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Motion segmentation from speed cues

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Motion segmentation from speed cues in transparent and corrugated displays

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Abstract

Motion transparency requires that the visual system distinguish different motion vectors and selectively integrate similar motion vectors over space into the perception of multiple surfaces moving through or over each other. Using wide-field displays containing two populations of random-dots moving in the same (horizontal) direction but at different speeds, we examined speed-based segmentation by measuring the speed-difference thresholds above which observers perceived two moving surfaces as opposed to one. We systematically investigated this "speed-segmentation" threshold as a function of speed and stimulus duration and found that it increases sharply for speeds at and above 16deg/sec and decreases exponentially with stimulus duration out to ≈ 500 msec. In contrast, under matched conditions, speed-discrimination thresholds are lower and stay low at least out to 32deg/sec. To examine the spatial interactions that may underlie this threshold difference, we examined the effect of corrugation on speed-segmentation thresholds. Corrugating the patterns into adjacent bars with alternating speeds generally results in significantly lower thresholds but, as the bar width decreases below ≈ 3 deg, the threshold increases and asymptotes close to that for transparent patterns at ≈ 0.4 deg. This transition between the low- and high-threshold regimes corresponds well with that between the perception of corrugation and transparency. We also examined the effect of "pairing", in which the two speeds were locally paired with an horizontal offset < 0.4 deg. Thresholds for the "paired" and "unpaired" conditions diverge as the vertical distance between the paired dots is decreased to a critical distance of ≈ 0.4 deg, which is only slightly sensitive to eccentricity. Below this, the "paired" thresholds rise dramatically and transparent motion is no longer possible even at speed differences of 80%. These results are consistent with previous studies of the spatial constraints underlying segmentation based on direction and extend them to speed-based segmentation. Furthermore, the small size and weak sensitivity to eccentricity of the critical pairing distance together with the fall-off in performance at rather low speeds provides further evidence for the view that transparency is supported by neurons early in the cortical visual motion pathway.

1 INTRODUCTION

Visual motion can be used to determine the three-dimensional structure of objects and to parse complex scenes (see Nakayama 1985 for a review). There is both psychophysical (e.g. Adelson & Movshon, 1982; Welch, 1989) and physiological (e.g. Movshon, Adelson, Gizzi & Newsome, 1985; Rodman & Albright, 1989) evidence that primate motion perception is a two-stage process. First, motion is represented by local measurements of speed and direction. At a subsequent processing stage, local motion measurements are combined to achieve a representation of pattern velocity. This

second stage is constrained by two competing segmentation processes: segregation, which detects changes in velocity across space and parses the image into regions of independent motion, and integration which smoothes local variations in velocity and connects the pieces of local motion associated to the same moving object (Braddick, 1993).

A particularly difficult challenge for these processes is transparency, the simultaneous representation of two or more objects/surfaces moving through or over each other, i.e two velocities represented at a single spatial location. For instance, superimposing random-dot patterns translating in different different directions, can produce

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the percept of two or more rigid structures moving transparently (e.g. Clarke, 1977; van Doorn & Koenderink, 1983; Andersen, 1989; Snowden, 1989; Mulligan, 1993). This phenomenon illustrates the fact that the visual system can segment motion signals even if they are juxtaposed in space and time. The transparent motion of two surfaces leads to the percept of a three-dimensional structure, with each surface associated with a different depth (Andersen, 1989). Alternatively, motion signals of similar characteristics can also be grouped together to form the percept of a rigid structure moving coherently (Adelson & Movshon, 1982; Snowden, 1989; Stoner et al., 1990).

Previous studies have pointed out two properties of motion transparency, that reflect the constraints on image segmentation. First, the segregation of two drifting, transparent surfaces moving at the same speed occurs only if the superimposed random dots move with sufficiently different directions. For instance, no transparency is perceived when the directions of motion of two translating random dot patterns differ by less than 30-40deg (van Doorn & Koenderink, 1983, Møller, 1992). This result suggests that proximity in direction promotes grouping or hinders segregation. Transparency from direction cues may depend on relative speed; even an orthogonally moving background can impair the detection of a second moving pattern (ostensibly by some grouping process), if the two patterns move with similar speeds (Snowden, 1990; Verstraten et al., 1996). This result indirectly suggests that proximity in speed may promote grouping or hinder segregation, but there is as yet no direct evidence without confounding direction cues.

Second, segmentation depends on the spatial distribution of the local motion vectors (van Doorn & Koenderink 1982a,b; 1983). The poor segmentation performance for small direction differences might therefore be explained by local interactions between population of units tuned for different directions. Qian and colleagues (1994ab) systematically investigated this issue both psychophysically and physiologically. A major outcome of their study was that transparency required locally unbalanced motion signals, i.e. local regions with net motion in one direction. When stimuli were finely spatially balanced by the pairing dots of opposite motion within a 0.4deg diameter, transparency was lost. Such local spatial interactions may also underlie the loss of motion gradient detection when the spatial distribution of motion vectors exceeds 3 cpd (van Doorn & Koenderink, 1982b). This result suggests that spatial proximity below a 0.4deg limit causes motion to be pooled.

In the present study, we used moving random-dot patterns to investigate how well speed differences, in the absence of any directional cues, can be used to support segmentation and to probe further the potential neural mechanisms underlying the segmentation process. Relative speed in the same direction is a powerful cue for the segregation of both overlapping (i.e. transparent) or non-overlapping surfaces as exemplified by motion parallax (Gibson et al., 1955) or structure-from-motion (Andersen, 1989). Bravo and Watanuki (1995) demonstrated that, in transparent displays where all dots move in the same direction, subjects are able to locally segregate motion measurements according to speed and to selectively integrate those local motion signals to produce a precise speed signal for one of the two transparent surfaces. Furthermore, studying the segregation process while manipulating differential speed alone avoids the confounding issues of interactions between direction channels and motion opponency. Our experiments have two specific goals. The first is to determine the speed-difference thresholds for distinguishing the presence of one or two surfaces and the dependence of this speed-segmentation threshold upon mean speed and duration. The second is to examine the spatial processing underlying speed-segmentation by measuring its dependency on the spatial distribution of the motion vectors at a range of eccentricities. Preliminary results have been previously reported in abstract forms (Mestre & Masson, 1997b; 1998; Masson & Mestre, 1997, 1998).

2 EXPERIMENT 1

In the main experiment (1-1), we measured the speed difference needed to detect the presence of two subpopulations moving at two different speeds within a pattern of random dots. In a yes/no task, observers were asked whether one or two moving surfaces was present in the stimulus. The effects of average speed and stimulus duration were examined. In a first set of control experiments (1-2), we measured and assessed potential eye movement artifacts. In a second set of control experiments (1-3), we measured, in the same observers, speed-discrimination and speed-segmentation thresholds using a 2IFC methodology. In the speed-discrimination task, observers sequentially viewed two intervals, each with a different uniform speed, and indicated which interval appeared faster. In the speed-segmentation task, observers sequentially viewed two intervals (one with two speeds present and one with a single uniform speed) and indicated which interval contained two surfaces.

2.1 Methods

2.1.1 Observers

Four observers (two authors and two naive observers) participated in this experiment. They had normal or corrected-to-normal vision. Naive observers were not familiar with visual psychophysical tests and gave their informed consent prior to the experiment.

