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A single motion system suffices for global-motion perception

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Abstract

Global-motion perception is the perception of coherent motion in a noisy motion stimulus. Thresholds for coherent motion perception were measured for different combinations of signal and noise speeds. Previous research [Edwards, M., Badcock, D. R., & Smith, A. T. (1998). Independent speed-tuned global-motion systems. *Vision Research, 38* (11), 1573–1580; Khuu, S. K., & Badcock, D. R. (2002). Global speed processing: evidence for local averaging within, but not across two speed ranges. *Vision Research*, 42 (28), 3031–3042.] showed that thresholds were elevated when signal and noise speeds were similar, but not when they were different. The regions of increased threshold values for low and high signal speeds showed little overlap. On the basis of this evidence two independent speed-tuned systems were proposed: one for slow and one for fast-motion. However, in those studies only two signal speeds were used. We expanded the results by measuring threshold-curves for four different signal speeds. Considerable overlap of the threshold-curves was found between conditions. These results speak against a bipartite global-motion system. Model simulations indicate that present and previous experimental results can be produced by a single motion system providing that the mechanisms within it are speed-tuned.
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1. Introduction

Motion information is abundant, and therefore a useful and often-used source of information.

Research on motion perception has suggested that the processing of motion information from the retina to perception consists of at least two processing steps (Adelson & Movshon, 1982; Kim & Wilson, 1996; Simoncelli & Heeger, 1998; Welch, 1989; Yuille & Grzywacz, 1988). Motion signals are initially picked up by cells that have receptive fields spanning less than a degree (Hubel & Wiesel, 1968; Reid, Soodak, & Shapley, 1991; Wurtz, 1969), hence this step is called the local-motion processing step. Often the gathered motion information is rather noisy, and pooling of velocity information may be essential to obtain a reliable indication of what the motion of the observed object was. Such a pooling process is thought to occur at a global-

motion processing stage in which information from several local-motion processing units are combined (Movshon, Adelson, Gizzi, & Newsome, 1985; Rodman & Albright, 1989; Stoner & Albright, 1994). In this study we are interested in the representation of velocity (i.e., direction and speed) at the global-motion processing level.

We are particularly interested in the question whether global-motion processing is achieved by one or several (independent) systems.

MT is the cerebral location where one thinks global-motion processing takes place.[1] Indeed, cells that process global motion have been found in MT (Movshon et al., 1985; Rodman & Albright, 1989; Smith, Majaj, & Movshon, 2005; Stoner & Albright, 1994). In MT the representation of direction changes smoothly over the cortex (Malonek, Tootell, & Grinvald, 1994). This structural

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[1] Area MST is also important in global-motion processing, but seems to be implicated in more complex motion analysis than MT (e.g., Born & Bradley, 2005; Vaina, 1998)

map is probably the resultant of an evolutionary pressure that pushes neurons that functionally interact closer to each other (Chklovskii & Koulakov, 2004). However, no clear-cut evidence exists for speed maps. Nevertheless, nearby cells have a tendency to have a similar speed preference (Liu & Newsome, 2003). These neurophysiological results are suggestive of a single motion system processing the whole range of directions and speeds, but they do not exclude the possibility of more motion systems.

Psychophysical data also suggests that direction information is processed in a single-system. Specifically, motion aftereffect (MAE) studies have found that adaptation to two motions of different directions (but identical speeds) results in a single motion aftereffect opposite to the vector-average of the two adapting components, suggesting that all the direction information is integrated (Mather, 1980; van der Smagt, Verstraten, & van de Grind, 1999). Furthermore, when two moving planes are presented simultaneously the difference in direction of motion between the two planes is perceived larger than veridical. This phenomenon is called motion repulsion or direction repulsion (Braddick, Wishart, & Curran, 2002; Dakin & Mareschal, 2000; Hiris & Blake, 1996; Kim & Wilson, 1996; Marshak & Sekuler, 1979; Mather & Moulden, 1980), and shows that long-range interactions exist in the direction-dimension. Motion repulsion takes place for angles between two motion vectors of up to 120° (Braddick et al., 2002; Mather & Moulden, 1980), again indicating that direction information is processed by a single-system.

On the other hand, other psychophysical data does give support to claims that multiple systems exist for speed processing. First, it is found that motion detection (Burr, Fiorentini, & Morrone, 1998) and discrimination (Gegenfurtner & Hawken, 1995) thresholds are higher for chromatic than for achromatic motion when stimulus speed is low, but these thresholds are identical when stimulus speed is high. These data suggest that there may be three motions systems: one for slow chromatic motion, one for slow achromatic motion, and one for fast (chromatic and achromatic) motion (Burr et al., 1998; Gegenfurtner & Hawken, 1995; Hawken, Gegenfurtner, & Tang, 1994). Second, MAE experiments show that for certain speed combinations of two motion-adaptation components, the resulting motion aftereffect is not opposite to the vector-average of these components. Adaptation to two adapting components of different speeds leads to two MAEs of differing speed, which may be brought about separately or simultaneously (van der Smagt et al., 1999; Verstraten, van der Smagt, Fredericksen, & van de Grind, 1999). These data have been interpreted as evidence for independent slow- and fast-motion systems. Within each motion system direction is integrated over the full 360°, but between systems no such integration takes place. Third, research on motion detection in noise has shown that motion detection is impaired when noise and signal dots move with similar speeds, but not when they move at very different speeds. Such was found for fast and slow signal

speeds (Edwards, Badcock, & Smith, 1998; Khuu & Badcock, 2002). Again the data were interpreted as evidence for independent fast and slow motion systems, this time for global-motion processing.

Although the psychophysical data are repeatedly interpreted in terms of two (or sometimes more) motion systems, direct neurophysiological evidence for such a division is absent. Moreover, some psychophysical counter-evidence has been reported (Metha & Mullen, 1997, 1998; van Boxtel, van Ee, & Erkelens, 2006). These studies show that the results that were interpreted as evidence for high and low speed systems may be reinterpreted in terms of a more parsimonious single-system explanation (see discussion section). For the last line of evidence (i.e., motion detection in noise) no such studies were found. Inspired by the previous studies reporting counter-evidence, we set out to investigate if the two systems that are proposed for global-motion processing could be united into a single-system.

Measuring thresholds for global-motion perception, we find that the detection of global-motion is impaired by noise that moves at similar speeds as the to-be-detected coherent motion, as reported by Edwards et al. (1998) & Khuu & Badcock (2002). However, when using more than two signal speeds, we find no indication of a division in fast and slow motion systems. Noise has a systematic degenerative effect on global-motion detection over wide ranges in the speed dimension, and the effect shows a tight link to the signal speed used and not to a particular speed range, which would be expected if it were linked to a speed-specific motion system. We developed a single-system model to investigate if the obtained pattern of results could be the result of a single continuous system, and found that this indeed appears to be the case.

