

# A Single System Explains Human Speed Perception

Jeroen J. A. van Boxtel, Raymond van Ee, and Casper J. Erkelens

## Abstract

■ Motion is fully described by a direction and a speed. The processing of direction information by the visual system has been extensively studied; much less is known, however, about the processing of speed. Although it is generally accepted that the direction of motion is processed by a single motion system, no such consensus exists for speed. Psychophysical data from humans suggest two separate systems processing luminance-based fast and slow speeds, whereas neurophysiological recordings in monkeys generally show continuous speed representation, hinting at a single system. Although the neurophysiological findings hint at a single

system, they remain inconclusive as only a limited amount of cells can be measured per study and, possibly, the putative different motion systems are anatomically separate. In three psychophysical motion adaptation experiments, we show that predictions on the basis of the two-motion system hypothesis are not met. Instead, concurrent modeling showed that both here-presented and previous data are consistent with a single system subserving human speed perception. These findings have important implications for computational models of motion processing and the low-level organization of the process. ■

## INTRODUCTION

The visual motion system has proven to be extremely versatile. This versatility has repeatedly been explained in terms of two (or more) separate and independent motion systems (Khuu & Badcock, 2002; van de Grind, van Hof, van der Smagt, & Verstraten, 2001; van der Smagt, Verstraten, & van de Grind, 1999; Burr, Fiorentini, & Morrone, 1998; Edwards, Badcock, & Smith, 1998; Verstraten, van der Smagt, & van de Grind, 1998; Gegenfurtner & Hawken, 1996; Gegenfurtner & Hawken, 1995; Nishida & Sato, 1995; Hawken, Gegenfurtner, & Tang, 1994; Barbur, Watson, Frackowiak, & Zeki, 1993; Gorea, Papathomas, & Kovacs, 1993; Cavanagh & Mather, 1989; Zihl, von Cramon, & Mai, 1983; Pantle & Picciano, 1976; Braddick, 1974). However, it is unlikely that all these motion systems exist, as this would lead to a very high number of motion systems (not to mention, all the possible interactions between those systems). We specifically investigated the widely supported division along the speed dimension, namely, the claim that human perception of motion is subserved by a fast and a slow motion system<sup>1</sup> (Khuu & Badcock, 2002; van de Grind et al., 2001; van der Smagt et al., 1999; Burr et al., 1998; Edwards et al., 1998; Verstraten et al., 1998; Gegenfurtner & Hawken, 1995, 1996; Hawken et al., 1994; Gorea et al., 1993).

The evidence for the proposed division in fast and slow motion systems comes from psychophysical and clinical research, which we shortly review.

Motion detection and discrimination thresholds for luminance-based (achromatic) and color-based (chromatic) motion are found to be identical for high-speed stimuli. However, it was found that at lower speeds thresholds were higher for chromatic than for achromatic stimuli (Burr et al., 1998; Gegenfurtner & Hawken, 1996). These results were interpreted as evidence for three different motion systems: one system for slow achromatic motion, one for slow chromatic motion, and a combined fast motion system (Burr et al., 1998; Gegenfurtner & Hawken, 1995, 1996; Hawken et al., 1994).

Stimulus adaptation has proven to be powerful in revealing neural mechanisms underlying visual perception. Motion adaptation—caused by prolonged viewing of unidirectional motion—is demonstrated by illusory motion in a subsequently viewed motionless (or motion-balanced) pattern (called test pattern): the motion aftereffect (MAE). Psychophysical MAE reports (van de Grind et al., 2001; van der Smagt et al., 1999; Verstraten et al., 1998) have shown that different MAEs are induced on different test stimuli. More specifically, for speed, it has been reported that fast motion induces MAEs with rapidly refreshed test patterns (called dynamic), whereas slow motion does so with slowly refreshed patterns (called static). A strict separation between these two types of MAE has been reported in the temporal frequency domain (van der Smagt et al., 1999): At test stimulus refresh frequencies below 20 Hz an MAE of slow adapting motion was observed, whereas at refresh frequencies above 20 Hz an MAE of fast adapting motion was observed. Both these kinds of MAE were seen

---

Utrecht University, The Netherlands

simultaneously when adaptation occurred to both slow and fast motion, and the test stimulus consisted of slowly and rapidly refreshed stimulus elements (dots), suggesting a complete independence of the slow and fast motion systems (van der Smagt et al., 1999).

Some clinical studies are taken as evidence for a division in fast and slow motion systems. Patients with lesions in V1 are unable to consciously perceive speeds below 6 deg/sec (Barbur et al., 1993), whereas patients with lesions in the middle temporal area (MT) are unable to perceive speeds above 6 deg/sec (Zihl et al., 1983), indicating that the slow and fast motion systems could be located in different brain areas.

Contrary to the findings in psychophysical research, neurophysiological work in monkeys has so far not suggested different motion systems for fast and slow speeds. The changes in speed preference are generally found to be continuous when measuring neurons in each other's vicinity (Liu & Newsome, 2003; Maunsell & Van Essen, 1983), although occasional large jumps in speed preference occur. Although the neurophysiological findings hint at a single motion system, they remain inconclusive as only limited amount of cells can be measured per study and, moreover, the putative different motion systems could be anatomically separate. Therefore, the nonconcordance of neurophysiological and psychophysical implies that data at present are inconclusive.

Although the psychophysical data have been interpreted as showing the existence for two motion systems, the different studies propose different underlying mechanisms. The slow motion signals are thought to be carried by sustained firing cells (van de Grind et al., 2001; van der Smagt et al., 1999) or parvocellular cells (Burr et al., 1998; Gegenfurtner & Hawken, 1996; Hawken et al., 1994); the fast motion signals are thought to be carried by transiently firing cells (van de Grind et al., 2001; van der Smagt et al., 1999), or magnocellular cells (Burr et al., 1998; Gegenfurtner & Hawken, 1996; Hawken et al., 1994). At a level lying after the slow and fast motion systems, the motion signals are thought to converge again to form a unified perceptual experience (Burr et al., 1998) or, instead, they are thought to have "a private line to consciousness" (van de Grind et al., 2001).

We note that the classifications such as static/dynamic, chromatic/achromatic, and also first-order/second-order depend on stimulus characteristics that may not be the characteristics the visual systems use. The dichotomized nomenclature, which does not allow intermediate conditions, forces one to assume that a finding of a dichotomy in the data using two different stimuli implies that two largely independent systems exist that are mainly activated by one or the other stimulus. However, one may actually have measured at two different spots in a continuum that is not best described by, for instance, "static/dynamic," but instead by, say, "speed."

By employing psychophysical methods, corroborated by a mathematical model based on neurophysiological principles, we approached the question from both psychophysical and neurophysiological sides. In the first part of this report, we show that the single-system model explains the experimental data on MAEs without necessitating a division in fast and slow motion systems. Instead, a single motion system—by which we mean a *continuum* of interconnected speed- and direction-tuned cells—suffices.

Model simulations gave the inspiration to execute three experiments, which are discussed in the second part of the report, together with explanatory model stimulations. We used an adaptation procedure to specifically gauge a system that adapts to motion, thereby excluding systems that may give rise to percepts of motion solely by means of position tracking, which are not motion systems *sensu stricto* (although such mechanism can nevertheless be very important in motion perception; Lu & Sperling, 2001). With these experiments, we demonstrate that the hypothesis of two independent motion systems fails both the necessity and the sufficiency criterion. The single motion system hypothesis is sufficient to explain the data (see Discussion), which therefore suggest that a single motion system underlies human motion perception.

## MODEL SECTION: A SINGLE-SYSTEM EXPLANATION

The model is a simplified functional representation of motion area MT, in which nearby locations have similar speed and direction tuning, which both change in a continuous manner (Liu & Newsome, 2003; Maunsell & Van Essen, 1983), and in which a motion opponency mechanism exists (Heeger, Boynton, Demb, Seidemann, & Newsome, 1999).

In the model, we assume that a test stimulus elicits a reaction in the motion system. The reaction is modulated by an adaptation-dependent modulation. We investigate whether such a model, without assuming any discontinuity in the form of motion systems, or channels, is able to produce the known MAE data.