2.1.2 Apparatus

Visual sequences were generated on a Silicon Graphics workstation (Indy, R4000) using OpenGL graphics primitives. Each dot trajectory was pre-calculated and a wrap-around procedure was used to keep dot-density constant at 0.5 dots/deg^2 . The trajectories were then stored on disk for later display. Random dots of luminance 4 cd/m^2 were back-projected onto a large tangent screen at a refresh rate of 76Hz, using a trichromatic projector (Electrohome Marquee 8000). The display contained 2048 dots, one pixel in size, and subtended $70\text{deg H} \times 56\text{deg V}$. The observer's head was stabilized by a chin and forehead rest, the image was at eye level and viewed binocularly from a distance of 1.2 meters. The display resolution was 1280×1024 pixels and, at the chosen viewing distance, each pixel subtended 0.055 deg . The screen background and experimental room were dark. Randomized presentation of the stimuli and recording of the responses (using response keys) were controlled on-line by a PC (HP 486, 66Mhz), connected to the graphics station by a serial RS232 interface.

2.1.3 Visual stimuli and procedures

Exp 1-1 and 1-2: Speed segmentation.

A single frame consisted of 2048 small dots randomly distributed over the whole image. One half of the dots moved at a speed of $v_1 = v(1 + \Delta v/2)$, while the other half of the dots moved at $v_2 = v(1 - \Delta v/2)$ with v ranging from 2 to 64 deg/sec and $\Delta v/v$ ranging from 0 to 80%. Each speed was randomly assigned to half of the dots. Motion direction was always horizontal and rightward. Given the pixel resolution and the refresh rate, the minimal motion generated by the displacement of one pixel across two frames was 4 deg/sec. However, given the high refresh rate, finer speed resolution could be obtained by varying the displacement over successive frames and desynchronizing the motion of the different dots over the frame sequence. For instance, a speed signal of 2deg/sec can be produced by moving one dot by one pixel every two frames. For a 260 msec

stimulus duration, 20 frame movies were generated. For half the dots, increasing (decreasing) the mean speed by 10% was done by adding (subtracting) a 1 pixel displacement in the sequence. Location of such addition (subtraction) within the sequence was randomized across dots to ensure desynchronization of local motion signals.

We used the method of constant stimuli. The stimulus was statically displayed for a random variable duration (between 800 and 1200 msec), then moved for a fixed duration. Predictive eye movements were minimized by the variable duration of the stationary interval. To minimize tracking eye movements further, a blue fixation cross ($1\text{deg} \times 1\text{deg}$, 0.1cd/m^2) was displayed at the center of the image.

For each of six mean speeds (2, 4, 8, 16, 32 and 64 deg/sec) and four durations (130, 260, 520 and 1040 msec), up to seven speed differences $\Delta v/v$ (0, 2.5, 5, 10, 20, 40, and 80%; for stimulus duration of 130 msec $\Delta v/v$ of 2.5 and 5 were randomly presented in blocks of 248 trials (2 trials per condition). Observers typically ran 10 blocks, so that 20 responses were collected for each condition. By pressing one of two response keys, the observer had to indicate whether the random-dot display contained one or two surfaces translating in the same direction. No feedback was ever provided.

Exp 1-3: Speed discrimination vs. segmentation

To compare speed-difference thresholds for segmentation and discrimination, we ran two control experiments using a 2-IFC procedure. A single frame of motion stimuli consisted of 2048 small dots randomly distributed over the whole image. For the speed-discrimination experiment, all dots within an interval moved rightward at the same speed across the visual field. Two intervals of motion, with speed difference Δv (again ranging between ± 5 and 80%) were presented sequentially for 260 msec each, with an Inter-Stimulus Interval (ISI) of 1000 msec. As before, the test intervals were always preceded by a stationary interval of random duration (from 800 to 1200 msec) to reduce predictive eye movements. The presentation order was randomized and 4 reference speeds (4, 8, 16 and 32 deg/sec) were interleaved in blocks of 280 trials (7 trials/condition). Observers had to indicate which interval appeared faster. Observers ran 10 blocks so that responses were pooled over 70 trials for each condition. For the speed-segmentation experiment, we repeated the first experiment using a 2IFC procedure. Observers were presented with two intervals, one with 0% speed difference (uniform speed) and the other with a speed difference of $\Delta v/v$ ranging between 5 and 80%. Observers had to determine the interval with two surfaces. The mean speeds, du-

ration, and ISI were identical to those used in the speed-discrimination experiment. Observers ran 10 blocks so that 30 trials were obtained for each stimulus condition.

2.2 Data Analysis

For each observer, responses were pooled across all runs to give one data point for each speed difference for each experimental condition. In the first motion-segmentation experiment, the data were plotted as the proportion of "two surface" responses versus the speed difference (in %), for each condition separately. With SigmaPlot software, the Marquardt- Levenberg algorithm was used to fit the yes-no psychometric data with a logistic function, Eq. (1):

$$p = \left[\frac{c - d}{1 + \exp(-b - (a.x))} \right] + d. \quad (1)$$

The 2IFC data were plotted as a proportion of correct ("2 surface") responses (ranging from .5 to 1) versus the speed difference, and fit with a Weibull function. For all experiments, the speed difference corresponding to 75% correct responses was defined as the threshold.

We fit descriptive functions to the data to compute estimates of optima and tuning bandwidths. Relationships between average thresholds (across subjects) and mean speed (\bar{v}) or stimulus duration (d) were fit with Eqs. (2) and (3) using the Simplex algorithm run with Matlab software:

$$thr = k_1 \cdot \exp(-a \cdot \bar{v}) + k_2 \cdot \exp(-b \cdot \bar{v}). \quad (2)$$

and

$$thr = a + b \cdot \exp \left[\frac{-(d - d_0)}{\tau} \right]. \quad (3)$$

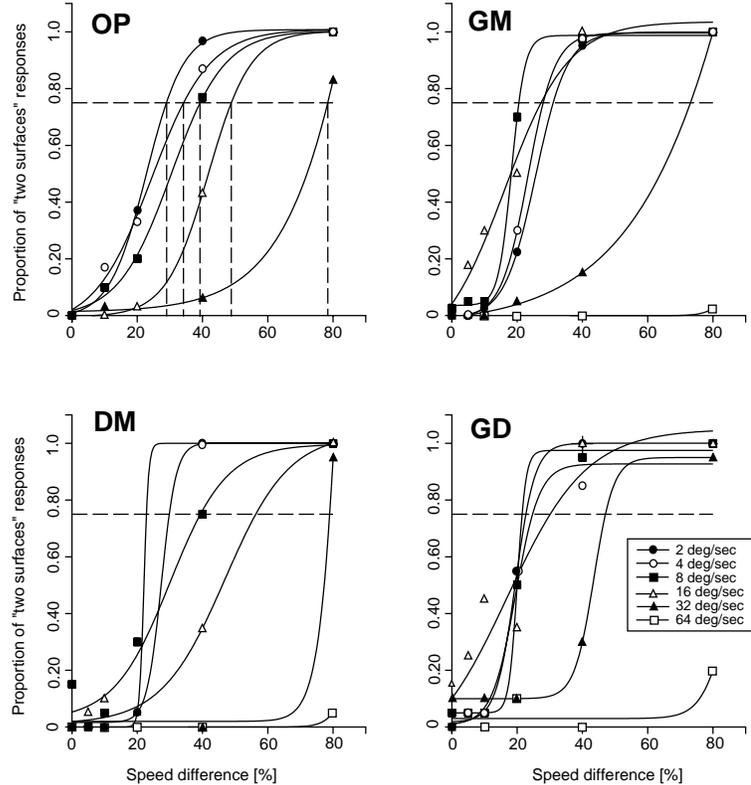


Figure 1: Psychometric curves for 4 observers. The proportion of trials for which observers indicated they perceived "two surfaces" is plotted against the speed difference (in %), for several mean speeds. The continuous lines are the best fits to the data using Eq. (1). Horizontal dotted lines indicate the 75% response criteria used to define our threshold for speed segmentation.

