction distributions, but were required to detect one particular direction of motion in a set. Their choice, therefore, needed to be based on an explicit representation of a set of directions and not on the comparison of the shape of two distributions without necessarily knowing at least one individual direction contributions. We also demonstrated that varying the number of dots assigned to each direction in a multiple direction transparent motion stimulus did have no major influence on this detection performance in both precued and uncued conditions, as long as dot density was above the bare minimum of a single dot moving in each direction.

4.1. Precues indicating direction

Within the range of stimulus conditions used here, the single most important factor affecting performance was whether observers were given a cue prior the onset of a stimulus, indicating a particular motion direction to attend to. Our results show that the provision of a directional cue prior to the motion sequence can activate a mechanism, which enhances the detectability of a specific direction and allows it to be separated from a second superimposed direction when its angular separation gets smaller, or from a larger number of superimposed directions in multiple direction stimuli. The strong correspondence between these effects suggest s that the cue might guide attention to narrow the directional sensitivity of local motion processing which is critical to separate adjacent directions. Indeed, the attentional state of an observer is known to play a crucial role in visual motion perception in various ways (Cavanagh, 1992; Dobkins & Bosworth, 2001; Raymond, 2000). Several studies have shown that attention enhances the simultaneous processing of motion information at early and late stages in the visual processing stream of humans and other primates (Alais & Blake, 1999; Treue & Trujillo, 1999). Physiological studies showed that neurons in areas V5/MT and MST, for example, roughly double their responses when a moving stimulus within the receptive field is the focus of attention (Alais & Blake, 1999). It seems that if there is competition for the same perceptual analyzers during simultaneous motion judgments, processing advantages gained in one neural stage would be transmitted to the next (Valdes-Sosa, Bobes, Rodriguez, & Pinilla, 1998). At later stages in the cortical stream a wider network of parietal and frontal cortex seems to be engaged by attention to motion but not by motion per se (Büchel et al., 1998). Again, such findings show that attention selectively enhances the representation of attended stimuli and reduces the influence of unattended stimuli (Treue & Trujillo, 1999). The pattern of inter-individual differences in our experiments mainly relate to utilizing the precue to improve performance, suggesting that some more experienced observers developed an ability to focus attention in a highly rehearsed task.

In the absence of directional cues our observers were able to identify one particular direction amongst 2–3 distinct directions, suggesting that the human visual system can accurately separate a small number of directions from transparent motion direction distributions. This could explain why a previous study on transparent motion indicated that the visual system may be fundamentally limited to segmenting 2–3 motion directions from spatially intermingled moving dots when observers were not attending to any specific direction (Hiris, 2001; Mulligan, 1993a). Although our experiments do not show whether observers can detect several directions of motion occupying overlapping regions of visual space *simultaneously*, the possibility to extract a particular cued direction of motion from transparent stimuli with 4 or more directions indicates that attention is attached to one of several superimposed motion surfaces and not to a specific location in the visual field (Treue & Trujillo, 1999).

4.2. Spatial and temporal integration

The fundamental problem for the visual system with motion transparency is to keep motion measurements from different objects or surfaces separate while integrating motion across time and space in order to reduce noise (Braddick, 1997) that is inherent to the stimulus and to the sensory system, generating broad motion direction distributions (Zanker, 2005). Our data suggest that temporal pooling of motion signals across a variable number of stimulus frames had only a minor effect on the thresholds for detecting a particular direction in a set of transparent directions, and that this small effect is restricted to the precued condition. Local and global motion signals could have been integrated in space and/or time to improve performance, as they are for other tasks (Watamaniuk & McKee, 1998). In transparent motion, however, large-scale spatial integration would merge and thus attenuate or extinguish, the motion signals from dots moving in different directions. Therefore spatial integration needs to be local, i.e. along the trajectories of individual dots and in the absence of dots moving in other directions in the close vicinity (Qian et al., 1994). A possible but not very strong role of small-scale spatial integration on separating transparent motion signals was indicated by the result of our second experiment, manipulating the average length of individual dot trajectories, which lead to results in close correspondence to those observed for manipulation of stimulus duration. The reason why we only found comparatively weak integration effects could be due to the fact that we restricted to values not larger than 600 ms because we wanted to reduce the possibility that observers switch attention between different motion directions in the transparent stimuli and detect several directions sequentially. Estimates of the minimum duration to find substantial temporal integration effects for coherently moving random dot patterns can vary from 500 ms to 3000 ms, depending on stimulus conditions (Burr & Santoro, 2001; Watamaniuk & Sekuler, 1992).

