



Speed tuning of motion segmentation and discrimination

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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 large-field ($7^\circ \times 7^\circ$) 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 above which observers can perceive two moving surfaces. We systematically investigated this 'speed-segmentation' threshold as a function of speed and stimulus duration, and found that it increases sharply for speeds above $\approx 8^\circ/\text{s}$. In addition, speed-segmentation thresholds decrease with stimulus duration out to ≈ 200 ms. In contrast, under matched conditions, speed-discrimination thresholds stay low at least out to $16^\circ/\text{s}$ and decrease with increasing stimulus duration at a faster rate than for speed segmentation. Thus, motion segmentation and motion discrimination exhibit different speed selectivity and different temporal integration characteristics. Results are discussed in terms of the speed preferences of different neuronal populations within the primate visual cortex. © 1999 Elsevier Science Ltd. All rights reserved.

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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 with the same moving object (Braddick, 1993).

A particularly difficult challenge for these processes is transparency, the simultaneous representation of two or more objects or 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 directions can produce the percept of two or more rigid structures moving transparently (e.g. Clarke, 1977; van Doorn & Koenderink, 1983; Andersen, 1989; Snowden, 1989; Mulligan, 1993; Qian, Andersen & Adelson, 1994). 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 often leads to the percept of three-dimensional structure, such that each surface is 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, Albright & Ramachandran, 1990; Lorenceau & Shiffrar, 1992).

Previous studies have pointed out several properties of motion transparency, that reflect the constraints on

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image segmentation (see Braddick, 1997). One of the most important is that 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 30–40° (Mather & Moulden, 1980; van Doorn & Koenderink, 1983; Møller, 1992; Wishart & Braddick, 1997). This result suggests that proximity in direction promotes grouping or hinders segregation. Transparency from direction cues may also depend on relative speed; even an orthogonally moving pattern can impair the detection of a second moving pattern (ostensibly by some grouping process), if the patterns move with at least broadly similar speeds (Snowden, 1989, 1990; Verstraten, Fredericksen, van Wezel, Boulton & van de Grind, 1996). This result indirectly suggests that proximity in speed may promote grouping or hinder segregation, but there is as yet little evidence without confounding direction cues (however see Verghese & Stone, 1997).

In the present study, we used unidirectional moving random-dot patterns to investigate how well speed differences, in the absence of direction cues, can support segmentation and to probe further the neural mechanisms underlying the segmentation process. Studying the segregation process by manipulating differential speed alone avoids the confounding issues of interactions across direction channels and of motion opponency. 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, Olum & Rosenblatt, 1955) or structure-from-motion (Andersen, 1989). Indeed, using transparent displays in which all dots moved in the same direction, Bravo and Watamaniuk (1995) demonstrated that, observers are able to locally segregate motion measurements according to speed alone and to selectively integrate those local motion signals to produce a precise speed signal for one of the two transparent surfaces.

This study has two specific goals. The first is to determine the speed-difference thresholds necessary for supporting the perception of two transparent surfaces and the dependence of this 'speed-segmentation' threshold upon mean speed and duration. The second is to compare speed-segmentation performance with the well studied ability of human observers to discriminate two motions based on their speed (McKee, 1981; De Bruyn & Orban, 1988; Stone & Thompson, 1992). Preliminary results have been previously reported (Mestre, Masson & Deharvengt, 1999).

2. Experiments

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 the two interval forced-choice (2IFC) segmentation task, observers were asked to detect in which of the two presentation intervals, two and only two moving surfaces were present in the stimulus. That is to say, observers had to locally segregate the different speed signals and selectively integrate them globally over the stimulus area to decide whether or not there were only two different speed signals in the test stimulus. To avoid perceptual judgments being based only on the existence of a local speed difference without having to rely on a global segmentation process, the comparison stimulus was made of five different speeds spanning the same speed range. In a second experiment (1-2), we compared the speed-segmentation and speed-discrimination thresholds for the same observers, under the same experimental conditions using the same psychophysical procedures. In the 2IFC speed-discrimination task, observers sequentially viewed two intervals, each with a different uniform speed, and indicated which interval appeared faster. For both tasks, we specifically examined the effects of mean speed and duration.

2.1. Methods

2.1.1. Observers

Four observers participated in these experiments. They all had normal or corrected-to-normal vision. Two naive observers (SD and YR) 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 (Octane MXE, 2 × R10000) using OpenGL graphics primitives. Each dot trajectory was pre-calculated and a wrap-around procedure was used to keep dot-density constant at 10.5 dots/deg². The trajectories were then stored on disk for later display. Random dots of luminance 4 cd/m² were back-projected onto a large tangent screen at a refresh rate of 76 Hz, using a trichromatic projector (Electrohome Marquee 8000). 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 m. The display resolution was 1280 × 1024 pixels, subtended 7° by 7°, and at the chosen viewing distance, each pixel was 0.05°. The screen background and experimental room were dark (background luminance < 0.01 cd/m²). Randomized presentation of the stimuli and recording of the responses (using response keys) were controlled

on-line by a PC (HP 486), connected to the graphics station by a serial RS232 interface. Stimuli always first appeared stationary for a random period of time (300–700 ms) and were then set into motion for a given duration. The inter-stimulus interval was always 500 ms. To minimize tracking eye movements, a blue fixation cross ($1^\circ \times 1^\circ$, 0.1 cd/m^2) was displayed at the center of the stimulus.

2.1.3. Visual stimuli and procedures

2.1.3.1. Experiment 1-1: speed segmentation. A single frame consisted of 512 small rectangular dots randomly distributed over the whole image. Each dot extended 2 pixels horizontally and 1 pixel vertically. Given the spatio-temporal resolution of our video projection system, the smallest speed which can be produced by shifting one pixel on every frame was $3.8^\circ/\text{s}$. To produce smaller speed differences, we used a sub-pixel animation procedure along the horizontal axis (Georgeson, Freeman & Scott-Samuel, 1996). The smallest difference in speed that could be generated was 2.5%, corresponding to $0.025^\circ/\text{s}$ for a reference speed of $1^\circ/\text{s}$.