2.3 Results

2.3.1 Exp 1-1: Speed segmentation.

Figure 1 plots raw data for all four observers and mean stimulus speeds, for a 260 msec stimulus duration. The proportion of "2 surface" responses is plotted against speed difference. Horizontal dotted lines indicate the 75% response level and, for observer OP, the vertical dotted lines correspond to threshold values. For all observers, the psychometric curves move to the right as the mean speed increases, indicating an increased segmentation threshold. Note that for the highest speed (64 deg/sec, open squares), observers never reached the 100% response plateau, so we did not compute a threshold for that speed.

Figure 2 illustrates speed-segmentation

thresholds as a function of the mean speed for each observer and stimulus duration. For all durations, the segmentation threshold is very sensitive to mean speed, with the speed difference required to segregate two surfaces increasing as the mean speed increases. At a 130-msec duration, the curves are highly idiosyncratic. Thresholds are never below 40% and the minima occur at various mean speeds, between 2 and 16 deg/sec depending on the observer, and rise to 80% at 32 deg/sec. At longer stimulus durations, the relationships between threshold and mean speed are similar across all observers. Thresholds are nearly constant ($\approx 25\%$; range 19-29%) for mean speeds between 2 to 8 deg/sec and increase sharply for higher mean speeds, independent of duration.

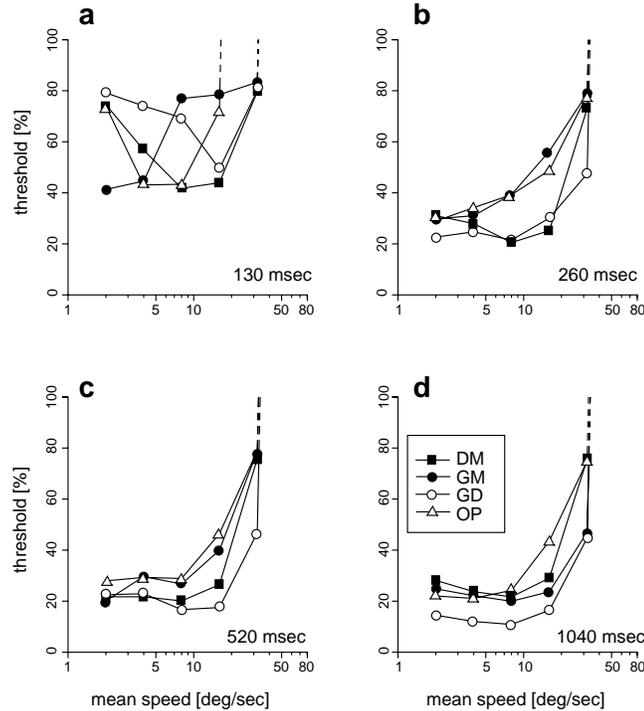


Figure 2: Speed segmentation thresholds (in %) vs mean speed, for all 4 observers and all stimulus durations.

Figure 3a plots the average (\pm sd) thresholds across observers, as a function of mean speed, for each stimulus duration. To estimate the minima, the data were fit with Eq. (2) and the best fits are shown as smooth curves (see Table 1). The minima were found between 2 and 8 deg/sec, and thresholds sharply increased for higher mean speeds. Moreover, increasing stimulus duration lowered the threshold in the 2-16 deg/sec range.

Figure 3b replots the same average (\pm sd) thresholds across observers as a function of stimulus duration for all reference speeds. The smooth curves are the best fits of the data to a single-exponential decay function, Eq. (3) (see Table 2). For the three lowest mean speeds, thresholds decreased from 60 to 20% as the stimulus duration increased from 130 to 520 msec. No further improvement of the performance was observed for the longest

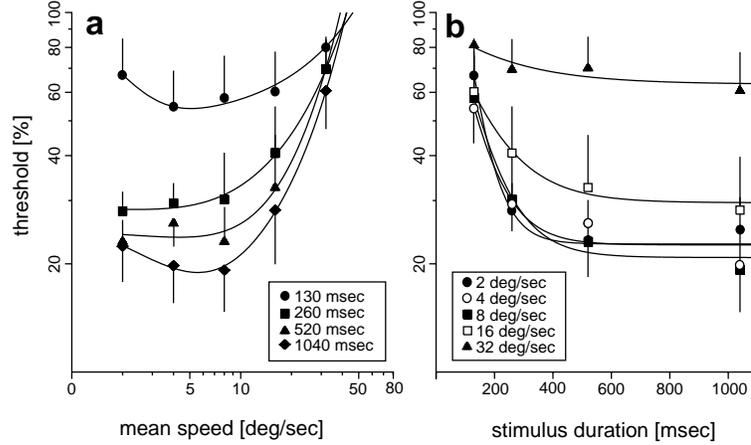


Figure 3: [a] The average (\pm sd across observers) speed-segmentation thresholds vs mean speed, for each stimulus duration. The continuous lines are the best fits to the data using Eq. (2) (see Table 1). [b] The average speed-segmentation thresholds vs stimulus duration, for each mean stimulus speed. The continuous lines are the best fits to the data using Eq. (3) (see Table 2).

stimulus duration. With higher mean speeds, the temporal integration lasted longer: the time-constant (τ) increased from 61 to 230 msec as the reference speed increased from 2 to 32 deg/sec. The asymptotic threshold value a reached a minimum for a mean speed of 8 deg/sec.

Table 1. Stimulus speed dependence

duration (msec)	k_1	k_2	b	c	v_{min}	$\Delta v/v$
130	49.24	113.46	-0.0154	0.965	5	54.09
260	23.09	6.22	-0.0344	0.231	2	28.65
520	13.25	12.02	-0.0519	0.120	4	23.74
1040	12.80	17.96	-0.0487	0.381	6	18.97

Table 2. Stimulus duration dependence

speed (deg/sec)	a	b	d_0	τ
2	22.71	44.65	129.85	61.4
4	22.58	32.13	129.51	88.8
8	20.83	36.92	130.24	97.8
16	29.59	30.58	129.11	135.1
32	63.19	18.41	109.14	228.3

Tables. Best-fit parameters when functions (2) and (3) were fitted to the velocity tuning curves (Table 1) and duration tuning curves (Table 2), respectively. In Table (1), the coordinates (v_{min} , $\Delta v/v$) of the function minimum are indicated for each stimulus duration.

2.3.2 Exp 1-2: Eye-movement controls

Eye movements were measured for three (GM, DM & GD) of the four observers over one session, using an infra-red limbus detector (Iris, Skalar Inc.). The smooth eye-movement responses were minimal under the experimental conditions used. Eye velocity ranged from 0.13 ± 0.11 deg/sec to 1.76 ± 2.02 deg/sec for stimulus durations of 130

and 1040 msec, respectively. Correcting for this in Fig. 3a would involve shifting the curves to the right by such a small amount as to have no significant impact on our conclusions. To examine further the possibility of eye-movement artifacts, we also reran Exp. 1-1 without a fixation point on the same 4 observers who ran Exp 1-1. Speed-segmentation thresholds were significantly lower (t-tests, $p < 0.05$ Buonferroni corrected for multi-

ple t-tests) for the two longer stimulus durations (520 and 1040 msec) but were indistinguishable (t-tests, $p > 0.25$) for the two shorter durations (130 and 260 msec). Furthermore, these shorter durations are not too dissimilar from the latency of human smooth-pursuit eye movements (Carl & Gellman, 1987) and of the optokinetic response to similar moving random dot patterns (Mestre & Masson, 1997a). We therefore conclude that, for stimulus durations of 260msec or lower, the effect of eye movements appear negligible. For that reason, a duration of 260 msec was chosen for the remaining experiments.