Eye movements could provide our observers with a possibility to change the retinal stimulus and could allow them to track individual motion directions. Smooth pursuit eye movements have been shown to improve direction discrimination due to spatial integration along the dot's path (Williams & Sekuler, 1984), but pursuit movements are only triggered by coherent motion lasting at least 200 ms (Watamaniuk & Heinen, 1999). One might suspect that attentional cues might change this temporal limit, but there is little influence of attention cues on the delays of fixation saccades (Findlay & Walker, 1999). The effect of eye movements in transparent motion stimuli is not straightforward because pursuit of one group of dots can not only reduce (or null) the motion of these dots, but also induce an additional motion component on all the dots in other motion directions, which may change their direction and speed. When we measured fixation stability in a control experiment, we found no evidence for substantial departures from the fixation target and no influence of cues given prior to the stimulation.

Even in the absence of eye movements, there could be the possibility that observers could benefit from attentional cues by applying a local processing strategy. Basically, they could restrict the attended region such that they detect the direction of individual dots and then either register the directions of individual dots within such small region sequentially, or split their attention to detect several directions simultaneously. In some previous studies (Smith, Curran, & Braddick, 1999) this strategy was prevented by the use of broad direction distributions for each of two transparent motion components, but this was not possible here because we tried to test the upper performance limit with very narrow direction distributions. It should be noted, however, that noise in the motion detector response automatically broadens the direction distribution (Zanker, 2005), which reduces the significance of this methodological difference considerably because the direction of each individual dot in a RDK can only be determined with some uncertainty. Indeed, a failed attempt to teach one of our observers with lower performance to focus on detecting local dot motion sequentially casts doubt on the possibility that our high-performing individuals were actually adopting such a local strategy to boost their performance for cued motion directions. (while remaining unaware of the strategy as such). Furthermore the efficiency of such a strategy would depend critically on dot density because additional dots moving in different directions in close neighbourhood would prevent the reliable determination of single dot directions. In experiment 4 we demonstrated that only one observer could improve performance for smaller number of dots, and only for the minimal number of dots per direction, suggesting that under such extreme condition some kind of simultaneous tracking might be used (cf. Pylyshyn & Storm, 1988).

In overall, our results indicate that cues guiding the observer to attend a particular direction in a dense dot transparent motion stimulus seems to activate mechanisms in the visual system that pool early motion signals along motion trajectories, thus avoiding the pooling of different transparent motion directions. The similarity of attentional effects for multiple direction (experiments 1 and 2) and variable separation (experiment 3) stimuli further suggests that the limiting computational demand is the angular separation of adjacent directions, and that such a mechanism therefore affects the effective width of the direction tuning for motion signals in the pooled region.

4.3. Angular separation

From a computational point of view, the limitation in the number of transparent directions of motion that can be encoded simultaneously should be directly determined by the minimum angular difference between two superimposed directions that can be separated. Initial data from the literature seem to suggest that this figure should be rather low (around 15°; Marshak & Sekuler, 1979; Mather & Moulden, 1980) and therefore the thresholds estimated in our first two experiments might result from some upstream limitation for the number of directions that are represented explicitly. However, the experimental conditions and task performed by observers are critical here, which becomes apparent in the direct comparison in experiment 3, using exactly the same stimuli and the same task. The minimum angular separation between two directions in transparent motion stimuli that still allowed identifying one directions individually was found in this experiment to be comparatively large, and to match the observer's performance in detecting a single direction within a larger number of directions, for both the cued and uncued condition. The causes for the difference between our lowest direction separation threshold (~60°) and the minimum difference between resolvable angles reported in previously (~15°) is most likely to be related to the nature of the task to be solved by the observers. In the experiments leading to very small separation thresholds observers were asked to adjust a pointer in the direction of a group of dots which was moving in a predictable direction or was labeled before motion onset (Marshak & Sekuler, 1979; Mather & Moulden, 1980), and therefore did not require explicit representation of both directions at the same time. In accordance with our data, evidence from creating perceptual metamers of multiple direction motion stimuli (Treue et al., 2000) suggests that in the neural population code transparent directions cannot be resolved individually if they are not separated by about 60°, although the overall shape of the directional distribution could be used to solve certain discrimination tasks with higher acuity.