Each two-interval forced choice trial consisted of two temporal intervals; in one interval, half of the dots moved at a speed of $v_1 = \bar{v} \cdot (1 + \Delta v/2)$, while the other half of the dots moved at $v_2 = \bar{v} \cdot (1 - \Delta v/2)$; in the other interval, five different speeds ranging from v_1 and v_2 were randomly chosen, such that the two intervals always had the same mean speed \bar{v} . We call these ‘test’ and ‘reference’ intervals, respectively. Observers were asked to indicate which of the two intervals was the test, i.e. contained two and only two speeds. Above thresholds, subjects reported perceiving two transparent surfaces sliding over each other in the test condition while the reference condition led to the perception of a cloud of horizontally moving dots. To reduce motion adaptation effects, the direction of motion was randomly leftward or rightward, on half of the trials. We used PEST (Taylor & Creelman, 1967) to staircase the speed difference between v_1 and v_2 as defined above, and up to five repeated runs to obtain each threshold. The smallest PEST step size was of 5%. No feedback was ever provided.

The dependence of the speed-segmentation threshold ($\Delta v/v$) on mean stimulus speed (\bar{v}) and stimulus duration (d) was investigated for five mean speeds ranging from 1 to $16^\circ/\text{s}$ and five durations ranging from 65 ms (five frames) to 520 ms (40 frames).

2.1.3.2. Experiment 1-2: speed discrimination. The same experimental procedure and general random-dot characteristics were used to investigate the speed-discrimination thresholds and compare them with speed-segmentation thresholds under identical experimental

conditions. For the speed-discrimination experiments, the test and reference stimuli were populations of random dots moving uniformly with either speed v_1 or v_2 , as defined above. The mean speed across the two intervals was kept constant but the speed difference between v_1 and v_2 was staircased using the same PEST procedure. Observers were asked to determine which interval moved faster. Again, the direction of motion was randomly leftward or rightward, and up to five runs were performed for each threshold. To minimize training or learning effects, speed discrimination and speed segmentation trials were run in interleaved blocks. Observers completed all threshold estimates for one mean speed \bar{v} for the two tasks with a given stimulus duration and then moved to the next stimulus duration, except for the 39 ms (discrimination) and 520 ms (segmentation) trials, which were run independently.

The dependence of the speed-discrimination threshold ($\Delta v/v$) on mean stimulus speed (\bar{v}) and stimulus duration (d) was investigated for five mean speeds ranging from 1 to $16^\circ/\text{s}$ and five durations ranging from 39 ms (three frames) to 260 ms (20 frames).

2.2. Data analysis

We fit both the segmentation and discrimination data with a Weibull function using the Simplex algorithm to find the speed difference yielding 75% correct. The relationships between the thresholds and mean speed (\bar{v}) and stimulus duration (d) were fit with Eq. (1) and Eq. (2), respectively, using the Simplex algorithm run with Matlab software:

$$\frac{\Delta v}{v} = k_1 \cdot \exp(-k_2 \cdot \bar{v}) + k_3 \cdot \exp(k_4 \cdot \bar{v}) \quad (1)$$

such that parameters k_1 , k_2 , k_3 and k_4 define a minimum (when $k_2 \cdot k_4 < 0$) at

$$v_{\min} = \frac{\ln\left(\frac{-k_1 \cdot k_2}{k_3 \cdot k_4}\right)}{(k_4 - k_2)}.$$

and

$$\frac{\Delta v}{v} = \left(\frac{\Delta v}{v}\right)_0 \cdot \exp[-\tau \cdot d] + \left(\frac{\Delta v}{v}\right)_{\text{as}} \quad (2)$$

such that $(\Delta v/v)_{\text{as}}$ is the asymptotic threshold for long durations, and $1/\tau$ is the time constant of the exponential decay.

3. Results

3.1. Experiment 1-1: speed segmentation

Fig. 1 plots the speed-segmentation thresholds, averaged across runs, as a function of the mean speed for

each observer and stimulus duration. For all durations, the speed-segmentation threshold is sensitive to mean speed, with the speed difference required to segregate two surfaces increasing as the mean speed increases. For the 65-ms duration, the curves are somewhat idiosyncratic and thresholds are barely below 40%. At longer stimulus durations, the relationships between threshold and mean speed are well behaved and similar across observers; all curves exhibit low-pass behavior, with thresholds sharply increased at 16 °/s. Some curves also show an increase in speed-difference thresholds when mean speed decreases below 2 °/s, suggesting a U-shape relationship between threshold and mean speed, at least for durations shorter than 260 ms. For all observers, increasing the stimulus duration for a given mean speed decreases threshold, down to an average of 13.2% (across observers and speeds) at the longest duration (520 ms), for mean speeds below 16 °/s. However, except for one observer (SD), at the longest stimulus duration (Fig. 1e), thresholds for speed segmentation are never below 20% at 16 °/s. The exceptional performance of this naive observer for this set of

conditions is likely the result of inadequate fixation; the intrusion of tracking eye movements would tend to reduce the mean retinal speed thus making the task easier.