2.3.3 Exp 1-3: Speed discrimination vs. segmentation

To compare the ability of human observers to segment multiple motions in a transparent display based on speed differences with the ability of the same observers to discriminate two different sequentially presented speeds, we ran an additional experiment on three of the subjects (GM, DM & GD) and show the data in Fig. 4. We were careful to keep all the visual stimulus conditions (dot density, luminance, contrast, display size) identi-

cal to Exp. 1-1. The average speed-discrimination thresholds (across observers, \pm sd) are plotted as the open circles. The average speed-segmentation thresholds (across observers, \pm sd) are plotted as open squares. The average speed-segmentation data (across observers, \pm sd) for the same three observers from Exp. 1-1 are re-plotted as closed squares. Two striking differences between the segmentation and discrimination thresholds are evident. First, for speeds above 4 deg/sec, the ability to discriminate speeds is better than the ability to segment random-dot displays based on speed, even though the former requires the accurate ordering of speeds and the latter ostensibly only requires the mere detection of two different speeds. Secondly, unlike segmentation performance, discrimination performance does not decrease as the mean speed increases at least up to 32deg/sec. Finally, segmentation thresholds did not depend much either on the type of psychophysical procedure or the type of psychometric function used to fit the data. Comparison of the open and closed squares in Fig. 4 indicates that thresholds for speed segmentation were not significantly different using either a yes/no or a 2-IFC paradigm (ANOVA, $F(1,2) = 1.12$; $p < 0.4$).

3 EXPERIMENT 2

The high speed difference required to segment transparent moving surfaces may be caused by spatial interactions within the human visual motion processing system. In Exp. 1, all local regions contained similar samples of intermingled speed signals, i.e. the stimulus was spatially homogeneous. To investigate spatial interactions directly, we used regionally heterogeneous stimuli, similar to those developed by van Doorn and Koenderink (1982b): moving random-dot patterns with horizontal bars of alternating speeds. In their original papers on the detectability of velocity gradients, van Doorn and Koenderink (1982a,b; 1983) made two observations. First they reported that a high signal-to-noise ratio (SNR) is necessary to detect a direction gradient in a dynamic random-dot pattern. Second, the required SNR changes according to the spatial layout of the display: for alternating bars with dots moving in opposite directions, SNR decreases monotonically with increasing bar width. Van Doorn and Koenderink also noted that the percept changed as the bar width was reduced, switching from corrugated to transparent and that transparent patterns required higher SNRs than corrugated pattern for detection.

The rather high speed-difference thresholds observed in the Exp. 1 might be related to the high SNR required for the perception of trans-

parency. If so, speed-segmentation thresholds should also be lower for patterns with wide horizontal bars and increase as bar width decreases, up to a value close to that corresponding to the perception of motion transparency. We therefore measured the speed-segmentation thresholds using stimuli in which the two speeds were assigned to two sets of interleaved bars and examined the effect of varying bar width.

A second way we examined spatial interactions was to "pair" moving dots (Qian et al., 1994a). In the standard "unpaired" condition, within each bar, the location of each moving dot was fully randomized, so that the distance between two different vectors was randomly distributed around a fixed mean defined by dot density. In a second, interleaved, "paired" condition, an additional constraint was imposed by pairing dots and assigning the two speeds to the members of the pair. Given that Qian et al. (1994a) reported that motion transparency perception fails when dots moving in opposite directions are locally paired within ≈ 0.4 deg of each other, we set the maximum horizontal offset allowed between two dots of a given pair (in our experiments moving in the same direction but at different speeds) to this same 0.4 deg critical distance. Because changing the bar width changes the vertical offset between paired dots, pairing should have little affect on percep-

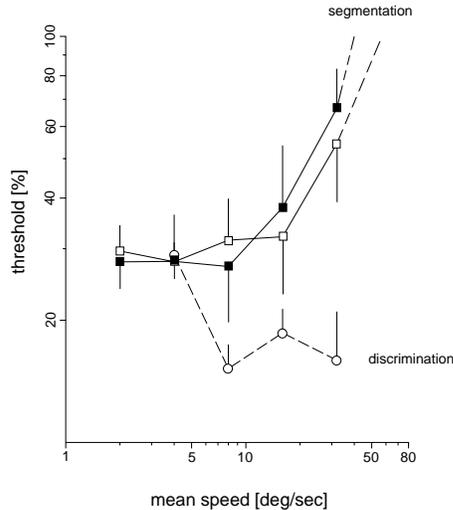


Figure 4: Comparison between speed segmentation and speed discrimination. Average (\pm sd, across observers) thresholds for speed segmentation (squares) and speed discrimination (circles) are plotted as a function of mean stimulus speed. Open symbols indicate data gathered with a 2IFC paradigm.

tion for bars widths $> 0.4\text{deg}$. For bar widths below this limit, if speed and direction signals are pooled similarly for segmentation, the perception of multiple surfaces should vanish and the percept should correspond to a coherent random-dot pattern, moving uniformly with a single speed.

3.1 Method

3.1.1 Observers

Five observers (2 authors and 3 naive observers) participated in the experiment, running several blocks daily.

3.1.2 Visual stimuli

Stimuli were as in Exp. 1 except for the spatial distribution of moving dots. The display was subdivided into bars with widths ranging from 0.025deg to 25.6deg . As in Exp. 1, the stimulus consisted of two populations of random dots moving at two different speeds (v_1 or v_2). However, in this experiment, the two population were presented in alternate bars so as to form a regular square-wave grating (Fig. 5). A central fixation cross was always displayed at the center of the display which always corresponded to a border between two bars. For the unpaired stimuli, the

distribution of dots within each bar was randomized. For the paired pattern, each dot moving at speed v_1 was paired with a dot moving at speed v_2 in an adjacent bar. Pairing was computed in such a way that the horizontal distance between two paired dots stayed below 0.4deg for the entire stimulus duration. Initial horizontal offset between two paired dots was randomized across pair of dots. The wrap around procedure was controlled so that when one dot disappeared, its companion also disappeared. Therefore, as illustrated in the right panel of Fig. 5, for bar widths equal to or smaller than 0.4deg , all local motion vectors v_1 and v_2 were paired within a 0.4deg diameter. The stimuli moved 260msec at a mean speed of 2deg/sec . This speed was chosen so that, for all speed differences, the horizontal offset between the paired dots could be kept below 0.4deg throughout the entire trial. Although this slow speed may have resulted in some spatio-temporal aliasing, our use of a high-frame rate (76Hz) minimized the visibility of any such artifacts. Furthermore, any motion aliasing would have been in the horizontal direction and therefore independent of the vertical corrugation, so our finding of a well-behaved corrugation effect cannot be accounted for by aliasing. This is further supported by the fact that results obtained in the unpaired condition were consistently reproduced with an higher mean speed of 9deg/sec (Mestre & Masson, 1998)