Representation of motion directions can be distorted by 'direction repulsion'—when two transparent directions are separated by *acute* angles the perceived global direction can be enhanced (Benton & Curran, 2003). Early reports of motion repulsion between two transparent directions moving at ⩽45° mention errors in directional judgments of up to 22° (Hiris & Blake, 1996; Marshak & Sekuler, 1979), and recent work indeed shows that attention can reduce repulsion (Chen, Meng, Matthews, & Qian, 2005). Although our smallest angular separations tend to be larger than those for which repulsion is observed, it could be possible that this effect contributes to our results by influencing the accuracy of identifying the direction asked for, when only two directions of motion are present in the stimulus. However, it would difficult to explain our results with RDKs containing several directions of motion along these lines, since the equal spacing between those directions would result in opposite shifts of perceived direction from motion directions on both sides of the one to be identified.

5. Conclusions

Transparent motion signals pose a substantial processing problem to the visual system, which has to separate several overlapping noisy distributions of motion signal. Our experiments show that human performance for identifying a particular direction in transparent motion stimuli is rather limited, both in terms of separating two neighbouring directions at variable angular difference and in terms of separating a variable number of transparent motion directions. However, we demonstrated that attentional cues enhance our ability to solve both of these tasks in a similar way, suggesting that attention is narrowing motion signal distributions, making use of local spatio-temporal integration mechanisms, which allows to separate smaller angles between neighbouring directions, and as a consequence, to identify a direction in more directions being represented at the same time within the same region of the visual field. Future experiments will have to show how many directions can be detected simultaneously, which is beyond the scope of our present task, but from the experiments presented here we know that the number of directions that can be separated from the encoded motion signals in the early visual system, which is limiting the simultaneous perception of multiple directions, is already severely limited.

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References

Alais, D., & Blake, R. (1999). Neural strength of visual attention gauged by motion adaptation. *Nature Neuroscience, 2*(11), 1015–1018.

Benton, C. P., & Curran, W. (2003). Direction repulsion goes global. *Current Biology, 13*, 767–771.

Borst, A. (2000). Principles of visual motion detection. *Nature, 3*, 1168.

Borst, A., & Egelhaaf, M. (1989). Principles of visual motion detection. *TINS, 12*(8), 297–306.

Braddick, O. J. (1997). Local and global representations of velocity: transparency, opponency, and global direction perception. *Perception, 26*, 995–1010.

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

Braun, J. (2000). Intimate attention. *Nature, 408*, 154–155.

Büchel, C., Josephs, O., Rees, G., Turner, R., Frith, C. D., & Friston, K. J. (1998). The functional anatomy of attention to visual motion. A functional MRI study. *Brain, 121*, 1281–1294.

Burr, D. C., & Santoro, L. (2001). Temporal integration of optic flow, measured by contrast and coherence thresholds. *Vision Research, 41*, 1891–1899.

Castiello, U., & Umiltà, C. (1992). Splitting focal attention. *Journal of Experimental Psychology, 18*(3), 837–848.

Cavanagh, P. (1992). Attention-based motion perception. *Science, 257*, 1563–1565.

Chawla, D., Rees, G., & Friston, K. J. (1999). The physiological basis of attentional modulation in extrastriate visual areas. *Nature Neuroscience, 2*(7), 671–676.

Chen, Y., Meng, X., Matthews, N., & Qian, N. (2005). Effects of attention on motion repulsion. *Vision Research, 45*, 1329–1339.

Crick, F. (1984). Function of the thalamic reticular complex: The searchlight hypothesis. *Proceedings of the National Academy of Sciences (U.S.A.), 81*, 4586–4590.

Cropper, S. J. (2001). Local and global motion signals and their interaction in space and time. In J. M. Zanker & J. Zeil (Eds.), *Motion Vision—Computational, Neural, and Ecological Constraints*. Berlin, Heidelberg, New York: Springer Verlag.

Dobkins, K. R., & Bosworth, R. G. (2001). Effects of set-size and selective spatial attention on motion processing. *Vision Research, 41*, 1501–1517.

Driver, J., & Baylis, G. C. (1989). Movement and visual attention: the spotlight metaphor breaks down. *Journal of experimental Psychology [Human Perception and Perfection], 15*, 448–456.

Efron, B. (1979). Bootstrap methods: another look at the jackknife. *The Annals of Statistics, 7*, 1–26.

Efron, B. (1982). *The Jackknife, the Bootstrap and Other Resampling Plans*. Philadelphia: Society for Industrial and Applied Mathematics.

Eriksen, C. W., & St. James, J. D. (1986). Visual attention within and around the field of focal attention: A zoom lens model. *Perception and Psychophysics, 40*, 225–240.

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

Findlay, J. M., & Walker, R. (1999). A model of saccade generation based on parallel processing and competitive inhibition. *Beh.Brain Sci., 22*, 661–721.