## Materials and Methods

### *Single Motion System Model*

We assume that a test stimulus elicits activation of the motion system. The activity is modulated by an adaptation-dependent factor. Responses to the test stimulus are modeled as spontaneous activity (arbitrarily set to unity) plus a test stimulus-induced activity, caused by the matching of different stimulus-elements between subsequent frames. The test stimulus-induced activity is described by a distribution of velocities that are present in the test stimulus, and is represented as a

Gaussian blob  $[Gb(\mu_{\text{test}}, \sigma_{\text{test}})]$ .  $\mu_{\text{test}}$  is the speed that is most present in the test stimulus, and is set to zero to simulate zero net motion.  $\sigma_{\text{test}}$  is the variable test velocity-distribution width (TVD width), which is larger for dynamic test displays than for static ones.<sup>2</sup> The final formula describing the test-induced activation is:  $1 + kGb(\mu_{\text{test}}, \sigma_{\text{test}})$ . The constant  $k$  is set to 8 to increase the influence of the test stimulus substantially above spontaneous activity (the exact value of  $k$  is unimportant for the qualitative results of the model).

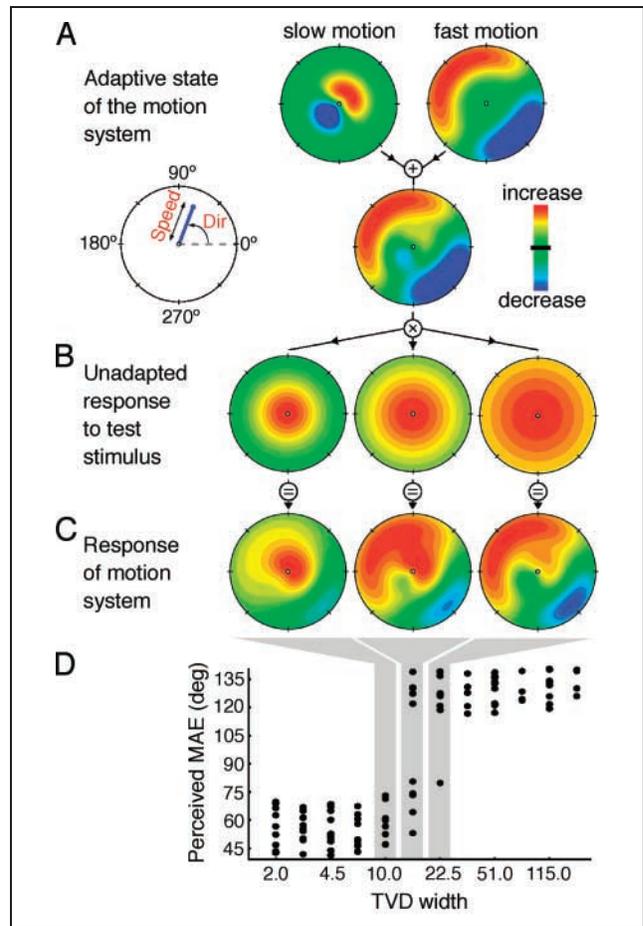
The test-induced response is multiplied by a modulation factor defined by the preceding adaptation:

$$1 - \sum_{n=1}^m [(G(\mu_n, \sigma_n)_s - G(\mu_n, \sigma_n)_{-s})M'(\beta_n, \kappa_n^e, \kappa_n^i)],$$

where  $m$  is the number of adapting motions,  $G$  is a Gaussian distribution, and  $M'$  is a circular Mexican hat-shaped function that we will describe below. The modulation factor is made up of two main parts. The first part,  $G(\mu_n, \sigma_n)_s - G(\mu_n, \sigma_n)_{-s}$ , describes the adaptation profile along the speed dimension, which depends on motion opponency.  $\mu_n$  represents the speed at which the motion system is most adapted by stimulus  $n$ , and  $\sigma_n$  represents the spread in the speed dimension. Motion opponency in the human visual system may be accomplished by subtracting the activity of motion sensors that are sensitive to opposite motions. We implemented it therefore as a subtraction of the value in the Gaussian distribution  $G(\mu_n, \sigma_n)$  at position  $-s$  from that at position  $s$ , for all values of  $s$ . In the function this is represented as a subtraction of  $G(\mu_n, \sigma_n)_{-s}$  (the distribution's tail at negative  $s$ ) from  $G(\mu_n, \sigma_n)_s$  (the tail at positive  $s$ ) for all  $s \geq 0$ . If  $\sigma$  was infinitely large, the visual system would be equally adapted to all speeds.

The second part of the modulation factor is  $M'(\beta_n, \kappa_n^e, \kappa_n^i)$ , which describes the adaptation profile along the direction ( $d$ ) dimension.  $M'(\beta_n, \kappa_n^e, \kappa_n^i)$  is a Mexican hat-shaped function:  $M(\beta_n, \kappa_n^e) - M(\beta_n, \kappa_n^i)$ , where  $M$  is the von Mises distribution (here also dependent on  $\kappa$ ),  $\beta$  is the mean direction, and  $\kappa$  is the concentration parameter ( $\kappa = 0$ , means a uniform distribution). The von Mises distribution is a circular analog of a normal distribution and is defined on the range of  $\beta \in [0, 2\pi]$ :  $M(\beta, \kappa) = e^{\kappa \cos(d - \beta)} / 2\pi I_0(\kappa)$ , where  $I_0(\kappa)$  is the modified Bessel function of the first kind of the order 0, and  $d$  is the direction variable, along which the function varies. The first and second parts of the modulation factor are multiplied to obtain an adaptation profile along both the speed and direction dimensions. This profile is used to modulate the test-induced response.

We investigated the importance of the parameters  $\kappa^e$  and  $\kappa^i$  by repeating the simulation in Figure 1 with many different combinations of  $\kappa^e$  and  $\kappa^i$ . We found that the



**Figure 1.** Model results showing that a single motion system explains the discontinuity in perceived direction of motion aftereffects (MAEs). The model stages: (A) modulation through adaptation, of the slow, fast, and the combined components; (B) response to test stimuli of different test velocity distribution (TVD) width in an unadapted state; (C) the final response of the motion system. Velocities are represented by a vector, the length of which is the speed, and the angle is the direction. Shades of red and blue represent increased and decreased activity, respectively. (D) The single-system model reveals a discontinuity in the perceived MAE directions, shown for different TVD, replicating previously reported data that led to the prevailing conclusion that slow and fast motion systems exist.

results could be obtained when parameter  $\kappa^e$  was smaller than about  $0.6\pi$ , and  $\kappa^i$  was smaller than about  $0.25\pi$ , resulting in a width-at-half-height excitation and inhibition larger than about  $90^\circ$  and  $120^\circ$ , respectively. We set  $\kappa^e$  to  $0.3\pi$  (width at half height  $\sim 100^\circ$ ) and  $\kappa^i$  to  $0.1\pi$  (width at half height  $\sim 160^\circ$ ) in all subsequent simulations, which are values close to those used in previous simulations with a model similar to ours (Grunewald & Lankheet, 1996), and not unlike known physiological data (Snowden, Treue, Erickson, & Andersen, 1991; Albright, 1984). Due to the later subtraction from 1, the physiological meaning of excitation and inhibition are actually inhibition and disinhibition, respectively (Grunewald & Lankheet, 1996).  $\sigma$  and  $\mu$  have units in deg/sec,  $\beta$  in rad. For Figures 1, 3, and 4, local maxima

were found, starting at random locations within twice the size of  $\sigma_{\text{test}}$  from the origin. This effectively models a noisy winner-take-all mechanism. Thirty degrees of uniform noise was added to the obtained direction for illustrational purposes, 10 repetitions were executed.

*Parameters of Figure 1:*  $\sigma_{1,2} = 6$ ,  $\mu_1 = 2$  and  $\mu_2 = 20$ ,  $\beta_1 = -3\pi/4$ ,  $\beta_2 = -\pi/4$ .  $\sigma_{\text{test}}$  was varied. Contour plots were scaled separately.

### *Relation to Other Models*

Our model was designed to answer a sufficiency question: Can the known MAE data be explained in a single motion system framework? The model also served to answer a necessity question: Is a two-motion system framework necessary to explain the known MAE data? To this end, the model was kept devoid of large amounts of detail, and included just a motion opponency stage (Heeger et al., 1999), and a continuous representation of direction and speed (Liu & Newsome, 2003; Maunsell & Van Essen, 1983).