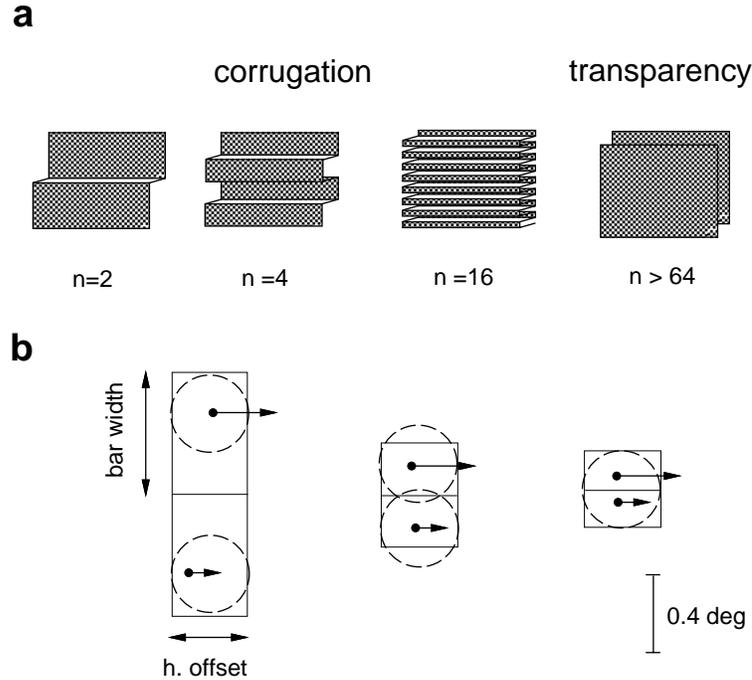


Figure 5: Schematic depiction of the displays in Experiment 2. [a] The large field display is divided into an even number of alternating horizontal bars. One speed is attributed to the odd bars while a second speed is attributed to the even bars. The speed difference is manipulated as well as the bar width. For large bar widths, above the speed-segmentation threshold, a “corrugated” pattern is perceived, with alternating bars moving at different speeds. Below a critical bar width, observers reported they perceived two transparent surfaces moving with different speeds in the same direction. [b] In the paired condition, two dots moving with different speeds, and thus located in different bars, are constrained to have their horizontal offset < 0.4 deg (dotted circles). The barwidth (continuous thin line) is reduced progressively until the dots are paired within a 0.4 deg diameter area.

3.1.3 Procedure

The data-gathering procedure was identical to that used in Experiment 1: in a yes/no paradigm, the observers had to indicate if there was one or two moving surfaces present in the stimulus. Before the first block, observers were instructed that surfaces could be transparent or square-wave corrugated. There were 11 different bar widths, 2 pairing conditions and 5 speed differences. All conditions were randomly interleaved. Each observer ran 25-30 blocks of 220 trials, so that 50-60 responses were collected for each condition. Data were analyzed as in Exp. 1-1.

3.2 Results

3.2.1 Exp 2-1: Effect of bar width on speed segmentation

Figure 6 illustrates the psychometric curves for one naive observer (FG) for different bar widths,

for both the unpaired and paired conditions. Fig. 6a shows the clear progression of the psychometric curves in the unpaired condition: for large bar widths (> 3.2 deg), speed-segmentation thresholds were lower, and for small bar widths (< 0.8 deg), thresholds were higher. Figure 6b illustrates psychometric curves corresponding to the same bar widths but in the paired condition. The curves corresponding to the larger bar widths were largely identical while those corresponding to small bar widths were dramatically affected by pairing. The small bar-width curves were shifted to the right. For bar widths below 0.2 degrees, performance never reached 75% correct at least for speed differences up to 80%. Speed differences greater than 80% could not be used: for a mean speed of 2 deg/sec and stimulus duration of 260 msec, an 80% speed difference would have resulted in a horizontal displacement greater than the 0.4 degrees required to keep the dots paired.

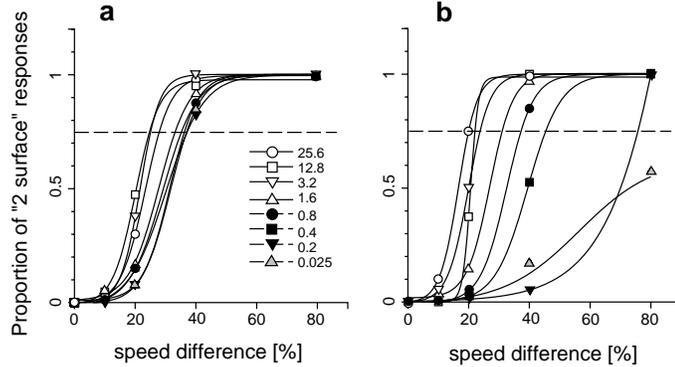


Figure 6: Psychometric curves for one naive observer (FG). The proportion of "two surfaces" responses is plotted as a function of speed difference for different bar widths in both unpaired [a] and paired [b] conditions.

Figure 7 illustrates the results from 5 observers, together with the average (\pm sd) data across observers. Speed-segmentation thresholds are plotted versus bar width. The first main result is that, for all observers, speed-segmentation thresholds in the unpaired condition increase as a sigmoid function of bar width. On the righthand side of the sigmoid, threshold reaches a plateau between 30 to 40%, for bar widths below 0.4deg. This value is very close to the thresholds reported in Exp. 1 for a fully randomized transparent pattern. Note that no significant differences were observed between thresholds for bar widths ranging from 0.2 and 0.05 deg and a bar width of 0.025 deg. With this latter condition, dots with different speeds were co-linear and therefore no corrugation was present. For that reason, data for a 0.025 deg bar width are indicated with a different color in Figures 6 and 7. On the other side of the curve, thresholds were lower at \approx 20% for coarsely corrugated patterns, and, for all but one observer (DM), little change in threshold was observed as the bar width decreased from 25.6deg to 4.7deg.

The second main result is that, for all observers, the threshold curves for the paired and unpaired conditions diverge at 0.4 deg bar width. At this limit, a significant difference in the average threshold in the paired and unpaired conditions becomes evident ($t(8) = 5.03$, Buonferroni corrected; $p < 0.01$). Above this limit, the thresholds in the two conditions were indistinguishable. Furthermore, in the paired condition, thresholds increase dramatically for bar widths under 0.4 degrees. No plateau is evident and observers consistently perceived only one surface even at speed differences of 80% (see Fig. 6b). Lastly, this critical bar width is surprisingly close to that at which the plateau onset is observed in the paired condition.

3.2.2 Exp 2-2: Perceptual transitions

Above the speed-segmentation threshold, for large bar widths, observers reported perceiving a square-wave corrugated pattern with alternating stripes moving at different speeds, yet for small bar widths, they perceived transparent surfaces moving over or through each other at different speeds. Below threshold, by definition, observers perceived only one surface. The lower right panel in Fig. 7 illustrates the mean (\pm s.d.) speed-segmentation threshold across observers. Threshold vs bar width curves for the paired and unpaired conditions divide the space into three distinct regions. The three areas correspond to three distinct perceptual states: coherency (bottom), transparency (upper right), and corrugation (upper left). By changing the horizontal (i.e. pairing) offset, the vertical offset (i.e. bar width) or the speed difference, one can switch from one perceptual state to another. The data indicate that the transition from coherency to corrugation is supported by lower speed differences than that from coherency to transparency.