Geisler, W. S. (1999). Motion streaks provide a spatial code for motion direction. *Nature, 400*, 65–69.

Grunewald, A. (2000). Two directions at the same location? *Trends in Cognitive Sciences, 4*(3), 76–77.

Hiris, E. (2001). Limits on the perception of transparency from motion. *Journal of Vision, 1*(3), 377a.

Hiris, E., & Blake, R. (1996). Direction repulsion in motion transparency. *Visual Neuroscience, 13*, 187–197.

Intriligator, J., & Cavanagh, P. (2001). The spatial resolution of visual attetion. *Cognitive Psychology, 43*, 171–216.

Juola, J. F., Crouch, T., & Cocklin, T. (1987). Voluntary control of attention near the fovea. *Acta Psychologica, 64*, 207–217.

Marshak, W., & Sekuler, R. (1979). Mutual repulsion between moving visual targets. *Science, 205*, 1399–1401.

Mather, G., & Moulden, B. (1980). A simultaneous shift in apparent direction further evidence for a distribution-shift model of direction coding. *Quarterly Journal Experimental Psychology, 32*, 325–333.

McCormick, P. A., Klein, R. M., & Johnston, S. (1998). Splitting versus sharing focal attention: comment on Castiello and Umiltà (1992). *Journal of Experimental Psychology, 24*(1), 350–357.

Mulligan, J. B. (1993a). Motion transparency is restricted to two planes. *Investigative Ophthalmology and Visual Science, 33*, 1049.

Mulligan, J. B. (1993b). Nonlinear combination rules and the perception of visual motion transparency. *Vision Research, 33*, 2021–2030.

Posner, M. I. (1980). Orienting of Attention. *The Quarterly Journal of Experimental Psychology, 32*, 3–25.

Pylyshyn & Storm (1988). Tracking multiple independent targets: Evidence for a parallel tracking mechanism. *Spatial Vision, 3*, 179–197.

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

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

Raymond, J. E. (2000). Attentional modulation of visual motion perception. *Trends in Cognitive Sciences, 4*(2), 42–50.

Shipp, S. (2004). The brain circuitry of attention. *Trends in Cognitive Sciences, 8*(5), 223–230.

Smith, A. T., Curran, W., & Braddick, O. J. (1999). What motion distributions yield global transparency and spatial segmentation? *Vision Research, 39*(6), 1121–1132.

Snowden, R. J., & Verstraten, F. A. J. (1999). Motion transparency: making models of motion perception transparent. *Trends in Cognitive Sciences, 3*(10), 369–377.

Treisman, A. M. (1964). Verbal cues, language, and meaning in selective attention. *American Journal of Psychology, 77*, 206–219.

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

Treue, S., & Trujillo, J. C. M. (1999). Feature-based attention influences motion processing gain in macaque visual cortex. *Nature, 399*, 575–579.

Valdes-Sosa, M., Bobes, M. A., Rodriguez, V., & Pinilla, T. (1998). Switching attention without shifting the spotlight: object-based attentional modulation of brain potentials. *Journal of Cognitive Neuroscience, 10*, 137–151.

van Doorn, A. J., & Koenderink, J. J. (1982). Temporal properties of the visual detectability of moving spatial white noise. *Experimental Brain Research, 45*, 179–188.

Watamaniuk, S. N. J., & Heinen, S. J. (1999). Human smooth pursuit direction discrimination. *Vision Research, 39*, 59–70.

Watamaniuk, S. N. J., & McKee, S. P. (1998). Simultaneous encoding of direction at a local and global scale. *Perception and Psychophysics, 60*, 191–200.

Watamaniuk, S. N. J., & Sekuler, R. (1992). Temporal and spatial integration in dynamic random-dot stimuli. *Vision Research, 32*, 2341–2347.

Williams, D. W., & Sekuler, R. (1984). Coherent global motion percepts from stochastic local motions. *Vision Research, 24*(1), 55–62.

Zanker, J. M. (2000). Motion transparency and multiple motion directions. *Investigative Ophthalmology and Visual Science, 41*, S720.

Zanker, J. M. (2001). Combining local motion signals: a computational study of segmentation and transparency. In J. M. Zanker & J. Zeil (Eds.), *Motion Vision—Computational, Neural, and Ecological Constraints*. Berlin, Heidelberg, New York: Springer Verlag.

Zanker, J.M., (2005). A computational analysis of separating of motion signals in transparent random dot kinematograms. Spatial Vision, in press.

Zanker, J. M., & Taylor, J. (2003). On the role of attention in the processing of transparent motion. *Perception, 32*, S43–S44.