The model is closely related to the multiple-direction opponency model used by Grunewald and Lankheet (1996), as the interactions along the direction dimension are similar, but in our model, the speed variable has been included, and the time dimension was not. The model framework is also similar to that of Wilson and Kim (1994), which has a first level of opponent motion interactions and a second level of short-range excitation plus long-range inhibition along the direction dimension, much as in our model. The current model does not include explicitly the interactions among the Fourier components in the stimuli (Krekelberg & Albright, 2005), although it does include them implicitly by defining MAEs in a velocity space (Wainwright & Cavanagh, 1997).

## **Model Results**

### *Discontinuous MAE Data from a Continuous Model System*

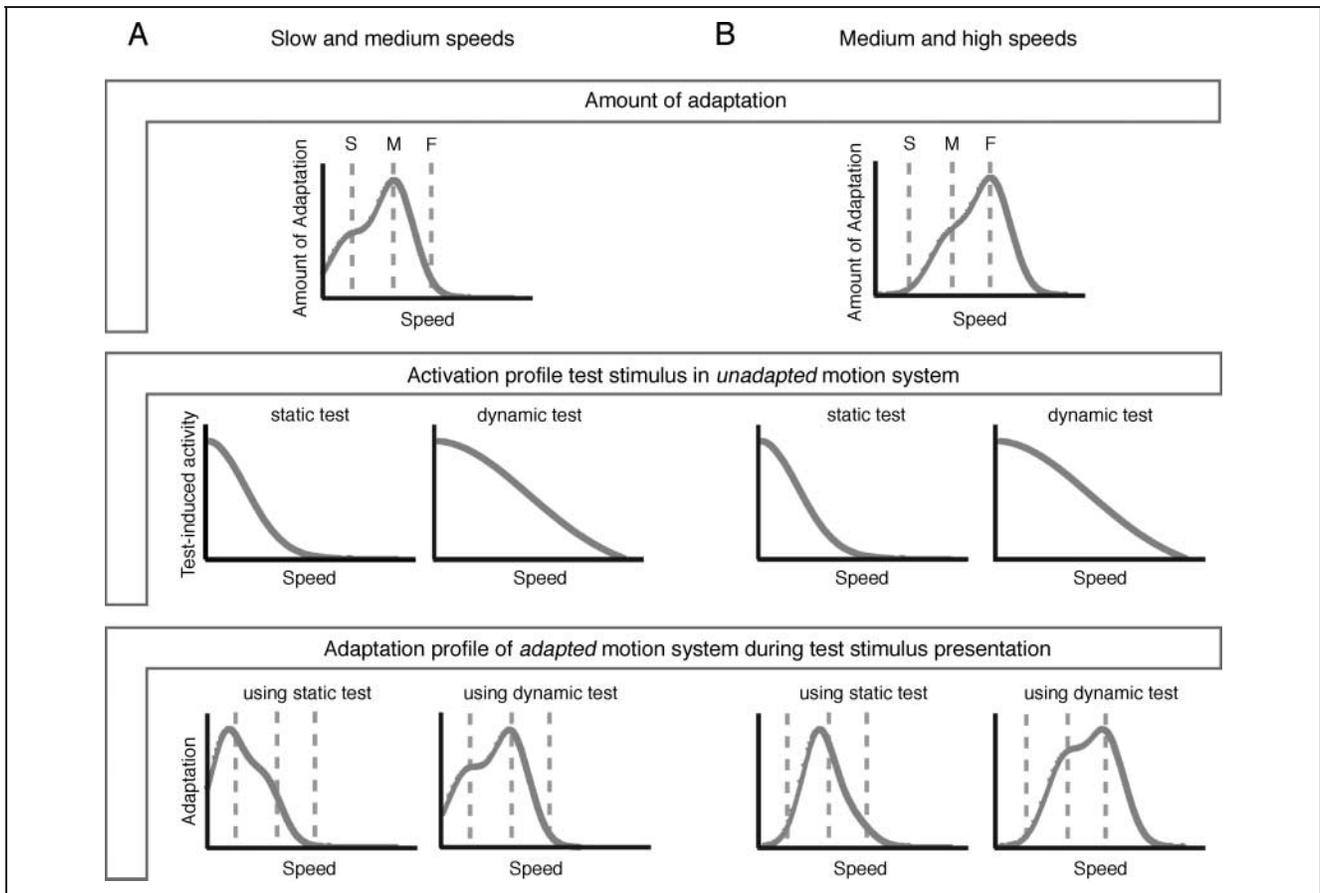
The motion system's response after adaptation was modeled by its response to the test stimulus in the non-adapted state multiplied by an adaptation-dependent modulation. The motion system's response to the test stimulus was explicitly modeled, taking into account the velocity content of the test stimulus, as static (low test refresh frequency; low TRF) and dynamic (high TRF) test stimuli have highly dissimilar velocity contents. A Gaussian blob centered at zero velocity modeled the velocity content of the test stimulus (Figure 1B). Its width, representing the width of the test stimulus velocity distribution (TVD), is the model's analog of the experimental parameter TRF (see footnote 2). The motion system's response after adaptation was readout by a noisy winner-take-all mechanism, giving perceived

MAE directions. Our single-system model reproduces the previously reported discontinuity in MAE directions (see van der Smagt et al., 1999, and our Figure 1D). The discontinuity has been taken as evidence for two independent motion systems (van de Grind et al., 2001; van der Smagt et al., 1999; Verstraten et al., 1998). Using the model, we may explain the occurrence of the discontinuity as follows: Adaptation causes an increased responsiveness at two separate spots (opposite the two adapting velocities; Grunewald & Lankheet, 1996) in the direction-speed space. Only one of these spots (at the high speed) is a global peak (Figure 1A, bottom). A ridge, slowly decreasing in height, runs from this peak to the spot opposite the slow adapting speed, after which it rapidly declines to basal levels (Figure 1A, bottom). Without explicitly putting a decreased sensitivity to slow motions in this model, such behavior is observed. The model produces this behavior because the motion opponency stage cancels out much of the low speed signals as much of the normally distributed adaptation of the velocity-sensitive cells falls on motion cells of opposite motion specificity when low speeds are used, but not when high speeds are used. The resulting larger adaptation at high velocities seems consistent with the literature that observes an ever-increasing responsiveness with increasing speed in motion area MT for the speed range we used in this study (Maunsell & Van Essen, 1983). This causes the following effect: With narrow TVDs, only the lower end of the ridge is read out, and a slow MAE is produced; with increasingly wide TVDs, the high-speed peak will eventually absorb the lower peak, thus creating fast MAEs (Figure 1B and C).

It thus seems that previously reported influential experimental results (van der Smagt et al., 1999) may be the footprints of a differential readout of a continuous system, in which a dichotomous response distribution arises because of sufficiently large speed differences between the adapting motion components.

## **PSYCHOPHYSICAL TESTS OF MODEL PREDICTIONS**

If a mechanism similar to our model is operational in the visual system, the following four predictions should be true: *Prediction 1:* The occurrence of an MAE after adaptation to slow or fast motion is not strictly dependent on the type of test stimulus. The static test stimulus activates mostly the lower part of the speed spectrum, whereas the dynamic test stimulus also activates large parts of the higher speed spectrum (Figure 2, second row). The static test will therefore support an MAE of the slower of two adaptation motions, independent of the exact speed (Figure 2, third row). The dynamic test will support an MAE of the faster of the two adapting motions. This will only hold if the faster



**Figure 2.** Schematic representation of the model predictions in cases of adaptation to slow and medium speeds (A), and medium and high speeds (B). The first row shows the amount of adaptation caused by the stimuli. The model shows less adaptation to slower speeds, both in A and B. The dashed lines indicate the adaptation speeds for slow (S), medium (M), and fast (F) components, although only slow and medium speeds were presented in A, and medium and fast speeds in B. The second row shows activation caused by static (left panels in A and B) and dynamic (right panels in A and B) test stimuli. Dynamic patterns show a wider range of activation. The third row shows the final readout of the amount of adaptation by the test stimulus (a multiplication of the first row by the second row). A static test pattern causes a maximum adaptation to be read out at the slower speed of the two adaptation components; a dynamic pattern has a maximum at the higher speed. This pattern of results occurs in both A (slow–medium speed adaptation) and B (medium–high adaptation). The transition can be discontinuous (i.e., a jump) or continuous, depending on model/experiment parameters.

motion induces a stronger activation than the slower motion (as shown in Figure 2); if this is not the case, one may observe two MAEs on a single test stimulus (as is found in Experiment 2, Figure 4). *Prediction 2:* With the right parameters, three different speed-dependent MAEs can be induced with a single adaptation stimulus. *Prediction 3:* Using three different refresh frequencies for the test stimulus should produce a maximum-duration MAE at three different speeds. *Prediction 4:* The discontinuous transition from slow to fast MAEs should exist only for rather large speed differences in the adaptation stimulus. If speed differences are small, no transition should be found, or it should be continuous rather than discontinuous, even if one speed falls within the range of the putative slow motion system, and the other in the range of the fast motion system. None of the predictions are made by a dual-motion system account for luminance-based motion that supposes independence of the two motion systems.