In a control experiment, we verified that the perceptual transition between corrugation and transparency corresponds to the sharp segmentation threshold transition seen in Fig. 7. For a fixed speed difference well above threshold (80%), we varied the bar width from 3.2 to 0 deg (with 0 deg corresponding to a fully transparent display). In a yes/no paradigm, observers had to decide whether they perceived a corrugated or a transparent display. The critical bar width for corrugation detection was defined as the value yielding 75% "corrugated pattern" responses. Across 5 observers (including those from Exp 2-1), the average (\pm sd) bar width for detection of a square-wave corrugated pattern was 0.90 ± 0.22 deg. This

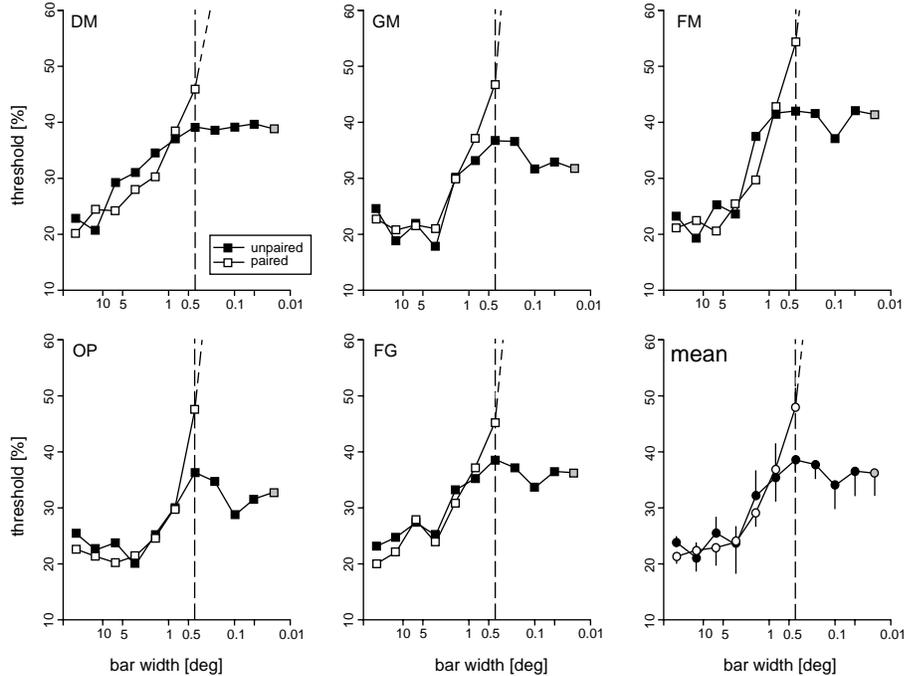


Figure 7: The dependence of speed difference threshold (in %) on the horizontal bar width (in deg, axis goes from large to small bar width) in both the unpaired (solid symbols) and paired (open symbols) conditions. Data are illustrated for each observer with the average (\pm s.d.) in the bottom righthand plot. The vertical dotted line indicates the critical bar width for which paired and unpaired conditions diverge.

perceptual transition point falls nicely into the transition zone in which the speed-segmentation thresholds transition from low to high, although

it is slightly higher than the point at which the paired and unpaired curves diverge.

4 EXPERIMENT 3

Results from Exp. 2 suggest that there is some critical distance over which speed signals are pooled. Below this critical distance, transparency is lost and the dots are perceived to move coherently within a single surface, despite large speed differences. The pooling distance was found to be ≈ 0.4 deg. This critical offset appears to represent the spatial scale at which motion segmentation occurs, but the stage in the primate cortical motion pathway where segmentation is implemented remains unclear. Psychophysically, Qian and collaborators (1994a) found a similarly small critical distance using dots moving in opposite directions. Their neurophysiological data however were somewhat contradictory because paired opposite motions were found to have little effect on V1 neurons (despite their appropriately small receptive fields) but large, suppressive effects on MT neurons (despite their inappropriately large receptive fields). Because of this, Qian et al. (1994b)

suggested that suppressive effects on MT neurons of pairing motion in opposite directions might be due to inhibition within MT sub-units integrating inputs from pooled populations of V1 neurons with opponent direction-selectivity. The results of Exp. 2 suggest an extension of this view to a more general velocity-averaging which occurs even when the directions are identical. To examine further the contribution of early (i.e. smaller) and late (i.e. larger) spatial scales of motion processing along the cortical motion pathway, we investigated the effect of pairing at different eccentricities. We re-measured speed-segmentation thresholds for both paired and unpaired stimuli, as a function of the bar width, but did so for a range of eccentricities, by using annular stimuli centered around the fixation point (Fig. 8). Our goal was to determine the effect of eccentricity on the critical bar width.

4.1 Method

Three observers (two authors and one naive observer) participated in the experiments, running several blocks daily. Stimuli were annular random-dot patterns varying in size and eccentricity, covering 4 eccentricity ranges: 0 to 1.75 deg; 1.75 to 3.5 deg; 3.5 to 7 deg; and 7 to 14 deg (Fig. 6). The stimulus area was increased with eccentricity (from 10 to 500 deg^2) roughly compensating for cortical magnification. Dot density was kept constant at 4 dot/ deg^2 . Mean speed was

2 deg/sec and 6 speed differences were used (0, 10, 20, 40, 60, 80%). Four bar widths were used: 1.76, 0.88, 0.44, and 0.22 deg. Thirty-two different conditions were randomly interleaved. Each observer typically ran 10 blocks of 288 trials for each annulus, such that 60 responses were collected for each condition. The procedure was otherwise identical to that used in Exp. 2: in a yes/no paradigm, observers had to indicate if there was one or two moving surfaces present in the stimulus. Data analysis was as in Exp. 2.

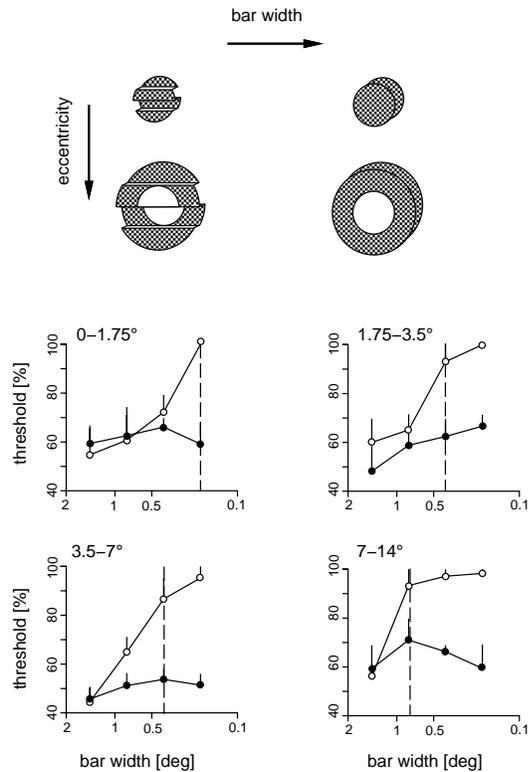


Figure 8: The dependence of The critical bar width on eccentricity. The top panels illustrate the annulus stimuli centered on the fixation point. The bottom four plots illustrate the relationship between segmentation threshold and bar width in the paired (open symbols) and unpaired (solid symbols) conditions. From top-left to bottom-right, eccentricity increases. The vertical dotted lines indicate the point at which the two conditions diverge. Note that, as the eccentricity increases, the dotted line shifts slightly to the left, toward larger bar widths.