Fig. 2a plots the speed-segmentation thresholds, averaged across observers, as a function of mean stimulus speed, for each stimulus duration. The data show a clear trend; the smallest thresholds were found for slow speeds, between 1 and 4 °/s, and they increased dramatically at 16 °/s for all stimulus durations. For instance, at 200 ms duration, the mean threshold was 21.7% for 1 °/s and increased to 76.5% for 16 °/s. The speed difference of 21.7% around a mean speed of 1 °/s, leads to a relative displacement between fastest and slowest dots of about 0.05° over the 15 frames. Over the same period of time, a speed difference of 76.5% around a mean speed of 16 °/s leads to a relative displacement around 2.42°. This indicates that the observed speed cut-off is due to a low-pass speed limitation in the motion-segmentation mechanism and not merely a lack of temporal integration of relative displacement. The best-fits with Eq. (1) give estimates of local minima

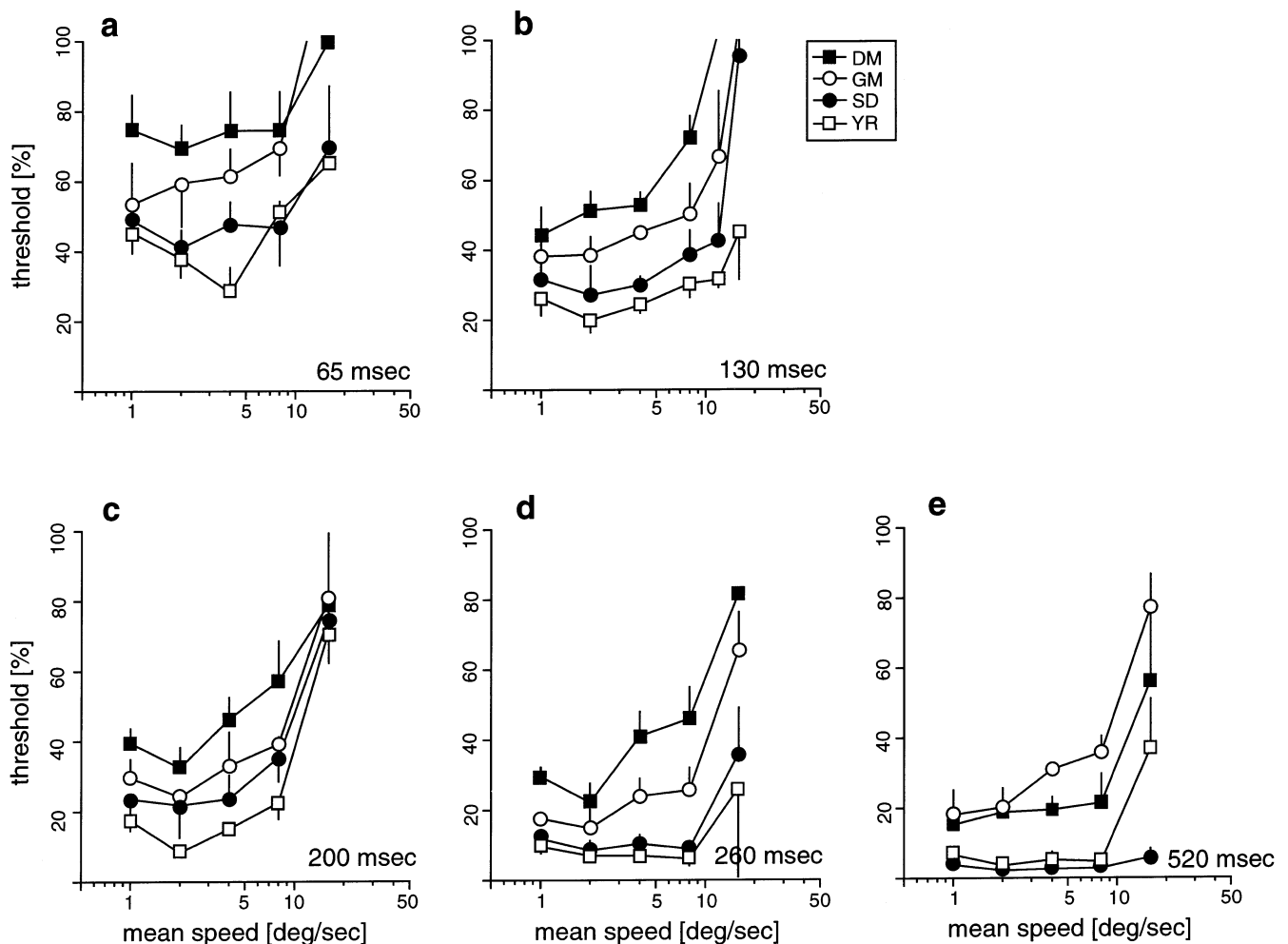


Fig. 1. Speed segmentation thresholds versus mean speed, for all four observers and all stimulus durations. Data are means (\pm S.D.) across runs.