Before continuing we would like to clearly define the terminology we adopt in this paper. The word "system" is, as it is generally done, used to imply that the processing of the information in question differs from that of other information. The processing of two systems is independent, and may involve different mechanisms/algorithms, and may also take place in different brain areas and often involves different modalities. Two motion systems respond therefore to different kinds of stimuli. For example, in MAE experiments it is assumed that the slow motion system responds specifically to non-dynamic test stimuli, and the fast-motion system specifically to dynamic ones (e.g., van der Smagt et al., 1999). Or that one activates different motion systems with colored (isoluminant) and luminance-defined motion stimuli (e.g., Hawken et al., 1994), on the bases of the finding that both have different contrast-dependencies. The word "channel" has three main usages, (1) it is the term for the psychophysically obtained profiles of the threshold-curves using masking-procedures; (2), it may be used to describe a set of units (e.g. neurons) that in a functional way form an entity that spans a specific and rather well-delineated region of the investigated domain; for example such a channel would be the main entity that

codes for speeds of, say, 3–7 deg/s. The entity would be the direct neuronal implementation of the psychophysically measured channel and would as such have the same tuning characteristics as the psychophysically measured channel. It would consist of a fixed set of units that responds as a whole to part of the investigated domain. Other channels consist of a completely different set of units, which may however partly overlap in their tuning to, e.g., speed. When these channels are shown to be truly independent, one could argue that they represent separate (independent) systems. (3) The word channel may also refer to a single unit (neuron) that codes for a limited part of the investigated domain.

As is clear from this list of definitions, the word channel is used to describe different things that are obviously related but may happen at quite different stages in the visual system, which complicates discussions on these issues. We will use the terms ''psychophysical channel'', ''neurophysiological channel'', and "neuron" or "unit" for definitions 1, 2, and 3, respectively.[2]

2. Experiment 1

Previous studies (Edwards et al., 1998; Khuu & Badcock, 2002) investigating the detection of coherent motion in noise, have found that noise impairs global-motion detection only when the speeds of noise dots were similar to that of the signal dots (carrying the coherent motion signal).

The following paradigm was used. Stimuli consisted of 75 dots, containing a variable number of signal dots that defined the coherent motion, the other dots being noise dots. The number of signal dots necessary to correctly identify a movie-sequence as containing a coherent motion, was measured and called the detection threshold. Signal and noise dots had identical speeds, but the noise dots had an individually assigned random direction of motion. The thresholds in this condition functioned as a comparison for conditions in which *additional* noise was added. The 75 additional noise dots also moved in random directions, but had a speed that varied over trials, which could be different from or identical to the speed of the signal dots. In the case that the speed of the additional noise dots was identical to the signal (and the other noise) dots, thresholds increased as expected. However, when the speeds differed, thresholds rapidly fell to comparison levels, as if no additional noise was added. The resulting threshold curve is a psychophysical channel.

Using slow (1.2 deg/s) and fast (9.6 deg/s) signal speeds there was little or no overlap between the psychophysical channels (i.e., the speed ranges where the increased thresholds were found) (Edwards et al., 1998; Khuu & Badcock, 2002). On the basis of this finding the authors concluded that at least two independent speed-tuned global-motion

systems exist.[3] However, these authors used just two signal speeds, which were rather far apart. To test if the regions of increased thresholds are indeed separable along the speed dimension, and identifiable as separate and independent systems, we decided to increase the number of signal speed conditions. Furthermore, we decided to measure thresholds for higher values of noise speed, to investigate if thresholds indeed remained elevated for high-noise conditions, when high signal speeds were used (Edwards et al., 1998; Khuu & Badcock, 2002).

We show in this report that these separate channels may not be interpreted as independent motion systems when their profiles show little overlap.

2.1. Method

2.1.1. Observers

Three subjects with normal or corrected-to-normal vision participated as observers, two were experienced (JB, first author; TK), one (AK) was an inexperienced observer. AK was naïve as to the purpose of the experiment.

2.1.2. Stimulus

The stimuli were brief motion sequences of random dot patterns that did or did not contain a coherent motion embedded in noise.

All sequences contained 150 white dots that were divided into two groups: a signal-containing group of dots, and a group of additional noise dots, each 75 dots large. Dots were of high luminance (about 70 cd/m^2), sized 3.1 arcmin, and were displayed on a black background (about 0.06 cd/m^2). The dots were randomly positioned on the first frame, and had an 'infinite' life-time. Of the first group a variable number of dots was assigned to be signal. Those signal dots moved *en group* in a certain direction (chosen randomly every trial), and with a given signal speed. The other dots of the first group were noise dots that moved in random directions (changing every frame transition) and had the same speed as the signal dots. At each frame transition, dots from the signal-containing group were assigned anew to be signal or noise.

The second group of dots (the additional noise dots) moved in random directions (changing every frame transition) and with a certain speed (not necessarily the same as that of the signal-containing group).

The display was 10.3° by 10.3° of visual angle and was surrounded by a single row of high-contrast stationary and filled squares (12.6 arcmin), that were positioned 25.2 arcmin from each other, and had a 70% chance of being visible (i.e., about 30% of the positions were left empty). Motion dots that moved outside the display were wrapped

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[2] Note that within a system several channels may be found.

[3] The authors did not mean psychophysical channels as they were speculating that the two systems could have functions that a single system could not have (Edwards et al., 1998; p. 1574) and could possibly involve different cortical processing (Khuu & Badcock, 2002, p. 3041).

around. Each sequence consisted of 30 frames, refreshed at 75 Hz, yielding 400 ms long movie sequences. A small fixation mark (size: 3.1 armin) was present at the center of the display.

2.1.3. Procedure

A two-interval forced-choice procedure was used to determine the number of signal dots needed for a coherent motion to be detected. One of the two-intervals contained a coherent motion signal, whereas the other contained only noise movements. The two-intervals were separated by a 500 ms blank period. Observers indicated in which interval a coherent motion was perceived.

We used the Quest procedure (Watson & Pelli, 1983) to find the number of signal dots needed for the observer to correctly identify in 75% of the trials the sequence with coherent motion, called the threshold for coherent motion perception. The procedure started with 18 coherently moving dots, and was aborted when, within a staircase, the Quest procedure gave two successive threshold-estimations that differed by less than 0.001 dots (this value was determined in tests that showed that the then-reached threshold (in number of dots) would remain the same irrespective of the subjects subsequent answers).

