

Brief communication

Test stimulus characteristics determine the perceived speed of the dynamic motion aftereffect

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Received 8 June 2005; received in revised form 15 March 2006

Abstract

Using a speed-matching task, we measured the speed tuning of the dynamic motion aftereffect (MAE). The results of our first experiment, in which we co-varied dot speed in the adaptation and test stimuli, revealed a speed tuning function. We sought to tease apart what contribution, if any, the test stimulus makes towards the observed speed tuning. This was examined by independently manipulating dot speed in the adaptation and test stimuli, and measuring the effect this had on the perceived speed of the dynamic MAE. The results revealed that the speed tuning of the dynamic MAE is determined, not by the speed of the adaptation stimulus, but by the local motion characteristics of the dynamic test stimulus. The role of the test stimulus in determining the perceived speed of the dynamic MAE was confirmed by showing that, if one uses a test stimulus containing two sources of local speed information, observers report seeing a transparent MAE; this is despite the fact that adaptation is induced using a single-speed stimulus. Thus while the adaptation stimulus necessarily determines perceived direction of the dynamic MAE, its perceived speed is determined by the test stimulus. This dissociation of speed and direction supports the notion that the processing of these two visual attributes may be partially independent.

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Keywords: Motion perception; Motion aftereffect; Adaptation

1. Introduction

The motion aftereffect (MAE) is a well known phenomenon in which prolonged viewing of a moving pattern results in the perception of opposite motion in a subsequently viewed directionally balanced test pattern (Mather, Verstraten, & Anstis, 1998). This effect reveals an important aspect of motion processing—at some point(s) the outputs of neurons tuned to different directions are compared. If (as in the MAE) a subset of directionally tuned neurons show reduced responsiveness due to adaptation, then the net output of directionally tuned neurons will signal motion where there is none. The MAE has two forms—the static and dynamic MAE. While the former is induced in static test patterns, the latter is induced in dynamic test patterns

defined by either counter-phase flicker (Ashida & Osaka, 1995; Nishida & Ashida, 2000) or local motion (Hiris & Blake, 1992; van der Smagt, Verstraten, & van de Grind, 1999). While the term ‘dynamic MAE’ is often used to cover MAEs found with both types of test stimuli, there is some evidence that they may reflect different mechanisms (Tao, Lankheet, van de Grind, & van Wezel, 2003).

There are a number of key differences between the static and dynamic MAE. On the one hand the static MAE is temporal-frequency tuned (Pantle, 1974), exhibits partial inter-ocular transfer (Moulden, 1980), displays a storage effect (Thompson & Wright, 1994), and is not induced by second-order motion (Anstis, 1980; Derrington & Badcock, 1985). Conversely, the dynamic MAE shows evidence of speed tuning (Ashida & Osaka, 1995), undergoes complete inter-ocular transfer (Nishida, Ashida, & Sato, 1994), does not exhibit a storage effect (Verstraten, Fredericksen, & van Wezel, 1996), and is induced by both first- and second-

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order motion (McCarthy, 1993). Consequently it is held that the dynamic and static MAEs reflect adaptation of different neural mechanisms (Verstraten, van der Smagt, Fredericksen, & van de Grind, 1999; Verstraten, van der Smagt, & van de Grind, 1998; von Grunau, 2002). It is thought that the static MAE reflects neural adaptation of low-level motion-sensitive neurons (Ashida & Osaka, 1995; Kohn & Movshon, 2003; Nishida & Sato, 1995; von Grunau, 2002), with cortical areas V1 and V2 (which are rich in local motion detectors) identified as likely sites. The dynamic MAE, on the other hand, is thought to reflect adaptation of higher-level neurons sensitive to global motions (Nishida & Ashida, 2000; von Grunau, 2002); such as the pattern cells in area MT/V5.

Investigations of the MAE have employed a wide range of measurements; including nulling techniques, duration estimation, speed matching, and apparent direction (Pantle et al., 1998). Apart from the latter, these measurements are not without their problems (Wade & Verstraten, 1998). In the case of the speed-matching paradigm, one is faced with the difficulty of matching the speed of a stimulus containing both real motion and displacement information, with a MAE that appears to move without displacement. This is particularly problematic in the case of the static MAE, but may be avoided in the case of the dynamic MAE. If one uses dynamic random dot test and comparison stimuli, with the comparison stimulus containing an appropriate mix of signal and noise dots, motion in the latter is perceptually indistinguishable from apparent motion in the test stimulus (Hiris & Blake, 1992).