4.2 Results

As illustrated in Fig. 8, mean ($\pm s.d.$ across observers) speed-segmentation thresholds increased when bar width decreased, for both the paired and unpaired conditions, thereby replicating the results of Exp. 2. Again, the critical offset was defined as the bar width at which the two curves diverged significantly (Buonferroni corrected t-tests,

$p < 0.05$). This point is indicated by the vertical dotted lines. As the eccentricity increased, this critical value slowly moved toward larger bar widths. In the central 1.75 deg of the visual field, the critical bar width was ≈ 0.2 deg while in the 7-14 deg region of the visual field, the critical bar width was $\approx 0.4 - 0.8$ deg. Across observers, a significant linear relationship between mean crit-

ical offset (C) and eccentricity (Ec) was found ($C = 0.17 + 0.06.Ec; r^2 = 0.97$). This linear relationship is similar to that between receptive field size and eccentricity for V1 neurons ($RF_{V1} =$

$0.22 + 0.04.Ec$, Dow et al., 1981) but different from that for MT neurons ($RF_{MT} = 1.04 + 0.61.Ec$, Albright & Desimone, 1987) in primate cortex (Fig. 9b).

5 DISCUSSION

The human visual system can easily segment multiple motions that are transparently combined in an image sequence. Two classes of motion transparency stimuli have been extensively investigated over the last decade. The sum of two overlapping moving gratings with different orientations (a plaid), under some conditions, is perceived as two gratings moving transparently or sliding over each other (Adelson & Movshon, 1982; Stoner et al., 1990). In the same vein, two overlapping random-dot patterns moving in sufficiently different directions can be perceived as transparent surfaces moving through or over each other (Clarke, 1977; van Doorn & Koenderink, 1982a; Snowden, 1990). In the case of random-dot stimuli, direction-based segmentation has been extensively studied. Qian and colleagues (1994a) found that direction-based transparency is not represented at spatial scales smaller than about 0.4 deg. Local interactions between units tuned for different directions can explain the rather poor performance in direction segmentation compared to direction discrimination (Braddick, 1997).

We have extended these studies by examining segmentation of moving random-dot patterns based on speed signals alone. Our main findings are: 1) speed segmentation requires significantly higher speed differences than speed discrimination under matched conditions, 2) speed segmentation operates over a restricted range of speeds and fails at speeds higher than ≈ 16 deg/sec, 3) speed segmentation thresholds are sensitive to the spatial distribution of motion signals with coarsely corrugated patterns more easily detected than finely corrugated or transparent patterns, and 4) the pairing two speeds signals within ≈ 0.4 deg blocks segmentation, and 5) the spatial scale of this apparent "pooling area" is only weakly dependent on eccentricity.

5.1 Speed segmentation for motion transparency

In Exp. 1, we first investigated the ability of human observers to segregate two overlapping moving surfaces in a moving random-dot pattern, based only on their speed difference. Second, we compared this ability with speed-discrimination performance. We found that the speed differ-

ence required for segregating two transparent motions is higher than expected from human speed-discrimination data. For stimulus durations of 260 msec or longer, speed-difference thresholds were between 20 and 30% and sharply increased when the average speed of the random dots increased above 16deg/sec.

Our results illustrate two critical properties of motion segmentation, and does so in the absence of other segmentation cues such as hue, binocular disparity, size, or contrast polarity (for a review see Stoner & Albright, 1993). The first of these properties is that motion segmentation of a transparent display requires relatively large velocity differences. Several authors have previously examined segmentation based on direction differences. By having observers adjust the signal noise ratio of a transparent pattern, Van Doorn and Koenderink (1992b) found that superimposed motion streams can be segmented whenever the directions of the motion vectors differ by at least 30 deg. Wishart and Braddick (1997) recently re-examined this issue, using a performance-based measure of segmentation threshold. Their method ensured that directional information was available from both streams jointly and therefore performance was related to a genuine multi-valued representation of direction (see Braddick, 1997). Their experiment showed that observers can make judgments of the angle between random-dot motions with a precision of about 13 deg, which is more than twice as high as the direction discrimination threshold for judging the angle between the motion of a set of random dots relative to a stationary line (≈ 5 deg.). Apparently, there is some penalty associated with transparency. In the present study, we compared speed-based segmentation of a transparent display with simple speed discrimination under matched non-transparent conditions. We found that the perception of transparency requires speed differences of about 20 to 40%, while, under matched conditions, speed-discrimination thresholds are only around 15 to 20%. Several experimenters previously reported good performance for speed discrimination with random-dot displays (e.g. De Bruyn & Orban, 1988; Snowden & Braddick, 1991; Watamaniuk & Duchon, 1992). Our speed-discrimination thresholds are somewhat higher than the 5 to 17% thresholds reported by De Bruyn and Orban (1988), for

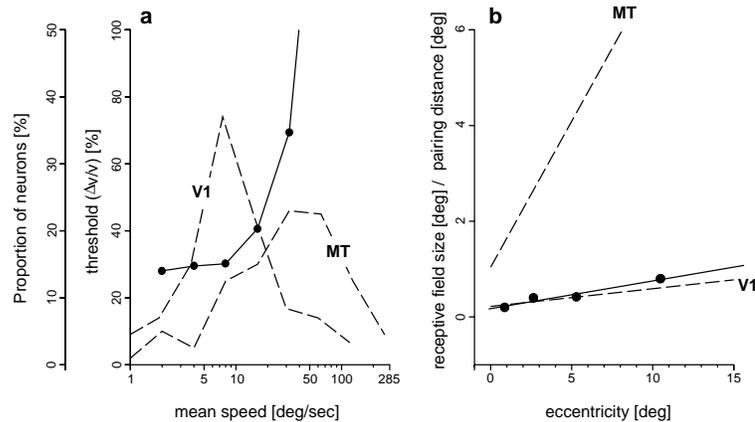


Figure 9: *Psychophysical and physiological signatures.* [a] The relationship between speed segmentation (solid circles) or motion discrimination (open circles) thresholds and mean stimulus speed. Superimposed are the distributions of speed sensitivities for V1 (upper velocity cut-off) and MT (optimal speeds) neurons in macaque monkeys (Orban et al., 1986; Cheng et al., 1994). [b] The relationship between critical bar width (averaged across observers) and eccentricity, together with the linear relationships found between receptive field size and eccentricity for MT (Albright & Desimone, 1987), and V1 neurons (Dow et al., 1981)

speeds between 0.5 and 64 deg/sec and a duration roughly the same (200 msec) as ours. Many differences between the experimental conditions could account for this quantitative difference (e.g. luminance, inter-stimulus interval duration, level of practice, etc.). Our results however are qualitatively consistent with theirs and with those of McKee (1981) for single targets: they found that speed discrimination exhibits a significant decrease at low speeds (below about 4 deg/sec) and high speeds (above about 60 deg/sec).

A second critical property of motion segmentation is the slow temporal build-up of perception. The dependence of speed discrimination thresholds upon stimulus duration have been previously reported for both random dots pattern (De Bruyn & Orban, 1988) and single targets (McKee, 1981). In both cases, asymptotic performance occurs at rather short durations ($\approx 100 - 150$ msec, De Bruyn & Orban, 1988; Snowden & Braddick, 1991). On the other hand, all experiments dealing with motion segmentation or structure-from-motion have reported rather sluggish dynamics. For instance, Treue et al. (1991) reported a rather slow temporal build-up for structure-from-motion perception and Mestre & Masson (1997a) demonstrated long (> 1 sec) reaction times for discrimination of stimuli made of either 1, 3, or 10 different speeds. This study found that short stimulus durations (130 msec) result in unreliable motion segmentation performance and that asymptotic speed-segmentation thresholds require durations longer than 250 msec, consistent with the findings

of Møller (1992). This relatively long asymptotic duration contrasts with the faster asymptote for motion detection (see Møller & Hurlbert, 1996 for a direct comparison) or speed discrimination (De Bruyn & Orban, 1988).