Thresholds were obtained for all combinations of 12 additional noise speeds and four signal speeds (noise speeds: 0.6, 0.8, 1.1, 1.6, 2.1, 2.9, 4.1, 5.6, 7.8, 10.6,14.5, 20.0 deg/s; signal speeds: 1.1, 2.1, 5.1, 10.6 deg/s). For every signal speed, the whole set was divided into three sessions, containing four interleaved Quest staircases each (session 1: 0.6, 1.6, 4.1, 10.6 deg/s; session 2: 0.8, 2.1, 5.6, 14.5; session 3: 1.1, 2.9, 7.8, 20.0 deg/s). The order of these sessions was random between subjects, and also within subjects between the three repetitions of each condition.

It has been shown that the used procedure really taps speed-tuned systems and not stepsize-tuned systems, and that the results are not dependent on refresh-frequency or perceived contrast (Edwards et al., 1998) in the range of parameters used in the present experiment.

2.1.4. Apparatus

Viewing was binocular. A Macintosh PowerPC G4 drove the experiment. Images were presented on a LaCie electron22blueIV monitor. Subjects used a chin-rest to stabilize head position. Experimental procedures were reviewed and approved by the Institutional Review Board and each subject gave informed consent.

2.2. Results and discussion

Figs. 1 and 2 show the results for one of the observers and of the averaged data, respectively. Shown are the threshold values (number of signal dots) for coherent motion perception plotted against the speed of the additional noise dots. Thresholds are low over rather broad ranges, but peak when the speed of the additional noise

dots is similar to the speed of the signal-containing group of dots. Considerable overlap between the curves exists. The size of the effects is of the same order as those reported previously (Edwards et al., 1998).

We fitted log-Gaussian curves to the mean results to identify the positions of the peaks of the different psychophysical channels and assess the width of the speed tuning. The fit-function is $\omega + \alpha G(\mu, \sigma)$, where ω is the offset, α the amplitude, μ is bias (i.e., the position of the maximum threshold), σ the width of the curve, and G is Gaussian function in log-space. All four parameters were free to vary. The resulting curves are shown in Fig. 2. Table 1 shows the obtained parameter values in the different conditions. From these results it can be concluded that with increasing signal speed, detection of coherent motion is easier (i.e., offset lower), also there exists a tight link between μ (bias) and the signal speed. The values of α (amplitude) increased with increasing signal speed, which means that best and worst performance deviated more and more from each other with increased signal speed. The values of σ were constant among all four conditions. A constant σ indicates that speed-tuning curves have a constant width in log-space (here being about 0.5 log-units, about 0.8 octaves) independent of the preferred speed, which is indeed found for macaque MT cells (Maunsell & Van Essen, 1983).

Edwards et al. (1998) & Khuu & Badcock (2002) compared curves with signal speeds of 1.2 and 9.6 deg/s, and found that the regions of increased threshold values hardly overlapped. They argued that because of the absence of overlap, at least two largely independent global motion systems could be assumed to exist: one for slow motions and one for fast-motions. Our dataset, however, also included two intermediate signal speeds. The finding that the two extreme channels in our study do not overlap suggests that the populations of neurons coding for 1.2 and 10.6 deg/s are not overlapping (i.e., operate independently) for our specific stimuli. However, when we follow the line of reasoning used by previous authors, we should conclude that the psychophysical channels at 1.1 and 2.1 deg/s are not independent of each other, and that those at 2.1 and 5.1 deg/s are not independent of each other, and that the 5.1 and 10.6 deg/s channels are not independent of each other. The evidence that the channel at 1.1 deg/s and that at 10.6 deg/s are independent of each other (in the current conditions), which might indicate separate speed-tuned systems, is overshadowed by the evidence that the series of channels are in fact part of a single-system. Furthermore, there is no indication of a discontinuity in the data. Instead, it seems that the position of the peak increases in a continuous manner with increasing signal speed.

Finally, it was previously reported that with high signal speeds the thresholds of coherent motion detection remained high even when noise speed was much higher than signal speed (Edwards et al., 1998; Khuu & Badcock, 2002). We measured thresholds over a more extended range, and found that for sufficiently high noise speeds
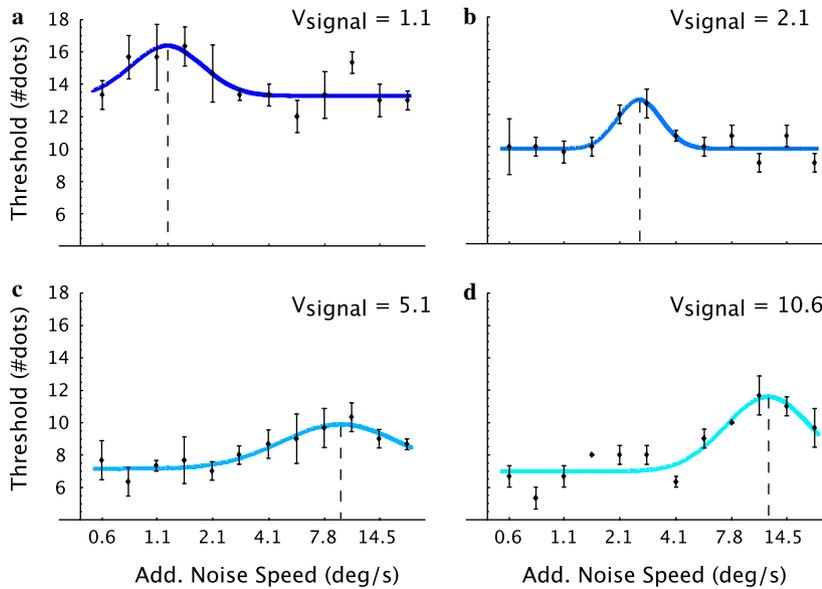
Fig. 1. Threshold values–in number of signal dots–for the detection of coherent motion in noise for Subject TK. Data points are means ± 1 SEM, in conditions where the signal speed is (a) 1.1 degr/s; (b) 2.1 degr/s; (c) 5.1 degr/s; and (d) 10.6 degr/s. For illustrational purposes log-normal fits through the data are also shown. The vertical dashed line shows the speed of the additional noise dots at which the highest thresholds are obtained. It can be seen that a strict link exists between the used signal speed and the additional noise speed at which the maximum is reached.
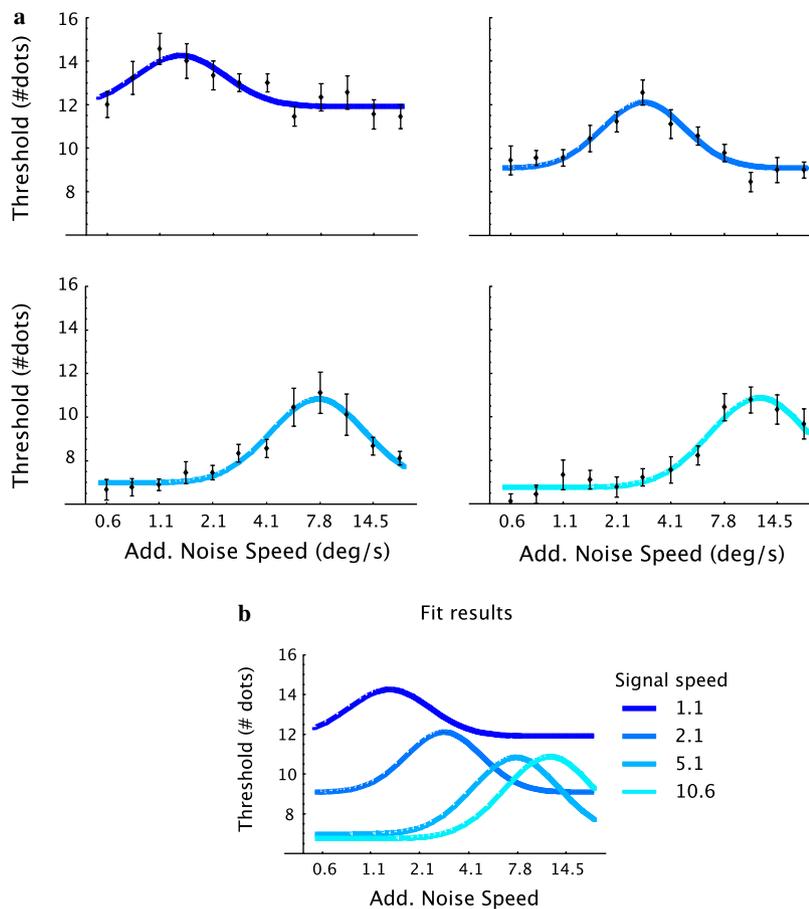