The following experiments use a speed-matching task to investigate the dynamic MAE's speed tuning. While speed tuning of the dynamic MAE has been investigated before (Ashida & Osaka, 1995), to our knowledge no-one has used a speed-matching paradigm. The results of our first experiment reveal that the perceived speed of the dynamic MAE is speed tuned. Data from experiment two reveal that the speed tuning of the dynamic MAE is determined by the local speed characteristics of the test stimulus, not by the speed of the adaptation stimulus. This influence of the test stimulus on the perceived speed of the dynamic MAE correctly predicts that, if the test stimulus contains an appropriate speed mixture, a single speed adaptation stimulus can induce a transparent MAE. Our results show that the perceived speed of the dynamic MAE is determined by the local speeds of the test stimulus whilst its direction is clearly determined by the adaptor. In other words, motion adaptation primarily influences the encoding of direction rather than speed; suggesting some independence between mechanisms underlying these two attributes.

2. Experiment 1: Speed tuning of the dynamic MAE

2.1. Apparatus and stimuli

The adaptation and test stimuli were random dot kinematograms (RDK), presented within circular apertures

(6.3 deg^2), with each RDK containing equal numbers of black and white dots against a mean luminance background. Dot density in each stimulus was set to 64 dots/deg^2 . Stimuli were presented to subject W.C. on a Sony GDM-F500R monitor. Mean luminance was 72.6 cd/m^2 , and viewing distance was 141 cm. Stimuli were presented to subject C.B. and J.L. on a Sony CPD-G500 monitor. Mean luminance was 58.3 cd/m^2 , and the viewing distance was 138 cm. The different viewing distances ensured that stimuli subtended the same visual angle for each subject in the different experimental set-ups. Each monitor was driven by a Cambridge Research Systems VSG 2/5 graphics board at a frame rate of 80 Hz.

2.2. Procedure

We used a speed-matching task to measure the speed tuning of the dynamic MAE. During the initial motion adaptation phase (60 s duration) observers were presented with two random dot stimuli, each moving behind a viewing aperture. All dots in the adaptation stimulus moved in an upward direction (100% motion coherence); in the other stimulus each dot took a random walk (0% motion coherence), being assigned a randomly chosen direction on each frame. The two stimuli were positioned in opposite hemifields, with a fixation point located midway between. In the test phase immediately following adaptation the coherent motion stimulus was replaced with a 0% motion coherence stimulus, and a 35% motion coherence comparison stimulus appeared where previously there had been 0% motion coherence (see Fig. 1). In the comparison stimulus 35% of the dots in each frame translated in the predetermined coherent direction (opposite direction to the MAE); the remaining 'noise' dots took random walks at the same speed as the signal dots. The motivation for having the comparison stimulus move in the opposite direction to the perceived MAE direction was to minimise eye tracking behaviour.¹ Whether a dot translated coherently or in a random direction was re-determined on each frame. The motion coherence level for the comparison stimulus was chosen because it is perceptually indistinguishable from apparent motion in the dynamic MAE (Hiris & Blake, 1992).

The observers' task was to judge whether the induced MAE in the 0% coherence test stimulus was moving faster or slower than the 35% coherence comparison stimulus. Test phases, which lasted 1 s, alternated with adaptation 'top-up' phases of 10 s duration. MAE speed was measured as a function of co-varying the dot speed (i.e., step size) in the adaptation stimuli and the 0% coherence test stimulus. The comparison stimulus speed was chosen by an adaptive method-of-constants procedure (adaptive probit estimation),

¹ While having the comparison and the dynamic MAE moving in opposite directions may result in an overestimation of MAE speed, this should not interfere with the aims of the experiments reported here; which are to test whether the dynamic MAE is speed tuned and whether its speed tuning is determined by the adaptor or test stimulus speed.