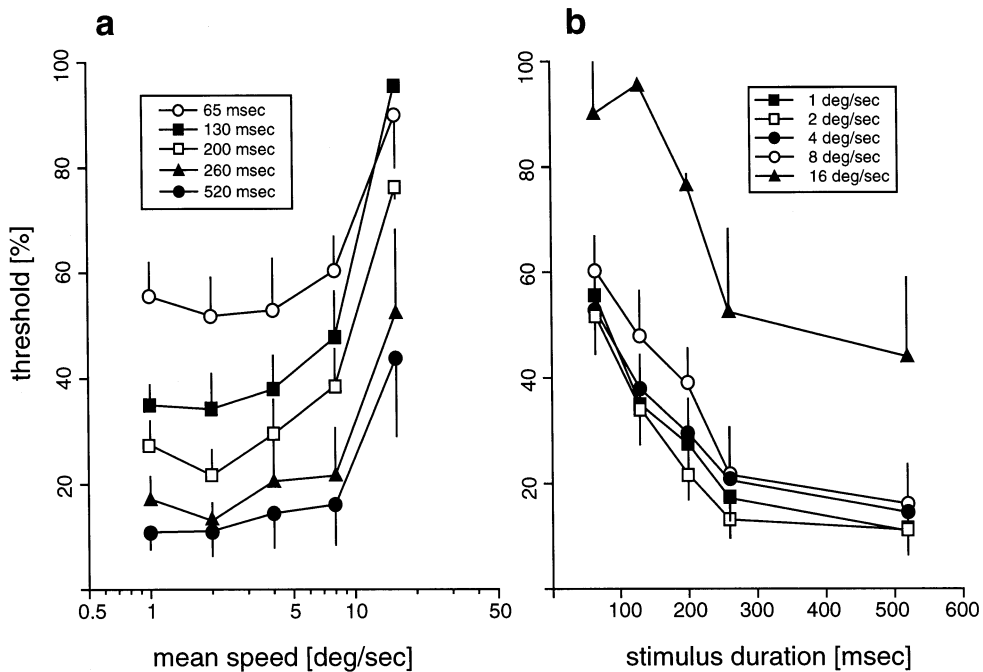


Fig. 2. (a) The average (\pm S.E. across observers) speed-segmentation thresholds as a function of stimulus mean speed, for each stimulus duration. (b) The average (\pm S.E.) speed-segmentation thresholds as a function of stimulus duration, for each mean stimulus speed.

between 0.5 and 3 $^{\circ}$ /s for stimulus durations between 65 and 200 ms.

The speed-segmentation threshold, averaged across mean speeds, ranged from 19.4% at 520 ms to 62.2% at 65 ms; an eightfold increase in the stimulus duration produced a threefold decrease in threshold. To examine the time course of this improvement, Fig. 2b plots the average thresholds, as a function of duration, for each mean speed. Again, the data show a clear trend; not surprisingly, increasing stimulus duration lowers the threshold at least out to \approx 200 ms. Little improvement in performance is observed at the longest duration. To estimate the time constant of this improvement, the average data were fit with a single exponential function [Eq. (2)] and the parameters of the best fits are shown in Table 1. The best-fitting time constant ($1/\tau$) was between 105 and 175 ms with no obvious change in ($1/\tau$) with mean speed. Asymptotic threshold, parameter $(\Delta v/v)_{as}$, was largely unaffected by mean speed, ranging from 9.3% at 2 $^{\circ}$ /s to 12.5% at 4 $^{\circ}$ /s. There was no significant difference between the estimated asymptote and the measured thresholds for stimulus durations higher than 200 ms, indicating that a plateau for segmentation performance was reached.

3.2. Experiment 1-2: speed discrimination

To compare the ability of human observers to segment multiple motions in a transparent display using only speed cues, with the ability of the same observers to discriminate two different sequentially presented speeds, we ran interleaved runs on the same four ob-

servers. We were careful to keep all the visual stimulus conditions (dot density, luminance, contrast, display size) identical to Experiment 1-1. Fig. 3 plots the speed-discrimination thresholds, averaged across runs, as a function of mean speed, for each observer and stimulus duration. Curves for the two shortest stimulus duration (39 and 65 ms) were somewhat idiosyncratic. For longer stimulus durations, the data are consistent with previous findings (McKee, 1981; De Bruyn & Orban, 1988); speed-discrimination thresholds decrease with increasing mean speed with a hint of a minimum between 5 and 10 $^{\circ}$ /s.

Fig. 4a plots the speed-discrimination thresholds, averaged across observers, as a function of mean stimu-

Table 1
Effects of stimulus duration^a

Speed ($^{\circ}$ /s)	$(\Delta v/v)_0$	$(\Delta v/v)_{as}$	$1/\tau$
<i>Segmentation</i>			
1	77.62	9.70	122
2	80.37	9.31	105
4	64.81	12.53	139
8	73.45	11.02	175
<i>Discrimination</i>			
1	45.40	18.54	98
2	52.17	16.03	60
4	40.30	15.75	35
8	31.30	9.56	72

^a Best-fit parameters when Eq. (2) was fitted to the duration tuning curves; for both segmentation and discrimination thresholds. The best-fits were not statistically significant for the fastest speed 16 $^{\circ}$ /s and are therefore not reported.