Fig. 2. Threshold values in number of signal dots for the detection of coherent motion in noise for all subjects combined. Data points are means ± 1 SEM. (a) Data is presented as in Fig. 1, but now for all the subjects together. (b) The fits from (a) are replotted together. The fits show a steady migration of the top to higher additional noise speeds when using increasingly high signal speeds. Two other points to note are that the offset (i.e. the minimum threshold value) of the curves decreases with increasing signal speeds, and the width of the curves (at the point halfway from the maximum to the offset) seems rather constant.

Table 1
Values of the fit parameters, and the R^2-values of these fits

	Signal speed in deg/s (log value in brackets)			
	1.1 (0.10)	2.1 (0.74)	5.1 (1.63)	10.6 (2.36)
Parameter				
ω	11.91	9.09	6.98	6.76
α	3.11	3.73	5.46	6.07
μ(log)	0.37	1.08	2.02	2.46
σ (log)	0.53	0.49	0.57	0.59
R^2	0.77	0.91	0.96	0.95

thresholds drop again (see Fig. 2a, bottom right panel), suggesting that the absence of a drop in thresholds (Edwards et al., 1998; Khuu & Badcock, 2002) was due to a too restricted range of noise speeds.

3. Model

The present experimental data oppose a division in fast and slow motion systems. In order to explain present and previous data, we decided to model a motion system based on the single-system assumption.

How could motion be represented in a motion system? When an object moves, it casts an array of signals on the retina that all have a certain speed and direction. Motion area MT processes both direction and speed information. Direction information is represented in an organized manner. Neurons responsive to similar directions are situated in cortical columns (Albright, Desimone, & Gross, 1984). Moreover, motion direction preference changes smoothly over the cortex (Malonek et al., 1994), and within MT connections exist preferentially between neurons of similar orientation preference (Malach, Schirman, Harel, Tootell, & Malonek, 1997; orientation preference is tightly coupled to direction preference in MT, e.g., Malonek et al., 1994). The representation of speed is much less well understood, but speed is represented in area MT (Liu & Newsome, 2003; Maunsell & Van Essen, 1983; Perrone & Thiele, 2001; Priebe, Cassanello, & Lisberger, 2003), and it seems that neurons positioned near to each other have similar speed preferences (DeAngelis & Newsome, 1999; Liu & Newsome, 2003).

A given motion stimulus activates neurons responsive to a variety of directions and speeds. More specifically, neurons optimally responsive to the stimulus' velocity will be activated most, but neurons optimally responsive to velocities slightly different from that of the stimulus, will be activated nonetheless, but to a lesser degree. In this way a population activity may emerge as depicted in Fig. 3b.

A global-motion stimulus contains a coherent motion signal, but also lots of noise, caused by spurious dot matching between successive frames. Both the noise and the coherent motion signal will activate the motion system. In the present experiment and those performed previously (Edwards et al., 1998; Khuu & Badcock, 2002), noise velocities were mostly limited to a certain speed-band, without a

predominance of any particular direction signal. Two examples of a population activity caused by this kind of noise are shown in Fig. 3c.

The extraction of motion signals from luminance changes on the retina can be seen as local motion extraction. A global-motion system may operate independently of this local-motion system, but it has been show that this is not the case. The global-motion system processes information obtained by the local motion system (e.g. Khuu & Badcock, 2002; Movshon & Newsome, 1996; Smith, Snowden, & Milne, 1994; Stoner & Albright, 1994).

Therefore the next step in our model, the global-motion extraction step, builds on the motion signals obtained by the local-motion system. We added the activity caused by signal and noise dots, and for every direction–speed combination we calculated a measure of how distinctly the model was activated at that direction–speed combination relative to other direction–speed combinations (see Section 3.1). High values mean a large distinctiveness for a direction–speed combination, which would translate into a low threshold for detection. Therefore, to compare the model and experimental results, we took the inverse of the maximum value of distinctiveness to obtain a measure comparable to a threshold for detection.

3.1. Methods

3.1.1. Motion representation

A motion stimulus of a particular direction–speed combination was assumed to activate a wide collection of neurons which themselves are maximally responsive to either the direction–speed combination of the stimulus, or a combination close to it. This dispersion of activity can be caused by both noise in the visual system and by (excitatory) interactions among neurons (e.g., Bosking, Zhang, Schofield, & Fitzpatrick, 1997; Malach et al., 1997).