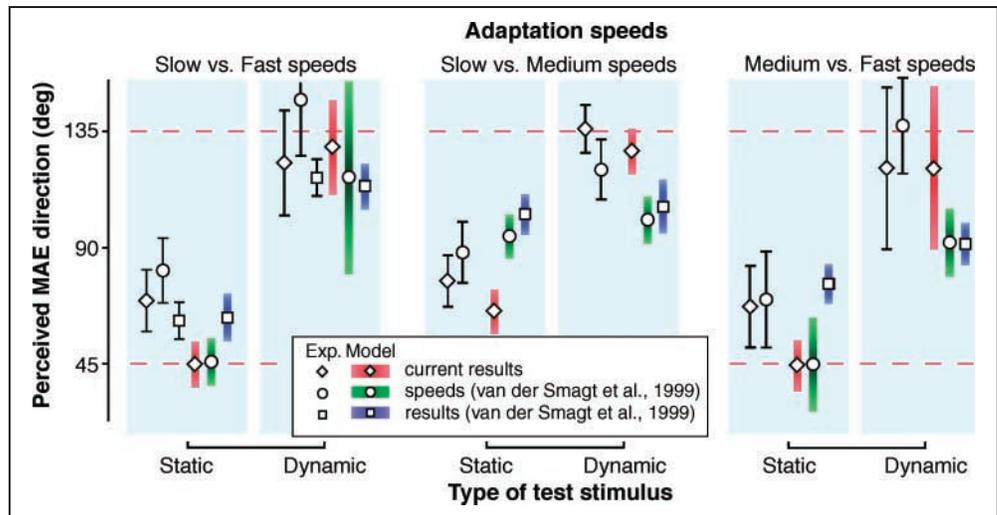
### Prediction 1: The Importance of Relative Speed Differences

In Experiment 1, we tested Prediction 1: The type of MAE is not dependent on the type of test stimulus. We pitted slow (6.4 deg/sec), medium (17 deg/sec), and fast (28 deg/sec) motions against each other in a pairwise fashion, and tested with static and dynamic test stimuli. According to Prediction 1, an intermediate speed should show an MAE on a static test pattern when a faster motion is simultaneously adapted to, but it should show an MAE on a dynamic pattern when the concurrent adapting motion was a slower one.

### Materials and Methods

*Experiment.* Movement was presented at 225° and 315° (counted counterclockwise from a horizontal rightwards direction) for slow and fast motions, respectively. Used

**Figure 3.** Perceived motion aftereffect (MAE) direction ( $\pm 1$  standard deviation) for static and dynamic test stimuli. Experimental (symbols only) and model results (having symbols matching the experimental data, and colored rectangular-shaped error bars) demonstrate a discontinuity in the MAE direction for all paired comparisons (slow–fast, slow–medium, and medium–fast speeds; diamonds). A previous influential article (van der Smagt et al., 1999) did not obtain such results (squares). However, using their parameter settings, we still observed a distinct discontinuity (right panel; circles). The single-system model encompasses all data by changing the adapting speeds (red to green) and the spread of velocity adaptation ( $\sigma$ ; green to blue).



were 6.4 versus 17 deg/sec, 17 versus 28 deg/sec, and 6.4 versus 28 deg/sec (diamonds in Figure 3). A similar experiment has been performed earlier (van der Smagt et al., 1999), and to be able to compare the data, we repeated the experiment with the speed reported in that study (circles in Figure 3): 1.3 versus 4 deg/sec (plotted in Figure 3: slow vs. medium), 4 versus 12 deg/sec (plotted in Figure 3: slow vs. fast), and 12 versus 36 deg/sec (plotted in Figure 3: medium vs. fast). Subjects G.B., A.K., and T.K. participated. Each direction was represented by 1000 white dots (9 arcmin/dot) on a black background. The stimulus size was  $18.4^\circ$ , it was surrounded by a 25-pixel-wide empty space, followed by a 50-pixel-wide border of randomly placed stationary dots, which were also visible during the test period. The test stimulus consisted of 3000 randomly placed dots. In static test conditions, the dots on the stimulus remain motionless on the screen for the duration of the test. In dynamic test conditions, patterns were refreshed at 33.3 Hz, meaning that for every 30 msec all dots were removed and repositioned at random locations. A test stimulus was presented for 4 sec, after which the subject indicated the strongest perceived MAE direction by means of a mouse-controlled dial. If subjects indicated that no MAE was seen, the datum point was excluded from analysis. A fixation mark (size: 18 arcmin) was present, surrounded by 16-pixel-wide empty space (1 pixel = 2.3 arcmin; monitor frame rate = 100 Hz).

Viewing was binocular. A Macintosh PowerPC G4 drove the experiment. Images were presented on a LaCie electron22blueIV monitor. Subjects A.K., T.K., and G.B. were naive as to the purpose of the experiment;

Subject J.B. is one of the authors. Subjects used a chin rest to stabilize head position. Experimental procedures were reviewed and approved by the Institutional Review Board, and subjects gave informed consent.

*Parameters simulations of Figure 3.* Red:  $\sigma_{1,2} = 3$ ; Left panel:  $\mu_1 = 1, \mu_2 = 20$ ; Middle panel:  $\mu_1 = 1, \mu_2 = 9$ ; Right panel:  $\mu_1 = 9, \mu_2 = 20$ . Green:  $\sigma_{1,2} = 3$ ; Left panel:  $\mu_1 = 4, \mu_2 = 17$ ; Middle panel:  $\mu_1 = 1, \mu_2 = 4$ ; Right panel:  $\mu_1 = 17, \mu_2 = 20$ . Blue:  $\sigma_{1,2} = 6, \mu_1$  and  $\mu_2$  as for the green plots.  $\sigma_{\text{test}}$  was 4 for static conditions and 34 for dynamic conditions.

### Results Experiment 1

Statistical tests showed that all pairwise comparisons between static and dynamic conditions were significant (one-tailed  $t$  test, all  $p < 10^{-3}$ ; the results from the different static conditions did not differ from each other, nor did the different dynamic conditions differ significantly from each other: all  $p > 0.1$ , two-tailed  $t$  test). Moreover, all means differed significantly from  $90^\circ$  (all  $p < 10^{-3}$ ,  $z$  test). The results (Figure 3, diamonds) show that for all pairs the slower of the two motions was linked to an MAE on static test stimuli, whereas the faster was linked to an MAE on dynamic test stimuli, *irrespective of their absolute speed* (see also Wainwright & Cavanagh, 1997). The medium speed (17 deg/sec)—falling well within the proposed range of the fast motion system (Verstraten et al., 1998)—induced an MAE on static or on dynamic test stimuli, depending on the

accompanying motion. These results speak against the existence of two motion systems. However, adapting speed differences are not the only factor determining the occurrence of the discontinuity in MAE direction, which is made clear by comparing our results with earlier research (van der Smagt et al., 1999). Similar speed differences between the adapting motions were used in this report and previous research, but the previous research found no discontinuity when pitting two rather slow (or two fast), but different, motions against each other, whereas we did find a discontinuity. This discontinuity did not disappear when we repeated the experiment with speeds identical to those from van der Smagt et al. (1999) (Figure 3, right panel, circles; pairwise comparisons between static and dynamic conditions,  $p < 10^{-3}$ ; all means were different from  $90^\circ$  [ $p < 10^{-2}$ ], except the slow vs. medium comparison,  $p > 0.7$ ).