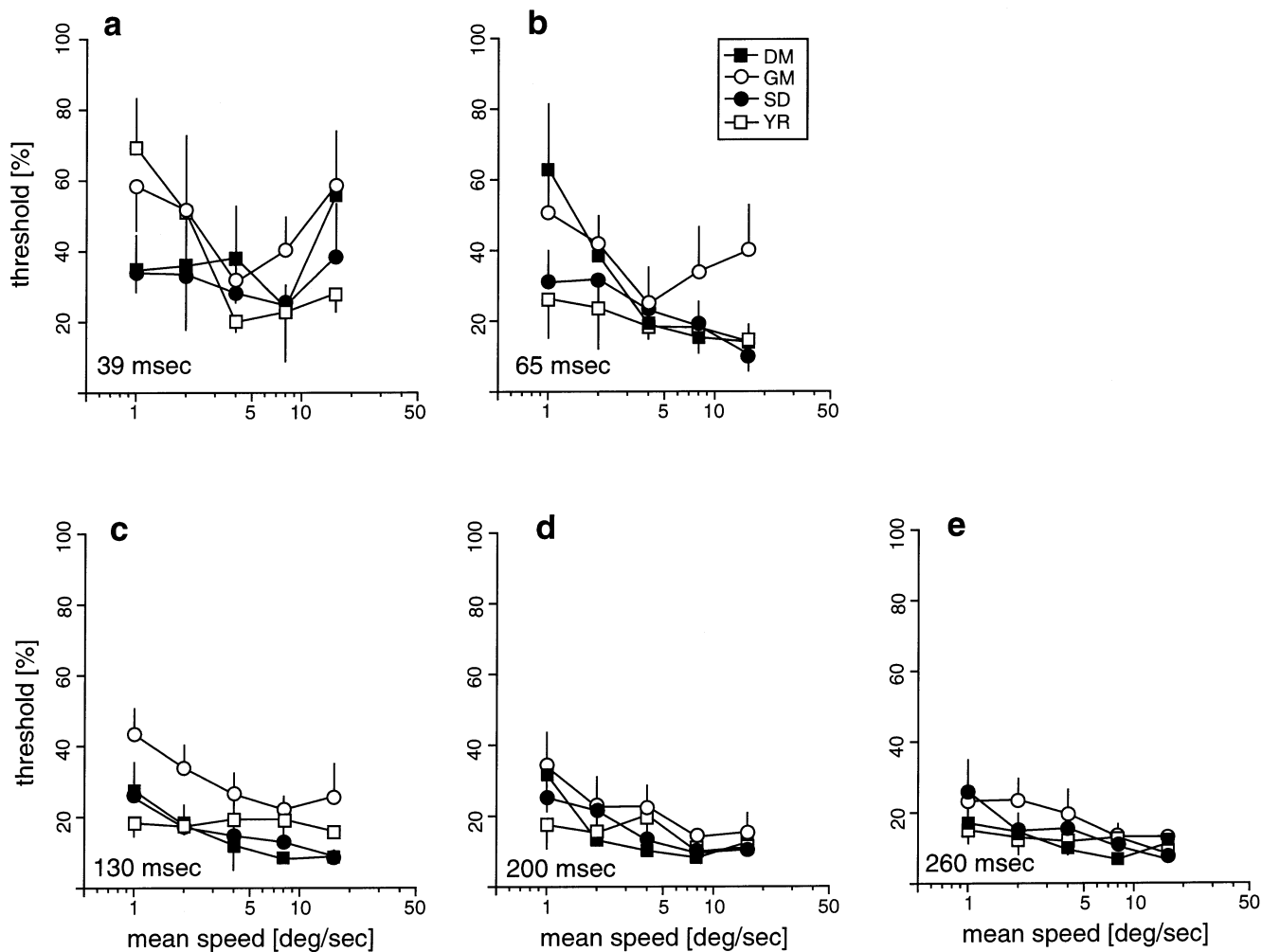


Fig. 3. Speed discrimination thresholds plotted against stimulus mean speed, for all four observers and all stimulus durations. Data are means (\pm S.D.) across runs. Symbols are the same as in Fig. 1

lus speed for each stimulus duration. To allow direct comparison between thresholds for a given stimulus duration, the same symbols are used as in Fig. 2a (except for the solid circles). The data show a clear trend; for durations above 39 ms, performance exhibits high-pass behavior with higher mean speeds associated with lower thresholds. The best-fit estimates of the local minima were found at 7 (39 ms duration), 9.9 (200 ms) and 11.2°/s (130 ms).

The discrimination thresholds, averaged across mean speeds, ranged from 14.4% at 260 ms to 39.0% at 39 ms; a nearly sevenfold increase in the stimulus duration produced a 2.5-fold decrease in threshold. To examine the time course of this improvement, Fig. 4b plots the speed-discrimination thresholds, averaged across observers, as a function of duration, for each mean speed. The data show a clear trend; not surprisingly, increasing duration decreased the discrimination threshold. The reduction was most dramatic for the fastest speeds (8 and 16 °/s) with thresholds changing by a factor of three between the 39 ms and 260 ms stimulus durations.

By comparison, thresholds changed by a factor of two for the slowest speeds (1 and 2°/s). To estimate the time constant of this improvement, average data were fit with a single exponential function [Eq. (2)] and the parameters of the best fits are shown in Table 1. The best-fitting time constant ($1/\tau$) was between 35 and 98 ms with no obvious dependence upon stimulus speed. Asymptotic threshold, parameter $(\Delta v/v)_{as}$, ranged from 9.6% at 8 °/s to 18.5% at 1 °/s. There was no significant difference between the estimated asymptote and the measured thresholds for stimulus durations longer than 65 ms (1, 2 and 8 °/s) or 130 ms (4 °/s), indicating that a plateau for speed-discrimination performance was reached.

3.3. Comparing motion discrimination and segmentation

A 3-way ANOVA was performed to assess the effects of the task, mean speed, and duration (in the range from 65 to 260 ms). All three factors had significant effects on the speed-difference thresholds. Mean

thresholds were significantly higher for motion segmentation than for motion discrimination ($F(1, 3) = 17.03$, $P < 0.025$, mean thresholds, 44.4 and 19.8%, respectively). In the same vein, stimulus duration had a significant effect ($F(2,9) = 44.18$, $P < 0.001$) as well as stimulus speed ($F(4, 12) = 46.54$, $P < 0.001$).

The first striking difference between speed segmentation and discrimination is their dependence on mean speed. Fig. 5a illustrates the relationship between the speed-difference threshold and mean stimulus speed for both motion discrimination (open symbols) and segmentation (closed symbols). The data are the average thresholds across the observers, for the 200 ms stimulus. This duration was chosen because it is the closest to asymptotic performance without being long enough to allow significant contamination from smooth eye movements (Mestre & Masson, 1997b). The continuous lines are best-fitting double-exponential curves [Eq. (1)]. As discussed above, over the range investigated, segmentation from speed cues shows low-pass behavior with an upper cut-off for speeds above about 8 °/s. The minimum speed-difference threshold is located at about 1.7°/s. The possibility of a lower cutoff needs to be investigated in future experiments using slower mean speeds. On the other hand, speed discrimination exhibits high-pass behavior with a minimum located around 9.5°/s. An upper cut-off, at speeds beyond the range that we tested, has been previously described (De Bruyn & Orban, 1988). Similar results were observed

for all other stimulus durations and a significant interaction between speed and task was observed ($F(4, 12) = 53.69$, $P < 0.001$). Post-hoc analysis revealed that there was no significant difference between the thresholds for motion segmentation and motion discrimination with a mean speed of both 1 and 2°/s ($P > 0.05$ Newman–Keuls test). On the contrary, segmentation thresholds were significantly higher across durations for mean speeds $\geq 4^\circ/\text{s}$ ($P < 0.05$, Newman–Keuls test).