The overall activation of the local motion sensors caused by the signal (i.e., the coherent motion) was modeled as:

$$S(d,s) = (G(s,\sigma)^+ - G(s,\sigma)^-)M(d,k),$$

being dependent on direction (d) and speed (s) of the signal dots, σ is the spread of the signal in the speed dimension, M is the von Mises distribution (a circular analogue of the normal distribution) modeling the spread in the direction-dimension, k is the concentration parameter of this distribution (with $k = 0$ representing a uniform distribution). G represents a Gaussian distribution in log-space. $(G(s,\sigma)^+ - G(s,\sigma)^-)$ represents motion opponency; if the spread along the speed dimension is large, a stimulus that moves in a 'plus' direction (say rightwards), will also active some neurons sensitive to 'minus' motions (say leftwards), in the motion opponency stage the activity in the left direction is subtracted from the activity in the right direction to obtain a clearer directional signal (see Fig. 6). Note that when σ is relatively small (as it is in our model), each stimulus will activate only part of the entire speed range in the
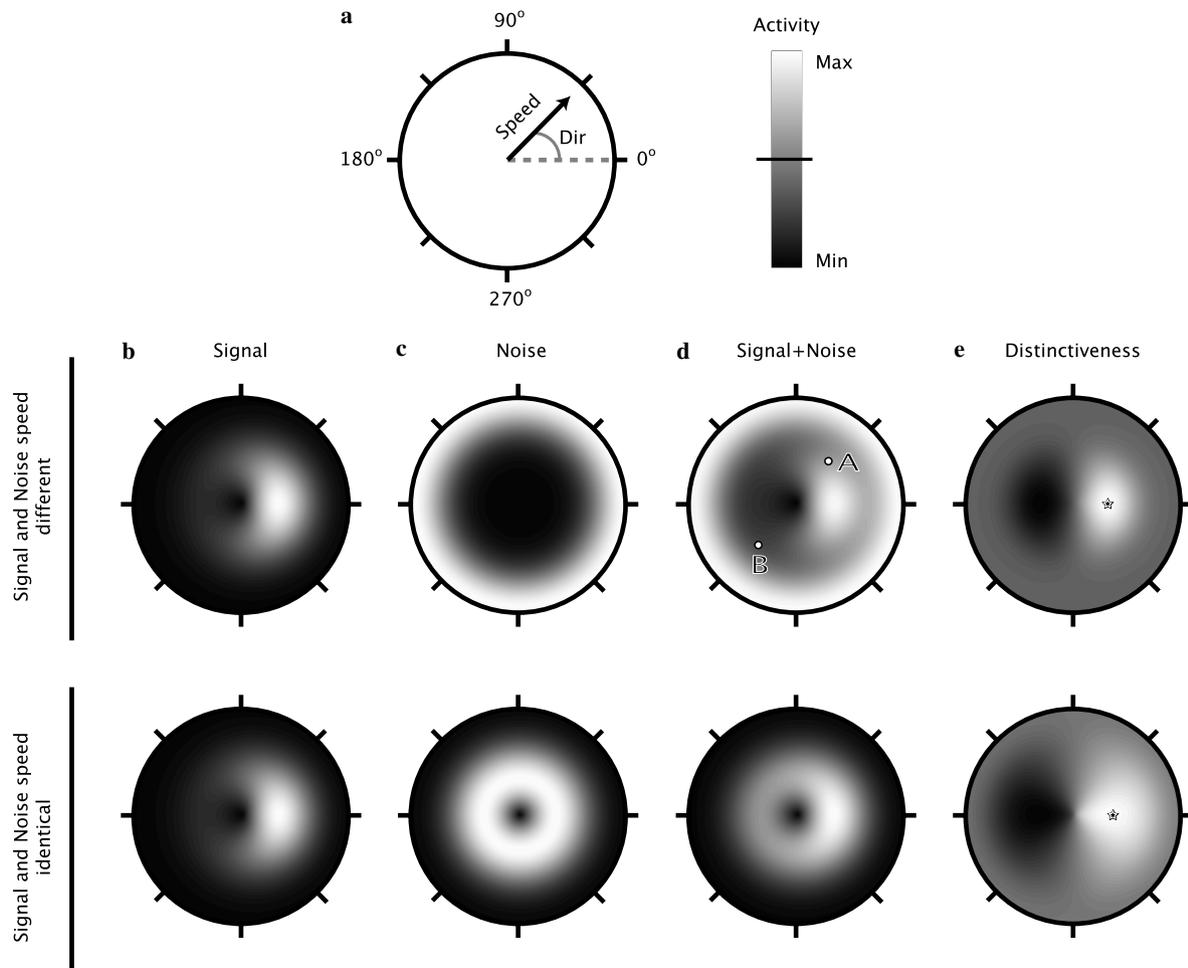
Fig. 3. The representation of velocity in the model. (a) Left, the polar plot shows a velocity vector, extending from the origin of the plot to a certain point in the velocity-space. The vector has an angle relative to a comparison direction (here right-horizontal), which is the direction component of the velocity. The length of the vector is the speed. (b–e) The top part shows a model condition in which signal and noise speed are different, the bottom part shows a condition in which they are identical. Plot grayscales are individually rescaled. (b) The motion signal is directed (here to the right), and the representation of it shows a spread in both direction and speed dimensions. There exists only one maximum in the representation, and it is positioned at the presented stimulus speed. (c) The noise is non-directed, and contains only a certain band of speeds. In the top part of the panel, this band of speeds is positioned at rather high values, in the bottom part it is centered at the signal speed. (d) The sum of signal and noise signals. (e) The distinctiveness measure (see Section 3.1). It is calculated at the ratio of a certain point (e.g., point A in (d)) and the point diametrically opposite to it (point B in (d)). If done for all points, one obtains the figures shown here. The star indicates the point of maximum distinctiveness.

system. It may therefore happen that two motions that are sufficiently different activate two non-overlapping populations of units in the system, causing them not to influence each other's processing.

The activity caused by the noise dots was modeled as:

$$N(s) = (G(s, \sigma)^{+} - G(s, \sigma)^{-})M(d, k),$$

k was set to zero, yielding a uniform circular distribution, meaning that the activity caused by the noise dots was not modulated along the direction-dimension.

The total activity (T) caused by the global-motion stimulus was modeled as:

$$T(d, s) = b + S(d, s) + N(s),$$

where b is a baseline activity.

3.1.2. Measure of distinctiveness

The global-motion system is assumed to base its processing on the information provided by the local motion system, described in the previous section.

Based on the local motion information the global-motion stage in the model computes a measure of distinctiveness (D) for every direction-speed combination as follows. It takes the value of activity at a certain speed and direction, and it divides this value by the value in the direction-speed space diametrically opposite to it (see two example dots in Fig. 3d):

$$D(d, s) = T(d, s)/T(d + 180°, s).$$

To obtain a measure comparable to a threshold for detection the inverse of the distinctiveness measure was taken, which we will call the model's threshold value.

The model has three parameters: k, σ, and b. k was set to $3\pi/10$, but its precise values did not change the results qualitatively. σ was set to 0.5, close to the widths obtained in the Gaussian fits in the previous experiment. b was arbitrarily set to 5; the qualitative results are independent of the exact value of b. Parameter b influences the signal-to-noise ratio, as b is part of the noise. It will show that for low speeds, signal-to-noise ratios will be low (partly due to b), and thresholds higher. With low b's this effect is greatly attenuated, but still present.