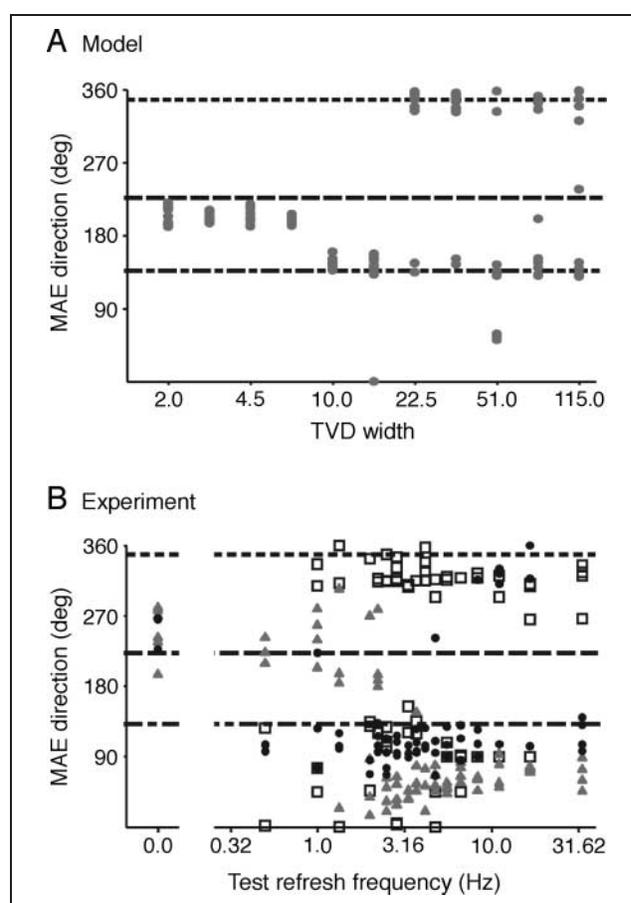
Our model reproduces our two sets of data by just changing the adapting speeds (see Methods) in similar ways as in the experiments (compare red [diamond] and green [circle] model results with corresponding experimental results; Figure 3). Without any further changes, it did not reproduce the results from van der Smagt et al. (1999). However, the stimuli used in both experiments were rather different: random dot patterns are used in the present study, whereas previous research used random-pixel arrays. (These stimuli look like checkerboards with the checks randomly assigned a white or black color.) Displaced random-pixel arrays (used in van der Smagt et al., 1999) contain more false matches, and thus noise, between subsequent views than do sparse random dot stimuli. Interestingly, when we introduce this notion into the model by increasing the range of speeds that adapts around the adapting speed (increasing  $\sigma$  in the model), the model reproduces the experimental data of van der Smagt et al. (blue model results in Figure 3).

There are therefore two factors determining whether a discontinuity in the MAE data occurs. First, the distance in speed between the two adapting motions. Second, the range of speeds that adapts in response to prolonged viewing of the adapting motion. In fact, the distance between the adapting speeds needs to be large relative to the width of the region that will be adapted by the stimuli to give rise to a discontinuity in the reported MAE directions with static and dynamic test stimuli, otherwise, a continuous transition is observed, or no transition at all.

### Prediction 2: MAEs in Three Directions

In a second experiment, we tested Prediction 2: Adaptation to three motions may produce three MAEs. It is proposed that within the slow and fast motion systems, information is averaged after adaptation, but between systems it is not (van der Smagt et al., 1999). This view is

supported by the finding that adaptation to two motions of similar, but not necessarily identical, slow (or high) speeds but different directions will result in an MAE opposite the average motion during adaptation, whereas adaptation to two motion components, of which one is a slow speed and the other is a high speed motion, leads to MAE opposite one or the other component (e.g., van der Smagt et al., 1999, but see our Experiment 1).<sup>3</sup> A prediction of a strict dual-motion system hypothesis is that a maximum of two MAEs can be obtained in response to any combination of adapting motions. However, under the condition that three simultaneously present adapting components are used, our single-system model predicted three MAEs opposite the adapting motion components (Figure 4A).



**Figure 4.** Perceived motion aftereffect (MAE) directions depending on test stimulus refresh frequency (or its model analog: the test velocity distribution [TVD] width) after adaptation to a stimulus containing three motions. The lines show directions opposite the adapting motion directions. Different subjects are denoted by different symbols. Both in the model (A) and in the experiment (B), three MAE directions were produced, contrary to the two MAE directions that would be predicted by a two-system account of the visual motion system. Intersubject variability causes the somewhat noisy appearance of the experimental data. Along previous lines of reasoning, the experimental data suggest the existence of three motion systems, but the model shows that a single motion system is sufficient to explain these experimental data.

## Materials and Methods

**Experiment.** Movement was presented simultaneously in following directions: 45°, 165°, and 315°, moving at 6.4, 17, and 28 deg/sec, respectively, or at 1, 12.7, and 28 deg/sec. We avoided motion in the four cardinal directions as we found in pilot studies that subjects are biased towards reporting MAEs in these directions. We avoided these directions to give all adapting motion components a more equal chance to be reported. The components were not equally spaced along the 360° as it turned out in pilot experiments that in such conditions subjects showed a continuous transition from the high-speed to the medium-speed MAE; the used motion directions resulted in discontinuous transitions in most subjects. Test pattern refresh frequencies varied. Other parameters were as in Experiment 1.

**Model parameters of Figure 4.**  $\sigma_{1,2,3} = 3$ ,  $\mu_1 = 1$ ,  $\mu_2 = 9$ , and  $\mu_3 = 20$ ,  $\beta_1 = \pi/4$ ,  $\beta_2 = 7\pi/4$ , and  $\beta_3 = \pi/12$ .  $\sigma_{\text{test}}$  was varied.  $\sigma_{1,2,3}$  and  $\mu_{1,2,3}$  are as those in the left panel in Figure 3 (Experiment 1).

## Results Experiment 2

We found that three different MAEs—opposite the adapting motion components—were reported (Figure 4B), in accordance with the model predictions that were based on parameters used in Experiment 1 (Figure 4A). The subject represented by the gray symbols does not show three groups of answers, but instead shows a group of answers around 225° (MAE of slow speed), and a group of answers that follows a continuous path from the intermediate speed MAE (at 345°) to the fast speed MAE (at 135°) as the TRF increases, without reaching either solution completely. Note here that the MAE direction is a circular variable. These results conform the single-system account (see Prediction 4). Furthermore, subjects indicated that sometimes two different MAEs were seen simultaneously on a single

test pattern. Both findings are in agreement with a single-system hypothesis.

## Prediction 3: Perceived MAE Durations for Intermediate Test Stimuli Refresh Frequencies

In Experiment 3, we tested Prediction 3: Intermediate TRFs show their longest MAEs for intermediate adapting speeds. (Predictions for a two-system hypothesis, proposed on the basis of the described results [Verstraten et al., 1998], could not be made, as they depend on the precise mechanisms that one assumes to underlie the division. So far, the proposed mechanisms are not articulated sufficiently precisely.) We tested our prediction experimentally (see Methods) with TRFs of 0, 19, and 75 Hz.

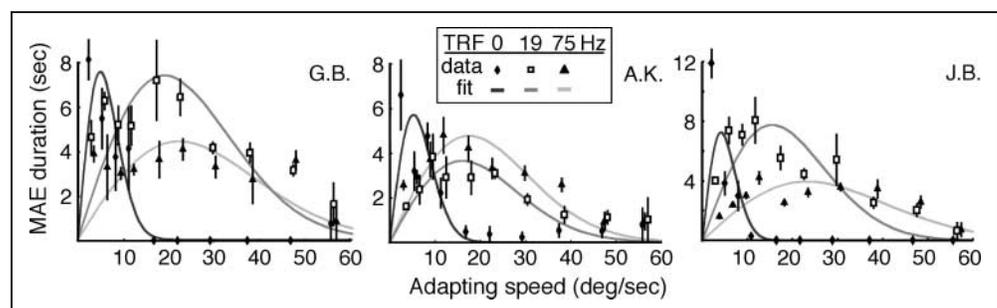
## Materials and Methods

**Experiment.** We used a setup and procedures similar to Verstraten et al. (1998). Adapting movement was 1 to 29 pix/frame (3 to 58 deg/sec). Stimulus size was 10.3 × 10.3 deg<sup>2</sup> (256 × 256 pix<sup>2</sup>). TRFs were 0, 19, or 75 Hz. The 19-Hz TRF was chosen close to the transition point between the putative slow and fast motion systems (van der Smagt et al., 1999) to maximize the responses of both systems. During the entire experiment, a 16-pixel-sized fixation cross was surrounded by a 28-pixel-wide square (intermediate gray). The monitor refresh rate was 75 Hz, 1 pixel was 2.4 arcmin wide. Subjects could indicate that no MAE was seen, this was analyzed as a zero second MAE. Subject G.B. performed four repetitions, whereas A.K. and J.B. each performed 5.