The second striking difference between speed segmentation and discrimination is their dependence on stimulus duration. Fig. 5b plots the relationship between speed-difference threshold and duration. The data are the average thresholds across observers for the 4°/s condition. This speed was chosen because it is mid-way between the optimal speed for segmentation and discrimination. The continuous lines are the best-fitting exponential curves [Eq. (2)]. Speed discrimination clearly improves faster than speed segmentation. The time constant for the former is 35 ms while that for the later is 139 ms. This difference was found for all other speeds tested (Table 1). There was no obvious dependence of the time constant on the mean speed for either segmentation or discrimination. Averaged across speeds, time constants were ≈ 60 ms for discrimination and ≈ 150 ms for segmentation. This difference reflects the significant interaction between task and duration in the ANOVA ($F(3,9) = 30.57$, $P < 0.001$).

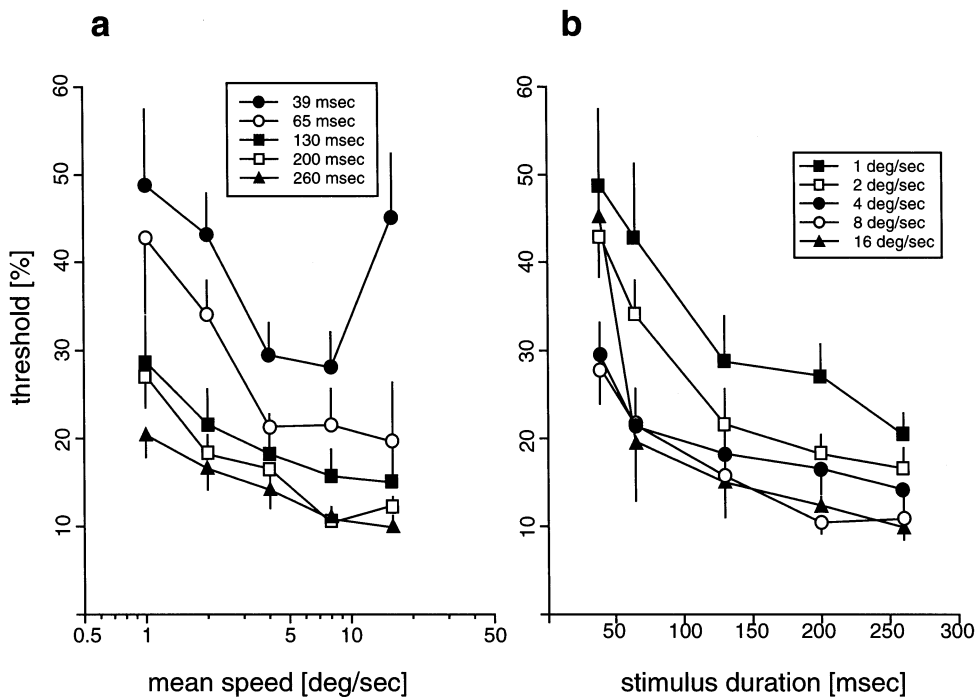


Fig. 4. (a) The average (\pm S.E. across observers) speed-discrimination thresholds plotted as a function of stimulus mean speed, for each stimulus duration. Notice that the abscissa is doubled and the ordinate is halved, compared to Fig. 2. (b) The average (\pm S.E.) speed-discrimination thresholds plotted as a function of stimulus duration, for each mean stimulus speed.