3.2. Results and discussion

In Fig. 4 we show the results of the model. The model results echo those of the experiment in its main characteristic, namely that the top of the curves moves to higher additional noise speeds with higher signal noise speeds
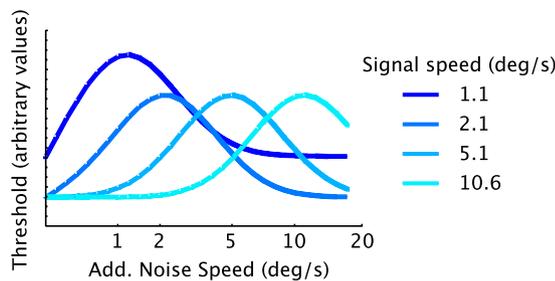

Fig. 4. Model results, simulating the experimental conditions. The different curves show the different signal speed conditions. The model shows clear resemblance to the experimental data (see Fig. 2b). Notably, it shows a lawful shift in the position of the top of each curve towards higher noise speeds for higher signal speeds. Moreover, the results also show an increased offset for low signal speed conditions, and a constant width of the different curves.

(compare Figs. 2b and 4). Clearly, a single continuous motion-system model is capable of producing the present and previous psychophysical findings of psychophysical channels that move to higher speeds ranges when higher signal speeds are used. The model produces the feature of psychophysical channels without having separate neurophysiological entities (i.e., neurophysiological channels) representing each individual psychophysical channel. Although the model contains units that are tuned to specific speeds, these units are not combined together as entities that span an a priori defined range of speeds (i.e. a neurophysiological channel) in order to produce the psychophysical channels.

Why does the model show these results? Fig. 5 shows a graph of the activity along the speed dimension, in the direction of the strongest signal; it is a horizontal slice through Fig. 3d ("signal + noise"). Fig. 5a shows the composition of the total activity in the case that noise and signal speeds are the same. Fig. 5b shows the same plots for the condition that noise speed is larger than the signal speed. The portions of activity that are caused by signal and noise have been denoted by "S" and "N", respectively. One can see that at various positions along the velocity dimension the signal makes up a large part of the total activity when signal and noise speeds are different. Its relative contribution to the total activity is smaller when noise and signal speeds are the same. Consequently, the distinctiveness of the motion signal is lower in Fig. 5a than in Fig. 5b, which is depicted in Fig. 5c. As a result of the low distinctiveness value, the threshold will be higher when noise is similar to the signal speed than when noise speed is different from signal speed, explaining why increased thresholds are found when noise and signal speeds are similar.
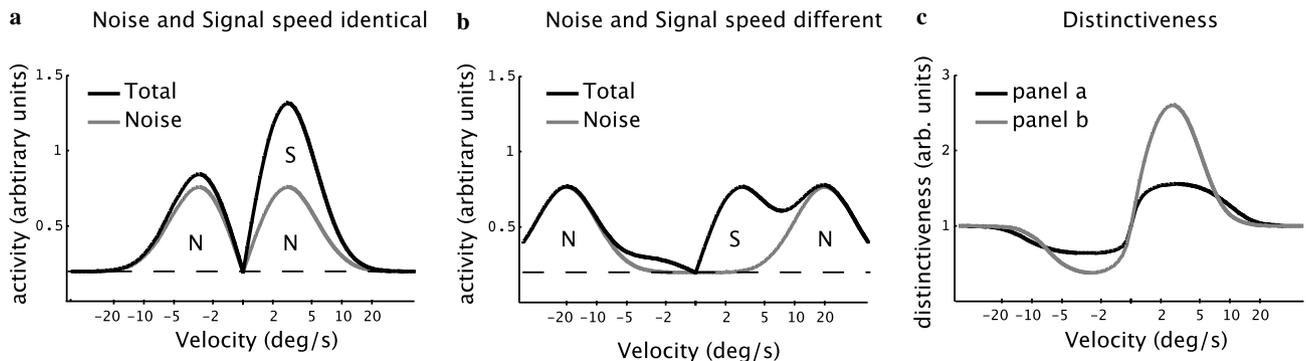

Fig. 5. Explanation of the increased thresholds when signal and noise speeds are similar compared to conditions where they differ. (a) A condition where noise and signal speed are identical. Shown are, the total activity (T) and the part of it that is caused by noise dots (N) and signal (S) dots. The figure is a slice through Fig. 3d, slicing through the origin and the maximum; negative and positive velocities in this graph represent therefore motions in opposite directions (the absolute value of the x-axis being the speed of the motion). The horizontal dashed line represents the baseline (b) in the model. (b) As in (a), but now for a condition in which signal and noise speeds differ. By comparing (a and b), one can see that the signal (S) constitutes a large part of the total activity over a wide range of velocities in (b) (from about 1 to 5 deg/s), whereas in (a) it is always accompanied by an increase in noise (in both "positive" and "negative" directions). Comparing the activities in opposite directions, as is done when calculating the distinctiveness measure (c), it is clear that the relative contribution of signal (S) is lower in the case when signal and noise speeds are identical, compared to when they differ. Therefore the final threshold (the inverse of the distinctiveness) will be higher for low-speed conditions of the noise.

Interestingly, the model also reproduces the finding that with low signal speeds, the lowest obtainable threshold is rather high compared to the lowest thresholds of the other signal speeds. Fig. 6 explains how the model gives rise to the raised thresholds. Fig. 6a shows the distribution of activity along the speed dimension at the motion opponency stage (the noise is left out for clarity). The gray curve shows the distribution of activity ($G^{\pm}$) caused by a motion stimulus of low (left panel) and high (right panel) speed. Part of the activity is present in the negative part of the graphs (G^{-}). For low speeds this part is larger than for high speeds. In the motion opponency stage this activity is subtracted from the activity in the positive part of the graph (G^{+}). The final activity after the motion opponency stage ($G^{+} - G^{-}$) is represented by the black curve, which is the difference between the gray dashed ($G^{-}_{mirrored}$) and continuous line. The top of the high-speed curve is higher than that of the low-speed curve, because it is less inhibited by its 'negative' tail