## Results Experiment 3

Prediction 3 was borne out by the findings: Intermediate TRFs led to distinct peaks in MAE duration at intermediate adapting speeds for all subjects (Figure 5). At first glance it may be argued that some curves show a

**Figure 5.** Perceived motion aftereffect (MAE) durations ( $\pm 1$  SEM) as a function of adapting speed for three subjects. Test patterns were static (diamonds), refreshed at 19 Hz (squares), or refreshed at 75 Hz (triangles). Fits through these data sets are shown (from dark to light gray: 0, 19, 75 Hz). Previously (Verstraten et al., 1998), fast and slow motion systems



were proposed on the basis of the finding that static and dynamic test stimuli exhibit the longest MAE at vastly different adapting speeds. The widely accepted division in fast and slow motion systems is at odds with here-presented data, as intermediate test refresh frequencies (TRFs; between static and very dynamic, 19 Hz) show the longest MAE durations for intermediate adapting speeds.

bimodal profile. However, this interpretation is dismissed, as for almost all these cases such an interpretation depends critically on a single data point that lies above or below the value expected from a unimodal dataset, and often (but not always) has a rather large *SEM* as compared to the other data points. Moreover, if one assumes that two systems cause two peaks, one should also see a small peak for the static curve at about 25 deg/sec (especially for observer A.K.). Such was not seen. Furthermore, if one adheres to the reasoning that many researchers follow when proposing the dual-motion system, Figure 4 suggests that three systems exist (as it shows three different MAE directions), and thus, that Figure 5 should show three peaks. Also, this was not observed.

To determine precisely the mechanism causing the different positioning of the peaks of the three curves, the experimental data were fitted with a function based on our model, of which the parameters have physiological interpretations:  $c[G(\mu, \sigma)_s - G(\mu, \sigma)_{-s}] G(\mu_{\text{test}}, \sigma_{\text{test}})$ , where  $G$  is a Gaussian distribution.  $\mu$  and  $\sigma$  characterize the adaptation state of the visual system,  $\mu$  represents the speed at which it most strongly adapts,  $\sigma$  represents the spread, and  $\sigma_{\text{test}}$  represents the TVD width,  $\mu_{\text{test}}$  represents the overall speed in the test stimulus, which is set to zero.  $\mu$ ,  $\sigma$ , and  $\sigma_{\text{test}}$  are expressed in degrees per second. All parameters were free to vary (except for the scaling factor  $c$ ). If different motion systems were at the origin of the experimentally found results, one would expect  $\mu$  and/or  $\sigma$  to increase with increasing TRF. If differences in the velocity content of the test stimulus were responsible for the found results—as predicted by the single motion system hypothesis—one would expect  $\sigma_{\text{test}}$  to increase with increasing TRF. The data from the different sessions were fitted separately (exemplar fits through the average data are shown in Figure 5 [curves]). Averaged values for  $\mu$ ,  $\sigma$ , and  $\sigma_{\text{test}}$  for 0, 19, and 75 Hz were:  $\mu = \{32, 15, 18\}$ ,  $\sigma = \{29, 26, 27\}$ ,  $\sigma_{\text{test}} = \{5, 25, 30\}$ . Linear regression analyses on all collected  $\mu$ ,  $\sigma$ , and  $\sigma_{\text{test}}$  values showed that only  $\sigma_{\text{test}}$  was significantly positively related to TRF ( $p < .0005$ ). These data suggest that the different positioning of the curves is not related to differences between adaptation states (characterized by  $\mu$  and  $\sigma$  and associable with different motion systems), but instead to differences in the velocity content of the various test stimuli (defined by  $\sigma_{\text{test}}$ ). Results were very similar among subjects.

#### **Prediction 4: Discontinuous Transitions Disappear with Small Speed Differences**

We did not test Prediction 4 in a separate experiment, but the model suggested that discontinuous transitions should not be observed when speed differences between the adaptation components are small relative to the width of adaptation in the speed dimension ( $\sigma$  in

the model). Assuming that adaptation processes differ between subjects, and that some subjects adapt a wider range of speed sensors than others in identical conditions, we could see continuous transitions for some subjects and discontinuous transitions for others, while stimulus conditions are the same. Indeed, in Experiment 2 (Figure 4B), the observer, denoted by the gray triangles, shows a continuous transition between fast and medium speeds, whereas the other subjects show a two-peaked distribution. Also, Subject F.V. in van der Smagt et al. (1999) shows a continuous transition between slow and fast MAEs, whereas the other two subjects do not.

## **DISCUSSION**

What are the mechanisms underlying our conscious perception of speed? Several studies have proposed a division in fast and slow motion systems, but have put forward different accounts of where in the brain and how this division is realized and until what stage it is sustained. It has been proposed that the division may occur early in the visual system, at the level of magnocellular and parvocellular cells (van de Grind et al., 2001; van der Smagt et al., 1999; Burr et al., 1998; Hawken et al., 1994), and may continue to exist until much of the motion processing is achieved and then come together at a perceptual level (Burr et al., 1998), or even that the two systems remain separated until the very end, and each have a “private line to consciousness” (van de Grind et al., 2001). Our results do not support claims of two separate motion systems, but instead show that a single motion system can explain the human perception of speed. We show that dichotomous data obtained with different stimuli cannot be interpreted as evidence of a bipartite (motion) system.

We have demonstrated that for the system processing luminance-based motion—arguably the most important source of motion information—(1) no strict link exists between adapting speed and type of test stimulus on which the strongest MAE is reported (Figure 3, diamonds for medium speeds); (2) simultaneous adaptation to three motions can bring about three different MAEs (Figure 4); (3) static test patterns support the longest MAE after adaptation to slow motion, dynamic test patterns do so for fast motions, but intermediately dynamic patterns support the longest MAE at intermediate adapting speeds (Figure 5); (4) depending on the speed differences among the different adaptation components and on the subject, discontinuous transitions become continuous transitions; (5) a single-system model explains all data (Figures 1, 3, and 4). The model shows (Figure 1) that discontinuities in experimental data do not necessarily indicate discontinuities in the visual processing. Discontinuous data are also produced by a single system along a sampled parameter dimension (e.g., the adapting velocity [Figure 5 and Verstraten et al.,

1998] and TVD [Figures 1, 3, and 4, and van der Smagt et al., 1999]) when the adaptation processes—taking place in two separate subpopulations—do not overlap extensively. None of the findings support the assumption of two independent speed-tuned motion systems.

Our results show how in different conditions transparent motions may lead to unidirectional and multidirectional aftereffects, depending on various stimulus parameters, and that all results are consistent with a single motion system. Our data further show that large-scale motion integration takes place in both direction and speed dimensions. Integration along the direction dimension may be precluded by large speed differences in the adapting stimuli, which is consistent with the research on plaid stimuli that has shown that the coherent motion perception (formed by motion integration) of the plaid decreases as the speed differences between its component motions increases (Kim & Wilson, 1993).

There exists, however, a large body of data that is interpreted as evidence for a distinction in slow and fast motion systems, both psychophysical and clinical. Below we will go to some length in discussing these data to show that the data are not necessarily indicative of two motion systems, and may be incorporated in a single motion system account.