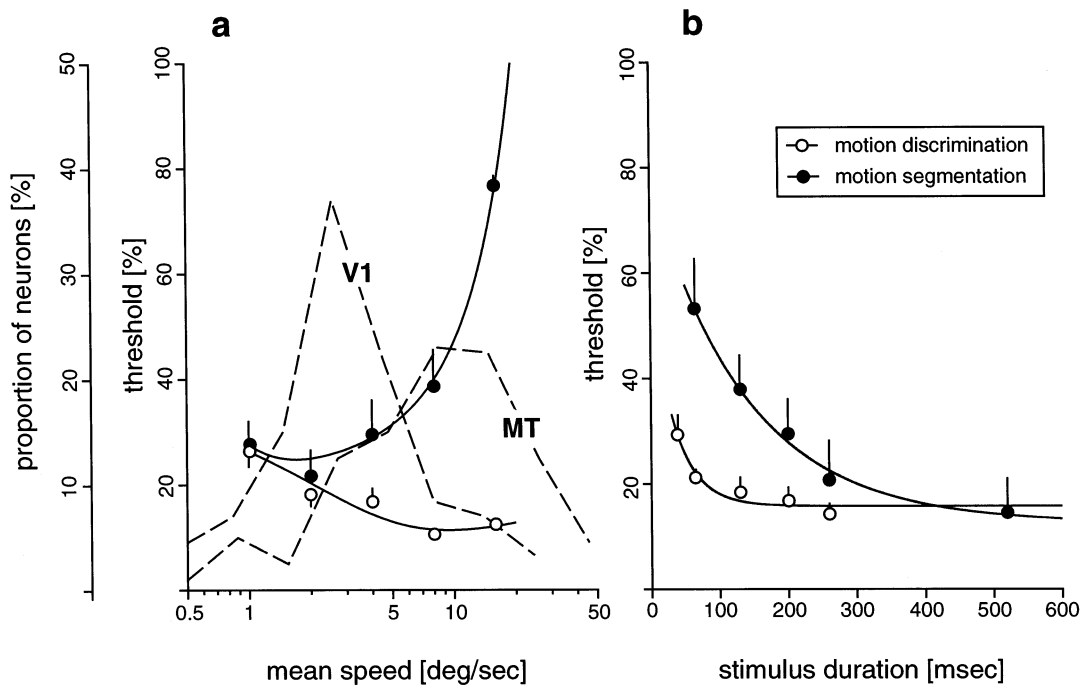


Fig. 5. Comparison between motion segmentation and motion discrimination. (a) Average (\pm S.E., across observers) thresholds for speed segmentation (closed symbols) and speed discrimination (open symbols) are plotted as a function of mean stimulus speed, for a stimulus duration of 200 ms. Similar differences were observed for all other tested stimulus duration (65, 130 and 260 ms). Superimposed are the distributions of speed sensitivities for V1 (upper velocity cut-off) and MT (optimal speeds) neurons in macaque monkeys (Orban, Kennedy & Bullier, 1982; Cheng, Hasegawa, Saleem & Tanaka, 1994). (b) Average (\pm S.E.) speed-segmentation (closed symbols) and speed-discrimination (open symbols) thresholds are plotted as a function of mean stimulus duration for a stimulus speed of $4^\circ/\text{s}$. Similar relationships were found with the other tested speeds (1, 2, 8 and $16^\circ/\text{s}$).

The 3-way interaction was also significant ($F(12, 36) = 3.01$, $P < 0.005$) indicating that thresholds were significantly different between segmentation and discrimination for some combinations of mean speed and duration, but not others. This was further investigated with post-hoc analysis (Newman–Keuls). As illustrated in Fig. 5a for the 200 ms stimuli, segmentation and discrimination thresholds were not statistically different for both 1 and $2^\circ/\text{s}$ ($P > 0.5$), but were significantly different for all other mean speeds ($0.001 < P < 0.04$). Interestingly, segmentation and discrimination thresholds were significantly different for all mean speeds at shorter stimulus durations (65 and 130 ms, $P < 0.007$). In brief, these results summarize the fact that for slow speeds, segmentation and discrimination thresholds converge to an identical, optimal performance, albeit with a different time course.

4. Discussion

The human visual system can segment multiple motions that are transparently combined in an image sequence (see Stoner & Albright, 1993; Braddick, 1997). 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 moving 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 or speeds can be perceived as transparent surfaces moving through or over each other (Clarke, 1977; van Doorn & Koenderink, 1982a, 1983; Andersen, 1989; Snowden, 1989, 1990; Bravo & Watamaniuk, 1995; Mestre & Masson, 1997a). We have extended these studies by directly comparing the speed tuning and time-course of the segmentation and discrimination of moving random-dot patterns based on speed signals alone. Our main findings are: (1) speed segmentation is low-pass, i.e. it operates over a restricted range of speeds and deteriorates dramatically at speeds higher than, $\approx 8^\circ/\text{s}$ and (2) motion segmentation requires a longer temporal integration compared to motion discrimination under matched conditions.

4.1. Speed segmentation for motion transparency

Our results illustrate two critical constraints on motion segmentation, and do so in the absence of other segmentation cues such as hue, binocular disparity, size,

or contrast polarity (for a review see Stoner & Albright, 1993). First, we found that speed discrimination and segmentation have different dependencies on stimulus speed. Fig. 5a illustrates this finding. The motion mechanisms underlying speed segmentation are tuned for low speeds (upper cut-off $\approx 16^\circ/\text{s}$). On the other hand, the motion processing underlying speed discrimination operates over a broader range with an upper cut-off between 40 and $60^\circ/\text{s}$ (McKee & Nakayama, 1984; Orban, de Wolf & Maes, 1984; De Bruyn & Orban, 1988).

Several experimenters previously reported good performance for speed discrimination with random-dot displays (e.g. De Bruyn & Orban, 1988; Snowden & Braddick, 1991; Watamanink & Duchon, 1992). Our speed-discrimination thresholds are somewhat higher than the 5–17% thresholds reported by De Bruyn and Orban (1988), for speeds between 0.5 and $64^\circ/\text{s}$ and a duration roughly the same (200 ms) as ours. Many differences between the experimental conditions could account for this difference (e.g. luminance, inter-stimulus interval duration, level of practice, etc.) (Orban et al., 1984). Nevertheless, the present results are qualitatively consistent with those of Orban and coworkers for large random dots stimuli and with McKee (1981) and McKee and Nakayama (1984) for single targets; they found that speed discrimination exhibits a significant decrease in performance at low speeds (below about $4^\circ/\text{s}$) and high speeds (above about $60^\circ/\text{s}$).

A second critical property of motion segmentation is the slow temporal buildup of the transparent percept. The dependence of speed-discrimination thresholds on stimulus duration has been previously reported for both random-dot patterns (De Bruyn & Orban, 1988) and single targets (McKee, 1981). In both cases, asymptotic performance occurs at rather short durations (≈ 100 – 150 ms, De Bruyn & Orban, 1988; Snowden & Braddick, 1991). Our results are in close agreement with those of earlier studies. The time constant of temporal integration for our speed-discrimination task is ≈ 60 ms, consistent with previously documented temporal integration times of about 100 ms for direction and speed discrimination (De Bruyn & Orban, 1988; Watson & Turano, 1995). On the other hand, experiments measuring motion segmentation, structure-from-motion, or other three-dimensional motion percepts have reported rather sluggish dynamics. For instance, Treue, Husain and Andersen (1991) reported a rather slow temporal build-up for structure-from-motion perception, Mestre and Masson (1997a) demonstrated long (> 1 s) reaction times for the discrimination of stimuli made of either one, three, or ten different speeds, and Stone and Perrone (1991) found that heading-from-optic-flow reached asymptotic performance at about 200 ms. The time constant of temporal integration for our speed-segmentation task is ≈ 150 ms, consistent with

the findings of Møller (1992). This sluggish behavior contrasts with the faster asymptote for motion detection (see Møller & Hurlbert, 1996 for a direct comparison) or speed discrimination (De Bruyn & Orban, 1988). The difference between segmentation and discrimination is clearly illustrated in Fig. 5b. The time constant for speed discrimination is much shorter than that for speed segmentation (see Table 1), irrespective of the mean stimulus speed in the range tested.