(G^{-}). This difference in maximum activity is found back in Fig. 6b where the total activity ($T(d,s)$) is depicted for both high-speed (black line) and low-speed stimuli (gray line). Fig. 6b is a slice through the velocity space similar to the one shown in Fig. 3d, and the small peak at the 'negative' side of the graph is some activity that has spread over 180° from the opposite side. Fig. 6c depicts the measure of distinctiveness for both low-speed- and high-speed stimuli, derived from the total activity. In our model calculations, the measure was only calculated for the point of highest activity (from, e.g., Fig. 6b), but one can see that this point coincides with the point of highest distinctiveness. One can see that the low-speed curve lies lower than the high-speed curve. It does so because the activity caused by the signal in the low-speed condition is small relative to the noise (mainly the baseline activity), since it was much reduced by the motion opponency stage. Importantly, a low value of distinctiveness translates into a high threshold of detection, explain-
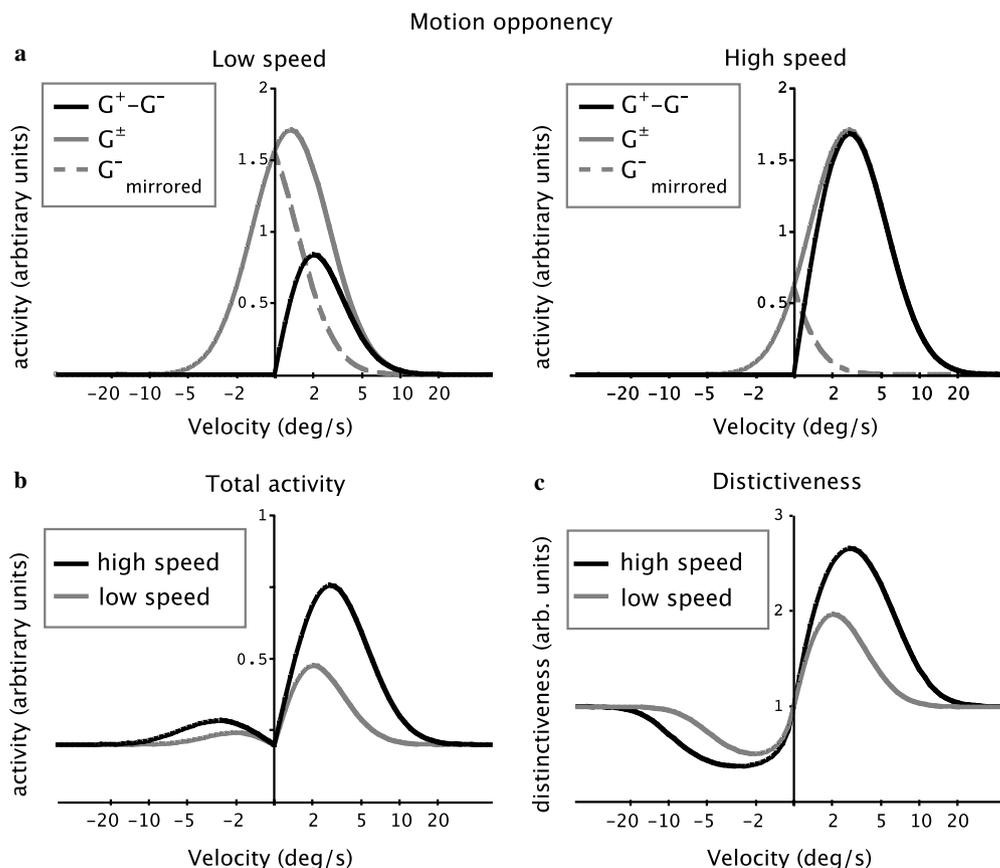

Fig. 6. Explanation of the increased thresholds at low signal speeds. At low signal speeds the smallest obtained threshold is much higher than at high signal speeds. (a) Left panel, a low signal speed condition; right panel, a high signal speed condition. The gray continuous line represents the activity caused by a moving stimulus before the motion opponency stage. A motion stimulus does not only activate neurons responsive to the speed of the stimulus, but also the neurons that are maximally responsive to slightly different speeds. A certain part of this activation is caused in neurons that are actually most responsive to motions in opposite directions (the part of the tail in the negative half of the graph). In the motion opponency stage this activity will reduce the activity of cells responsive to the direction of motion of the stimulus. Therefore, in the model the tail in the negative half of the graph is subtracted from the one in the positive half, yielding the activity after the motion opponency stage (black line: $G^{+} - G^{-}$). The subtracted amount in the high-speed condition is however much less than in the low-speed condition, because the part of the tail in the negative half of the graph is much smaller. (b) The resulting total activity in high-speed conditions (black line), and low-speed conditions (gray line). (c) The distinctiveness values for high-speed (black line) and low-speed (gray line) conditions. The maximum distinctiveness value is lower in the low-speed condition.

ing why low-speed stimuli are more difficult to detect. The modeling results suggest that the motion opponency stage plays a major role in the increase of thresholds for low signal speeds.

Although we find a general decrease in thresholds with increased stimulus speed, in previous reports (Edwards et al., 1998; Khuu & Badcock, 2002) it was stated that measurements were executed in a range (which is identical to our used speed range) in which coherence thresholds did not vary before performing the experiment. However, at least one and possibly two of the three subjects in (Edwards et al., 1998) study showed a decrease of thresholds with increased stimulus speed, just as our subjects. The thresholds of (Khuu & Badcock, 2002) indeed seem not to vary a lot, but they were only measured at two points along the speed dimension. One additional point is that (Khuu & Badcock, 2002) used rotational and radial motion and not translational motion, which may also have caused the difference in results. From a theoretical point of view, however, one *should* expect an increase of thresholds at low signal speeds, because in the limit of zero speed it is impossible to detect motion, and therefore thresholds should be immeasurably high.

4. General discussion

In this study we examined the existence of independent fast and slow speed-tuned global-motion systems. These independent motion systems have been proposed for both translational (Edwards et al., 1998) and rotational and radial (Khuu & Badcock, 2002) global-motion processing.

The existence of such independent systems was proposed on the basis of coherent-motion detection thresholds. Coherent motion detection was found to be impaired when noise was added that has similar speeds as the signal speed (i.e., the speed of the coherent motion). On the other hand such impairments were absent when noise and signal speeds were very different. Previous studies had used low-speed (1.2 deg/s) and high-speed (9.6 deg/s) coherent motion stimuli, and found that the increases of the thresholds for coherent motion detection (i.e. psychophysical channels) in these cases occurred in different speed ranges that did hardly overlap. These results pushed the idea of two independent motion systems: one for fast-motions and one for slow motions.

However, these studies used just two signal speeds. In the present study four different signal speeds were used covering the range from 1.1 to 10.6 deg/s. We found extensive overlap between the different psychophysical channels. The two extreme psychophysical channels in our study do indeed not overlap (suggesting independence). However, all other combinations of psychophysical channels do overlap, suggesting they resulted from the activation of the same range of speed-tuned neurons and are part of a single-system. No indication was found for a dichotomy along the speed axis: the four different signal speeds we used led each to an increase of threshold at very specific values for

noise speeds, tightly linked to the signal speed used. These results are not indicative of the existence of two independent global-motion systems.[4]

It may be argued that the two global-motion systems are not fully independent, but show some sort of interaction (as suggested by Curran & Benton, 2003). However, if one proposes interactions between the two systems the two-systems claim loses much of its value.