Slow chromatic and fast achromatic motion systems have been proposed in the psychophysical literature (Burr et al., 1998; Gegenfurtner & Hawken, 1995, 1996; Hawken et al., 1994; Gorea et al., 1993). Reaction time to motion onset (Burr et al., 1998), and motion identification thresholds (Gegenfurtner & Hawken, 1996) were found to increase more steeply for chromatic stimuli than for achromatic stimuli when using increasingly low physical stimulus speeds (or temporal frequencies). However, these increases were nearly identical for both conditions when replotted against *perceived* speed (Burr et al., 1998). These data were interpreted to mean that there exist separate motion systems for chromatic and achromatic motions, and that the outcome of these systems converges at a subsequent level (Burr et al., 1998). However, the differences between chromatic and achromatic conditions are well explained by just assuming different contrast-transduction properties of early temporal filters without assuming different motion systems (Metha & Mullen, 1997, 1998). Also, the discovery of low and high temporal frequency channels (Alais, Verstraten, & Burr, 2005; Anderson & Burr, 1985; Thompson, 1982) has incited claims that slow and fast motion systems exist. However, it has been suggested on theoretical (Hammett, Champion, Morland, & Thompson, 2005; Perrone & Thiele, 2002) and experimental (De Valois & Cottaris, 1998; Thompson, 1982) grounds that these channels operate not independently but jointly to create a representation of speed at a later stage. These findings can therefore be incorporated in the one-system hypothesis.

Research on motion detection in noise has shown that motion detection is impaired when noise dots move with similar speeds as signal dots, but not when both speeds are very different. Such was found for fast and slow signal speeds (Khuu & Badcock, 2002; Edwards et al., 1998). These results—although interpreted as evidence for two motion systems—are fully compatible with our findings that, under certain conditions, subpopulations of a single motion system may adapt to (and thus process) fast and slow motion without much interaction. Such a mechanism may also be the key to explain the data reported by van de Grind et al. (2001), who showed that presenting different motions to the two eyes results in binocular rivalry if both motions were slow, or fast, but results in transparency if one motion was fast and the other slow (cf. Kim & Wilson, 1993).

In clinical studies, it has been suggested (Ffytche, Guy, & Zeki, 1995) that there exist two separate pathways to motion area MT: one pathway projecting directly from the lateral geniculate nucleus (LGN) to MT (for fast motions,  $>6$  deg/sec), the other one relayed through V1. Although much of the data suggesting this pathway has been criticized (Azzopardi, Fallah, Gross, & Rodman, 2003), a direct LGN–MT pathway seems to have been found recently (Sincich, Park, Wohlgemuth, & Horton, 2004). The available data, however, suggest that the direct koniocellular LGN–MT projection (Sincich et al., 2004) is not involved in motion processing per se (Ruppertsberg, Wuerger, & Bertamini, 2003; Nguyen-Tri & Faubert, 2002; Azzopardi & Cowey, 2001; Morand et al., 2000), but may function as a fast attention-grabbing (and possibly directing) device. Such a device should be specifically sensitive to fast motions (Chawla et al., 1999; Ffytche et al., 1995) as they pose a greater threat to the survival of an organism (embodied in approaching predators, or e.g., cars and trains), for which the more time-consuming motion calculations in V1 should be bypassed. Therefore, the finding of a direct LGN–MT projection is not in conflict with our findings.

One other possibility is that slow and fast motion systems are located in anatomically separate brain areas. Consistent with this idea is the finding that a patient with a bilateral lesion in MT could not see motions faster than about 6 deg/sec (Zihl et al., 1983), whereas a patient with V1 lesions could not see motions slower than about 6 deg/sec (Barbur et al., 1993). However, patients with V1 lesions were unable to determine the direction of motion of the stimulus because of little position information (Azzopardi & Cowey, 2001). Similarly, the patient with MT lesions did show only saccadic pursuit for fast motions, and she did not perceive an MAE after prolonged periods of motion stimulation (Zihl et al., 1983). The rudimentary motion perception for both types of lesion seems to depend on a position tracking (and not a motion) system.

V3A is also an area that is found to be motion-sensitive. Much is still unknown about its motion

specificity, but it seems to have speed sensitivities almost identical to MT (Chawla et al., 1999), which speaks against a division of labor between V3A and MT along the speed dimension. Its inferior activity to motion stimuli relative to MT (Tootell et al., 1997) seems to suggest that V3A is not very specific for motion, which dovetails nicely with the suggestion that it processes 3-D shape or layout (Tsao et al., 2003), which can be derived from multiple cues, including motion information. Our results add to this idea that a single functional entity underlies the found MAEs, and it is then most parsimonious to assume that this is also a single anatomical substrate.

Overall, a single motion system is well able to explain the available data on motion processing. Our study reconciles a large body of research that lent support to the single-system account of motion perception with the psychophysical literature that repeatedly reported evidence for a division in fast and slow motion systems. We have demonstrated that a two-system hypothesis is neither sufficient (Experiments 1, 2, and 3) nor necessary (model) to explain the data on luminance-based motion perception. Therefore, we argue—opposing previous psychophysical studies (Khuu & Badcock, 2002; van de Grind et al., 2001; van der Smagt et al., 1999; Burr et al., 1998; Edwards et al., 1998; Verstraten et al., 1998; Gegenfurtner & Hawken, 1995, 1996; Hawken et al., 1994; Gorea et al., 1993), but in line with currently known neurophysiological findings in monkeys (Liu & Newsome, 2003; Perrone & Thiele, 2001; Maunsell & Van Essen, 1983)—that a single luminance-based motion system can explain human speed perception. This finding accords well with the generally accepted view of a single system for the processing of motion direction (Mather & Harris, 1998; Albright, Desimone, & Gross, 1984; Mather, 1980).

### Acknowledgments

We thank Dr. W. A. van de Grind for critical discussions and P. Schipphorst and T. Knapen for technical assistance.

Reprint requests should be sent to Prof. Dr. C. J. Erkelens, Department Physics of Man, Helmholtz Institute, Utrecht University, Princetonplein 5, 3584 CC Utrecht, The Netherlands, or via e-mail: c.j.erkelens@phys.uu.nl.

### Notes

1. We use the term motion system to refer to processes in the brain that give rise to motion percepts. Our use of motion systems is close to that of motion channels, in that motion channels perform identical calculations, but with different parameters, leading to different sensitivities, and so forth. However, it is of interest to note that authors often imply that the two-motion systems respond to different kinds of stimuli. It is assumed that the slow-motion system responds specifically to static test stimuli and the fast-motion system specifically to dynamic ones (e.g., van der Smagt et al., 1999). Or that one activates different systems with colored (isoluminant)

and luminance-defined motion stimuli (e.g., Hawken et al., 1994), on the basis of the finding that both have different contrast dependencies. A motion system may contain several motion channels.

2. We have followed the next reasoning: suppose we have two frames. Each contains randomly positioned dots, and the frames differ from each other. By presenting the two frames in sequence, the motion system matches all (or many) of the dots of frame 1 with all (or many) of the dots in frame 2. These spatial displacements, together with a certain time lag between the onsets of both frames, create a certain velocity distribution. Choosing the lag to be small (high refresh frequencies) gives rise to high speeds, choosing the lag to be large, but keeping the spatial displacements the same creates low speeds. Therefore, high refresh frequencies give rise to wider velocity distributions than low refresh frequencies in the stimuli we used.

3. Note that one need not expect any interaction between slow chromatic and achromatic motions if one assumes different systems to underlie these motion percepts.