It is possible that observers performed our speed-segmentation task using cues other than transparency. In our segmentation task, because the two intervals could be interpreted as ‘two frontoparallel surfaces’ or as ‘a volumetric cloud’, we cannot rule out the possibility that observers performed some kind of 3D structure-from-motion discrimination. However, in an earlier preliminary study (Masson & Mestre, 1997; Mestre & Masson, 1997b; Masson, Mestre & Stone 1998), to determine segmentation thresholds, we asked observers to discriminate a random-dot stimulus with two speeds/surfaces from one single speed/surface and therefore no 3D structure. The similarity between the performance in that task and the present one suggests that transparency, not 3D structure, is responsible for the high speed-difference thresholds in our segmentation task. It is also possible that observers used displacement or streaking to support their judgments. However, this possibility is difficult to reconcile with our finding that, in pairwise comparisons between conditions, better discrimination was often associated with shorter displacements. Lastly, it is possible that the higher thresholds in our segmentation task than in our discrimination task can be explained by the presence of the additional three speeds acting to reduce the relevant signal-to-noise ratio, without any specific reference to segmentation *per se*. However, it is difficult to see how the often more than fourfold and speed-dependent threshold differences observed could entirely be explained in this way. Moreover, the similarity with our previous results using a two versus a one speed/surface discrimination argues against this possibility as well.

Several authors have previously examined segmentation based on direction differences. By having observers adjust the signal to noise ratio of a transparent pattern, van Doorn and Koenderink (1982b) found that superimposed motion streams can be segmented whenever the directions of the motion vectors differ by at least 30° . 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 sets of random dots jointly and therefore performance was related to a genuine multivalued representation of direction (see Braddick, 1997). Our method of using five versus two speeds also forces observers to perform a global task by making a local speed difference an

unreliable cue. Their experiment showed that observers can make judgments of the angle between random-dot motions with a precision of about 13° , which is higher than the $\approx 7^\circ$ expected given the $\approx 5^\circ$ required for judging the angle between the motion of a set of random dots relative to a stationary line. Apparently, there is some penalty associated with transparency. In the present study, we also found a penalty associated with transparency at least at speeds higher than $2^\circ/s$. For instance, we found that, with a stimulus duration of 200 ms (Fig. 5a), the perception of transparency requires speed differences of about 25–40% (speed range: 2–8 $^\circ/s$), while, under matched conditions, speed-discrimination thresholds are only-around 10–25%. A similar difference is found between the higher thresholds for texture segmentation based on static orientation cues and simple orientation discrimination (Nothdurft, 1994).

4.2. Neurophysiological substrates

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, a view supported by a number of psychophysical studies of motion detection and discrimination (e.g. Adelson & Movshon, 1982; Welch, 1989; Smith, Snowden & Milne, 1994). These two stages have been associated with cortical areas, MT and V1, respectively (see Movshon et al., 1985; Albright & Stoner, 1995; Nowlan & Sejnowski, 1995). Within this scheme, it remains unclear where motion segregation (the distinction of multiple velocities) and selective integration (the grouping of similar velocities) occur. Andersen and colleagues (Snowden, Treue, Erickson & Andersen, 1991; Qian & Andersen, 1994) reported little or no change in V1 responses when opponent motions were paired within a V1-sized area, a manipulation that destroys perceived transparency. On the contrary, MT neurons were largely inhibited by pairing. This discrepancy led them to postulate that pairing might affect V1-sized 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. Indeed, several properties of MT neurons such as their large receptive fields (Maunsell & Van Essen, 1983; Albright & Desimone, 1987), broad speed tuning (Maunsell & Van Essen, 1983; Rodman & Albright, 1987; Lagae, Raiguel & Orban, 1993), sensitivity to segmentation cues (Stoner & Albright, 1992), and pattern-motion selectivity (Movshon et al., 1985; Rodman & Albright, 1989) suggest that area MT plays an important role in motion integration.

Although it remains unresolved where and how motion segmentation is implemented in the visual motion pathway, our data show that the segmentation mechanism shares its speed tuning with that of V1 neurons. Fig. 5a compares the speed tuning of the segmentation process together with that for V1 (Orban et al., 1982) and MT neurons (Cheng et al., 1994). There is a clear correlation between the limited low-pass tuning of motion segmentation and the range of preferred speeds of V1 neurons. In contrast, the higher bandpass tuning of speed discrimination is more similar to that of MT neurons, as previously suggested (De Bruyn & Orban 1988; Orban, Saunders & Vandebussche, 1995). Therefore, our psychophysical data support the view that motion segmentation and discrimination are implemented at different levels within the motion processing stream. Our results support the hypothesis that segmentation is initiated by a network of neurons with small receptive fields and low-pass speed tuning, as found in the early stages of motion processing such as V1. Indeed, the ability to segregate image motion at a small spatial scale (Qian et al., 1994; Masson et al., 1998) may constrain the segmentation process to have a rather low speed cutoff because of the natural trade-off between receptive field size and preferred speed (Mikami, Newsome & Wurtz, 1986; Chey, Grossberg & Mingolla, 1998).

In conclusion, the present study demonstrates that speed segmentation operates over a different, narrower range of speeds than speed discrimination. The speed tuning closely resembles that of neurons earlier in the motion pathway than MT (e.g. V1, V2 or V3) (Orban, Kennedy & Bullier, 1986; Mikami et al., 1986; Gegenfurtner, Kiper & Levitt, 1997). Investigating the speed-difference thresholds for motion segmentation provides a powerful tool for exploring the neural processing for motion integration and segregation. We are currently extending this approach to probe the spatial scale of the local interactions underlying motion segmentation from speed cues.

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