With our model we were able to show that a single global-motion system is able to produce the present and previous data. We assumed that speed is represented in a continuous manner, from very low to very high speeds. Interactions among speed-tuned units exist, but are limited to a small speed range. This last point causes noise to have a detrimental effect on coherent motion perception only when its speed is within this range. When signal speeds lie sufficiently far apart, the limited influence of noise speeds will automatically lead to an absence of overlap between the regions of increased threshold. The model indicates that this absence does not need to be a signature of two motion systems, but could very well be explained by a more parsimonious single-system account having a continuous range of speed-tuned units. The psychophysical channels were produced by our continuous model without having separate neurophysiological entities (i.e., neurophysiological channels) representing each psychophysical channel.

4.1. Position of the global-motion system

The extraction of global-motion from local motion signals is generally thought to take place in motion area MT (Movshon et al., 1985; Rodman & Albright, 1989; Stoner & Albright, 1994). Although our results do not constitute any direct evidence for the placement in MT, when we compare our curves of the different signal speed conditions (which are based on the combined activity of many motion sensitive neurons) to the speed tuning curves of single neurons, the tuning widths of our curves are similar to, though somewhat sharper, than those found in single cell recordings in monkey MT (Maunsell & Van Essen, 1983). Of course one should be careful when comparing two such very different processes as single cell measurements and psychophysically measured perceptual performance.

However, our model is able to reproduce the experimental psychophysical data to a great extent, by incorporating the known physiology of MT for direction representation and assuming that speed is represented in a continuous

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[4] We note that Khuu & Badcock (2002) used rotational and radial motion, whereas we used translation motion. Our experimental results may not be directly extrapolated to radial and rotational motion, especially since area MT is not very sensitive to rotational motion and area MST is (Vaina, 1998). However our results strongly suggest that the interpretation of Khuu & Badcock (2002) may need revision. Moreover, our model does not necessarily need to be interpreted in terms of translational motion, and may well be used to explain the results obtained with rotational and radial motion.

manner in MT as well. The correspondence between the model results and the experimental results further support the idea that speed is represented together with direction in a continuous manner in MT, in accordance with some motion aftereffect data (Schrater & Simoncelli, 1998).

4.2. Motion opponency

Our model data resemble quite closely the data from our human subjects. The model did not only show increased thresholds around the signal speeds in different conditions (i.e., psychophysical channels), but also a general increase of thresholds at low signal speeds. A finding that follows from the model is that low speeds should be more difficult to detect than high speeds signals, which we find in our global-motion stimuli, but is also reported for other motion stimuli (Burr et al., 1998). The occurrence of this increased difficulty was the result of interplay between a motion opponency stage and the existence of a baseline activity in motion-sensitive units in the model. Without the motion opponency this behavior would not be observed, suggesting that the motion opponency stage is an important step in (both local and global) motion perception. Indeed many models of local motion processing include a motion opponency stage (Heeger, Simoncelli, & Movshon, 1996; Kim & Wilson, 1996; Simoncelli & Heeger, 1998), and evidence from functional imaging is reported in humans (Heeger, Boynton, Demb, Seidemann, & Newsome, 1999).

4.3. Relation to other studies supporting independent fast and slow motion systems

Several other studies have reported evidence for independent motion systems. These studies have been reviewed more extensively in van Boxtel et al. (2006) than will be done here. Here, we focus on evidence from psychophysical studies that are most related to the findings in this report.

The evidence for fast and slow motion systems comes mainly from two kinds of study: differences in motion perception in chromatic and achromatic stimuli, and motion aftereffects with static and dynamic test stimuli.

It has been reported that reaction time to motion onset is faster for slowly moving achromatic stimuli than for chromatic stimuli, whereas no such difference exists for fast moving stimuli (Burr et al., 1998). Thresholds for motion identification were also found to be high for slow speed chromatic stimuli, but low for slow speed achromatic stimuli (Gegenfurtner & Hawken, 1995). And it has been reported that perceived speed was contrast-dependent for slow chromatic (isoluminant) stimuli, but contrast-independent for fast chromatic and all achromatic stimuli (Hawken et al., 1994). On the basis of these results, one proposed three different motion systems, one for slow chromatic motion, one for slow achromatic motion, and one for fast (chromatic and achromatic) motion (Gegenfurtner & Hawken, 1995; Hawken et al., 1994).

However for reaction time to stimulus onset the increases found for both types of stimuli were nearly identical when the results were plotted against perceived (and not physical) speed (Burr et al., 1998), indicating that these results stem from a single-system. Indeed, the differences between chromatic and achromatic conditions are well explained by just assuming different contrast-transduction properties of early temporal filters (Metha & Mullen, 1997, 1998). The difference is therefore not necessarily due to two different motion systems but is well explained by differences in the involved low-level detection mechanisms.

The second major group of studies reporting evidence for fast and slow motion systems has found differences in motion aftereffect (MAE) durations on static and dynamic test stimuli. A MAE is an illusory motion perception in a direction opposite to a moving stimulus that had been viewed for prolonged periods of time. Such MAEs are seen on stimuli presented after the prolonged adaptation (called test stimuli). The test stimuli may be static or containing balanced motion signals (such that the net motion is zero). These last test stimuli are called dynamic. It is found that adaptation to slow motion gives rise to motion aftereffects with static test stimuli, whereas adaptation to fast-motion does so with dynamic test stimuli (van der Smagt et al., 1999; Verstraten et al., 1999; Verstraten, van der Smagt, & van de Grind, 1998).

In a recent study (van Boxtel et al., 2006) we have shown that the seeming dichotomy may be explained in terms of a single motion system, much like we have done in the current report. Briefly, it was shown that static stimuli only read out the motion-adaptation to slow motions, because static stimuli only activate units sensitive to slow motion. Dynamic test stimuli contain many high-speed signals and will therefore also read out the adaptation of those units sensitive to high speeds.

5. Conclusion

The results of the current study indicate that there is little evidence for independent global-motion systems for fast and slow motion. Data interpreted previously as evidence for this division is well explainable in a single motion system model, within which each speed-tuned neuron covers part of the entire speed-domain. Other lines of evidence from achromatic/chromatic motion, and motion aftereffect experiments have already been shown to fit a single motion system account. In the absence of direct evidence for independent slow and fast-motion systems, one should embrace the more parsimonious explanation assuming a single motion system covering the full range of perceived speeds and directions.

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