### REFERENCES

- Alais, D., Verstraten, F. A., & Burr, D. C. (2005). The motion aftereffect of transparent motion: Two temporal channels account for perceived direction. *Vision Research*, *45*, 403–412.
- Albright, T. D. (1984). Direction and orientation selectivity of neurons in visual area MT of the macaque. *Journal of Neurophysiology*, *52*, 1106–1130.
- Albright, T. D., Desimone, R., & Gross, C. G. (1984). Columnar organization of directionally selective cells in visual area MT of the macaque. *Journal of Neurophysiology*, *51*, 16–31.
- Anderson, S. J., & Burr, D. C. (1985). Spatial and temporal selectivity of the human motion detection system. *Vision Research*, *25*, 1147–1154.
- Azzopardi, P., & Cowey, A. (2001). Motion discrimination in cortically blind patients. *Brain*, *124*(Pt 1), 30–46.
- Azzopardi, P., Fallah, M., Gross, C. G., & Rodman, H. R. (2003). Response latencies of neurons in visual areas MT and MST of monkeys with striate cortex lesions. *Neuropsychologia*, *41*, 1738–1756.
- Barbur, J. L., Watson, J. D., Frackowiak, R. S., & Zeki, S. (1993). Conscious visual perception without V1. *Brain*, *116*(Pt 6), 1293–1302.
- Braddick, O. (1974). A short-range process in apparent motion. *Vision Research*, *14*, 519–527.
- Burr, D. C., Fiorentini, A., & Morrone, C. (1998). Reaction time to motion onset of luminance and chromatic gratings is determined by perceived speed. *Vision Research*, *38*, 3681–3690.
- Cavanagh, P., & Mather, G. (1989). Motion: The long and short of it. *Spatial Vision*, *4*, 103–129.
- Chawla, D., Buechel, C., Edwards, R., Howseman, A., Josephs, O., Ashburner, J., et al. (1999). Speed-dependent responses in V5: A replication study. *Neuroimage*, *9*, 508–515.
- De Valois, R. L., & Cottaris, N. P. (1998). Inputs to directionally selective simple cells in macaque striate cortex. *Proceedings of the National Academy of Sciences, U.S.A.*, *95*, 14488–14493.
- Edwards, M., Badcock, D. R., & Smith, A. T. (1998). Independent speed-tuned global-motion systems. *Vision Research*, *38*, 1573–1580.
- Flytche, D. H., Guy, C. N., & Zeki, S. (1995). The parallel visual motion inputs into areas V1 and V5 of human cerebral cortex. *Brain*, *118*(Pt 6), 1375–1394.

- Gegenfurtner, K. R., & Hawken, M. J. (1995). Temporal and chromatic properties of motion mechanisms. *Vision Research*, *35*, 1547–1563.
- Gegenfurtner, K. R., & Hawken, M. J. (1996). Interaction of motion and color in the visual pathways. *Trends in Neurosciences*, *19*, 394–401.
- Gorea, A., Papathomas, T. V., & Kovacs, I. (1993). Two motion systems with common and separate pathways for color and luminance. *Proceedings of the National Academy of Sciences, U.S.A.*, *90*, 11197–11201.
- Grunewald, A., & Lankheet, M. J. (1996). Orthogonal motion after-effect illusion predicted by a model of cortical motion processing. *Nature*, *384*, 358–360.
- Hammitt, S. T., Champion, R. A., Morland, A. B., & Thompson, P. G. (2005). A ratio model of perceived speed in the human visual system. *Proceedings of the Royal Society of London, Series B, Biological Sciences*, *272*, 2337–2344.
- Hawken, M. J., Gegenfurtner, K. R., & Tang, C. (1994). Contrast dependence of colour and luminance motion mechanisms in human vision. *Nature*, *367*, 268–270.
- Heeger, D. J., Boynton, G. M., Demb, J. B., Seidemann, E., & Newsome, W. T. (1999). Motion opponency in visual cortex. *Journal of Neuroscience*, *19*, 7162–7174.
- Khuu, S. K., & Badcock, D. R. (2002). Global speed processing: Evidence for local averaging within, but not across two speed ranges. *Vision Research*, *42*, 3031–3042.
- Kim, J., & Wilson, H. R. (1993). Dependence of plaid motion coherence on component grating directions. *Vision Research*, *33*, 2479–2489.
- Krekelberg, B., & Albright, T. D. (2005). Motion mechanisms in macaque MT. *Journal of Neurophysiology*, *93*, 2908–2921.
- Liu, J., & Newsome, W. T. (2003). Functional organization of speed tuned neurons in visual area MT. *Journal of Neurophysiology*, *89*, 246–256.
- Lu, Z. L., & Sperling, G. (2001). Three-systems theory of human visual motion perception: Review and update. *Journal of the Optical Society of America. A, Optics, Image Science, and Vision*, *18*, 2331–2370.
- Mather, G. (1980). The movement aftereffect and a distribution-shift model for coding the direction of visual movement. *Perception*, *9*, 379–392.
- Mather, G., & Harris, J. (1998). Theoretical models of the motion aftereffect. In G. Mather, F. A. Verstraten, & S. Anstis (Eds.), *The motion aftereffect* (pp. 157–185). Cambridge: MIT Press.
- Maunsell, J. H., & Van Essen, D. C. (1983). Functional properties of neurons in middle temporal visual area of the macaque monkey: I. Selectivity for stimulus direction, speed, and orientation. *Journal of Neurophysiology*, *49*, 1127–1147.
- Metha, A. B., & Mullen, K. T. (1997). Red–green and achromatic temporal filters: A ratio model predicts contrast-dependent speed perception. *Journal of the Optical Society of America. A, Optics, Image Science, and Vision*, *14*, 984–996.
- Metha, A. B., & Mullen, K. T. (1998). Failure of direction discrimination at detection threshold for both fast and slow chromatic motion. *Journal of the Optical Society of America. A, Optics, Image Science, and Vision*, *15*, 2945–2950.
- Morand, S., Thut, G., de Peralta, R. G., Clarke, S., Khateb, A., Landis, T., et al. (2000). Electrophysiological evidence for fast visual processing through the human koniocellular pathway when stimuli move. *Cerebral Cortex*, *10*, 817–825.
- Nguyen-Tri, D., & Faubert, J. (2002). The perceived speed of drifting chromatic gratings is mechanism-dependent. *Vision Research*, *42*, 2073–2079.
- Nishida, S., & Sato, T. (1995). Motion aftereffect with flickering test patterns reveals higher stages of motion processing. *Vision Research*, *35*, 477–490.
- Pantle, A., & Picciano, L. (1976). A multistable movement display: Evidence for two separate motion systems in human vision. *Science*, *193*, 500–502.
- Perrone, J. A., & Thiele, A. (2001). Speed skills: Measuring the visual speed analyzing properties of primate MT neurons. *Nature Neuroscience*, *4*, 526–532.
- Perrone, J. A., & Thiele, A. (2002). A model of speed tuning in MT neurons. *Vision Research*, *42*, 1035–1051.
- Ruppertsberg, A. I., Wuerger, S. M., & Bertamini, M. (2003). The chromatic input to global motion perception. *Visual Neuroscience*, *20*, 421–428.
- Sincich, L. C., Park, K. F., Wohlgenuth, M. J., & Horton, J. C. (2004). Bypassing V1: A direct geniculate input to area MT. *Nature Neuroscience*, *7*, 1123–1128.
- Snowden, R. J., Treue, S., Erickson, R. G., & Andersen, R. A. (1991). The response of area MT and V1 neurons to transparent motion. *Journal of Neuroscience*, *11*, 2768–2785.
- Thompson, P. (1982). Perceived rate of movement depends on contrast. *Vision Research*, *22*, 377–380.
- Tootell, R. B., Mendola, J. D., Hadjikhani, N. K., Ledden, P. J., Liu, A. K., Reppas, J. B., et al. (1997). Functional analysis of V3A and related areas in human visual cortex. *Journal of Neuroscience*, *17*, 7060–7078.
- Tsao, D. Y., Vanduffel, W., Sasaki, Y., Fize, D., Knutsen, T. A., Mandeville, J. B., et al. (2003). Stereopsis activates V3A and caudal intraparietal areas in macaques and humans. *Neuron*, *39*, 555–568.
- van de Grind, W. A., van Hof, P., van der Smagt, M. J., & Verstraten, F. A. (2001). Slow and fast visual motion channels have independent binocular-rivalry stages. *Proceedings of the Royal Society of London, Series B, Biological Sciences*, *268*, 437–443.
- van der Smagt, M. J., Verstraten, F. A., & van de Grind, W. A. (1999). A new transparent motion aftereffect. *Nature Neuroscience*, *2*, 595–596.
- Verstraten, F. A., van der Smagt, M. J., & van de Grind, W. A. (1998). Aftereffect of high-speed motion. *Perception*, *27*, 1055–1066.
- Wainwright, M., & Cavanagh, P. (1997). Static and flicker motion aftereffects in a velocity space. *Investigative Ophthalmology and Visual Science*, *38*, S374.
- Wilson, H. R., & Kim, J. (1994). A model for motion coherence and transparency. *Visual Neuroscience*, *11*, 1205–1220.
- Zihl, J., von Cramon, D., & Mai, N. (1983). Selective disturbance of movement vision after bilateral brain damage. *Brain*, *106*(Pt 2), 313–340.