Furthermore, we found that speed discrimination and speed segmentation have different dependencies on stimulus speed (Fig. 4). Figure 9a illustrates the speed dependence of the segmentation threshold found in the present study. The motion mechanisms underlying speed segmentation are tuned for low speeds (upper cut-off between 10 and 20 deg/sec). On the other hand, the motion processing underlying speed discrimination operates over a broader range with an upper cut-off between 40 and 60 deg/sec (De Bruyn & Orban, 1988).

5.2 The spatial scale of motion segmentation

Several examples of detrimental effects of one motion signal on the detection of a second motion signal transparently displayed have been reported (e.g. Mather & Moulden, 1980; Snowden 1989; Wishart & Braddick, 1997). A possible explanation for these differences in the discrimination and segregation performance might be the interaction between neurons selectively activated by the disparate velocity vectors. Several psychophysical and neurophysiological studies point out the need for understanding the relationship between the spatial scales of these interactions (see Brad-

dick, 1997 for a review). Experiments 2 and 3 investigate the spatial scale of speed-segmentation.

Our results extend the findings of van Doorn and Koenderink (1982b) on direction-based segmentation to speed-based segmentation. They reported that observers perceive motion transparency when the corrugation of random-dot patterns is higher than 3 cpd. In Experiment 2, we found that the spatial limit lies between 0.4 and 0.8 deg (1.25 and 0.625 cpd). Segmentation below this spatial limit is characterized by high, asymptotic speed-segmentation thresholds, roughly identical to those obtained with fully randomized transparent displays. Moreover, speed-segmentation thresholds exhibit a steep transition for bar widths between 0.2 and 0.4 deg, as does the transition between corrugation and transparency perception. Note that below the speed-segmentation threshold, the two conditions are undiscernable as both perceived as coherently (i.e. uniformly) moving displays. Whether or not the coherent motion is perceived as moving at the average velocity requires further data, but it is likely given the previous reports of motion averaging in transparent random dots when the directions of motion were similar (Snowden, 1989; Mulligan, 1993, Braddick, 1997).

Our results extend the findings of Qian and colleagues (1994a,b) on opponent-motion based segmentation to speed-based segmentation. They reported that the pairing of dots moving in opposite directions to an area smaller than 0.4 deg blocks segmentation. We have shown that pairing of dots moving in the same direction but at different speeds within the same 0.4 deg area, blocks segmentation as well and results in the perception of a single coherently moving pattern, at least for dot speeds centered on 2 deg/sec. The fact that both studies found the same critical pairing distance suggests that transparent motion signals cannot be represented with a finer scale than about 0.4 deg. Moreover, we found that the pairing distance that blocks speed segmentation increases only slightly with eccentricity.

In summary, our data suggest that below the spatial-scale limit, two velocities falling in the same place are not resolvable. Furthermore, our data also suggest that the pooling of closely-spaced vectors is a true local-averaging process and not just a motion-opponency mechanism as suggested by Qian et al. (1994c).

5.3 Neurophysiological substrates

Three different motion perceptions can be triggered, depending on both the spatial distribution of dots and their relative speed. For speed differences below the segmentation threshold or for vec-

tor local separations below the pooling threshold, observers perceive a single surface moving coherently, i.e. only one velocity is represented in the visual system. At large speed differences with adequate spatial separation between individual vectors, two velocities can be simultaneously represented. Furthermore, the nature of the global motion percept (e.g. corrugation vs transparency) depends on the spatial distance between populations of similar vectors, i.e. on a second spatial limit that constrains the selective integration of identical local motion signals (e.g. see Nowlan & Sejnowski, 1995).

Visual motion processing is often assumed to be a two-stage mechanism in which a global motion integration stage follows a local motion measurement stage. These two stages have been attributed to cortical areas, MT and V1, respectively (see Movshon et al., 1985). Within this scheme, it remains unclear where motion segregation (the distinction of multiple velocities) and integration (the grouping of similar velocities) occur. For instance, contradictory results have been reported, concerning the level at which boundary detection might occur (Lamme et al., 1993; Marcac et al, 1995). A similar dilemma is true for motion transparency. Qian and Andersen (1994) reported little or no change in V1 responses when opponent motions were paired. On the contrary, MT neurons were largely inhibited by pairing. The discrepancy found by Qian et al. (1994a) between the small V1-sized pairing distance abolishing transparency and the lack of pairing effect on V1 responses, led them to postulate that pairing might affect MT sub-units receiving inputs from V1 neurons of opposite direction selectivity. Thus, MT neurons would then selectively integrate motion signals over a large part of the visual field, collecting inputs from opponent-tuned sub-units which receive convergent input from V1 neurons from the same retinal location. Several properties of MT neurons such as their large receptive fields, broad velocity tuning, sensitivity to segmentation cues, pattern-motion selectivity, suggest that area MT could play an important role in motion integration. Indeed, MT appears critical in the perception of motion transparency, as well as structure-from-motion, in random dot displays (Siegel & Andersen, 1988; Dodd et al., 1997). Their sensitivity to paired motion signals could however be due to interactions at an intermediate stage between V1 and MT (Qian et al., 1994b). A role for MT in the detection of corrugation is however tempered by the fact that the supra-threshold transition from transparency to corrugation occurs at bar widths below 1 deg. This finding strongly suggests that the selective integration or motion-boundary detection under-

lying the detection of corrugation is effected by neurons with receptive fields significantly smaller than MT's.

Although it remains unresolved where motion segregation actually occurs in the visual motion pathway, the segmentation mechanism must share with V1 neurons a small dependency upon eccentricity and small receptive field size. The global motion perception stage which supports corrugation vs transparency perception must also be implemented by a mechanism with rather small receptive fields. Neural networks within the earliest stages of primate visual cortex (V1, V2 and V3A) might therefore be responsible for both these phenomena (Marcar, Raiguel, Xiao, Maes & Orban, 1992; Reppas, Niyogi, Dale, Sereno & Tootel, 1997; Van Oostende, Sunaert, Van Hecke, Marchal & Orban, 1997). Our data provide two psychophysical signatures for the motion segregation process that can be compared with the physiological signatures of cortical areas (Fig. 9). Figure 9a illustrates the speed tuning of the segregation process together with that for V1 and MT neurons (Orban, Kennedy & Bullier, 1986; Cheng, Hasegawa, Saleem & Tanaka, 1994). There is a clear correlation between the limited band-pass of motion segmentation and that of V1 neurons. By contrast, the higher bandpass of speed discrimination is more similar to that of MT neurons, as previously suggested by others (De Bruyn & Orban, 1988; Orban, Saunders & Vandebussche, 1995). Figure 9b illustrates the linear relationship between the critical pairing distance and eccentricity, together with that between receptive field size and eccentricity for V1 and MT neurons (Dow et al., 1981; Albright & Desimone, 1987). There is again a clear correlation between the eccentricity tuning of speed segmentation and that of V1 neurons. In conclusion, the present study demonstrates that speed segmentation operates over a narrow low-pass range of speeds (Fig. 9a) and that its limiting spatial interactions are over relatively short distances that do not change much with eccentricity (Fig. 9B). Its properties more closely resemble those of neurons earlier in the motion pathway than MT (i.e. V1, V2 or V3). Our results together with those of Qian and colleagues (1994) point out the importance of examining more closely the role of V2 and V3 in motion processing in general and in motion segmentation in particular.

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