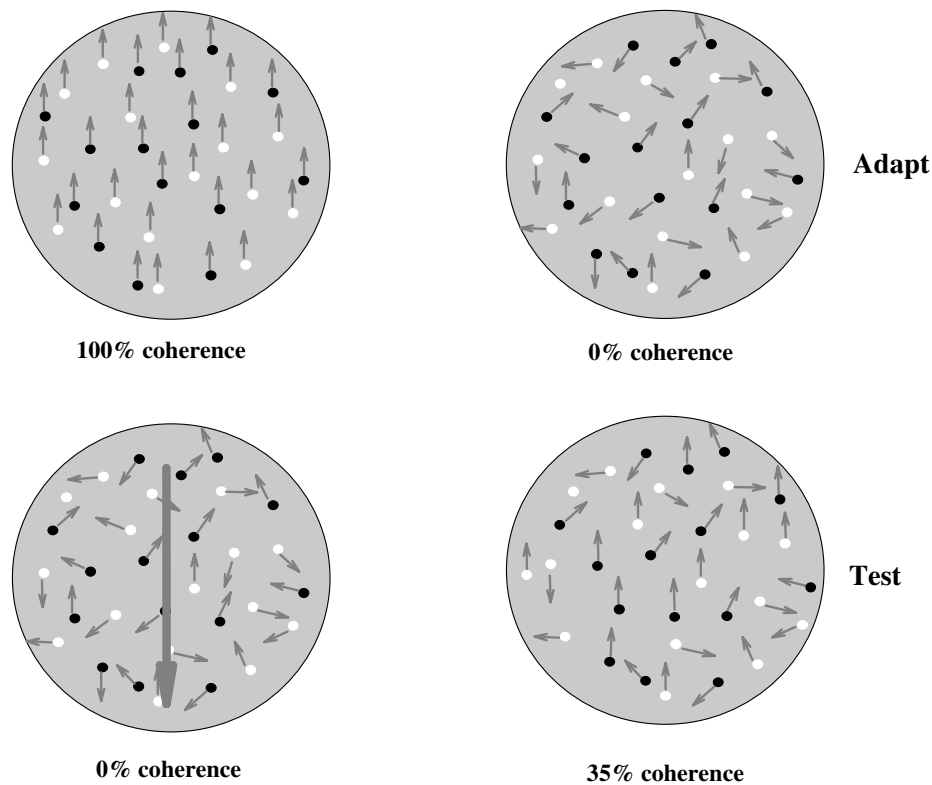


Fig. 1. The experimental procedure. After adaptation to coherent motion in one hemi-field (in this case, the left hemi-field), and 0% motion coherence in the opposite hemi-field, observers viewed a brief (1 s) presentation of a 0% and 35% coherent-motion stimuli. The grey line and arrow in the 0% coherence stimulus indicates the perceived direction of the MAE. The comparison stimulus, in which 35% of dots were uni-directional signal dots, moved in the opposite direction to the MAE and its speed varied from trial to trial (see Procedure). Observers judged which stimulus, the MAE or the comparison, was moving faster.

a method that dynamically updates the set of stimuli being presented depending on the observer's previous responses (Treutwein, 1995; Watt & Andrews, 1981). The stimulus values are selected to optimize the estimation of the 'point of subjective equality' (PSE), in our case the speed of the comparison set when it was perceived as moving at the same speed as the MAE.

Observers were tested with adaptation and test stimulus speeds ranging from 1 to 32 deg/s, and generated four psychometric functions per speed condition. Half the psychometric functions were generated following adaptation in each hemi-field; the interval between switching hemi-field adaptation was at least 4 h. The observer's PSE was taken as the average of the four PSEs, thus balancing for any potential side bias in responses. Data for each speed condition were collected on separate days.

2.3. Results and discussion

Fig. 2 plots the data from the speed tuning experiment, in which perceived MAE speed was measured as a function of *co-varying* the adaptor and dynamic test stimulus speed. These data reveal that the dynamic MAE is speed tuned. As noted above, the local speed information in the adaptation and test stimuli was always the same; thus it is not possible to determine whether the speed tuning

function is driven solely by the speed of the adaptation stimulus, or whether the test stimulus has a role to play. We attempted to answer this question in the next experiment.

3. Experiment 2: The influence of local speed information

The methods and procedure were the same as in experiment one, with one exception. Rather than co-varying dot speed in the adaptation and test stimuli, dot speed was fixed in one of the stimuli while MAE magnitude was measured as a function of varying dot speed in the other stimulus. Thus adaptation stimulus speed remained constant while dot speed in the test stimulus was varied, and vice versa. In order to avoid ceiling or floor effects, the fixed-speed stimulus in each condition was anchored at 8 deg/s for observers C.B. and J.L., and 4 deg/s for WC.

3.1. Results and discussion

Fig. 3 plots results for the test and adaptor speed conditions. The speed tuning functions generated in experiment one are included in the plots for comparison purposes. It is clear from these data that the speed tuning obtained when varying just the test stimulus local speed (Figs. 3a, c, and e) is almost identical to the original tuning functions of exper-

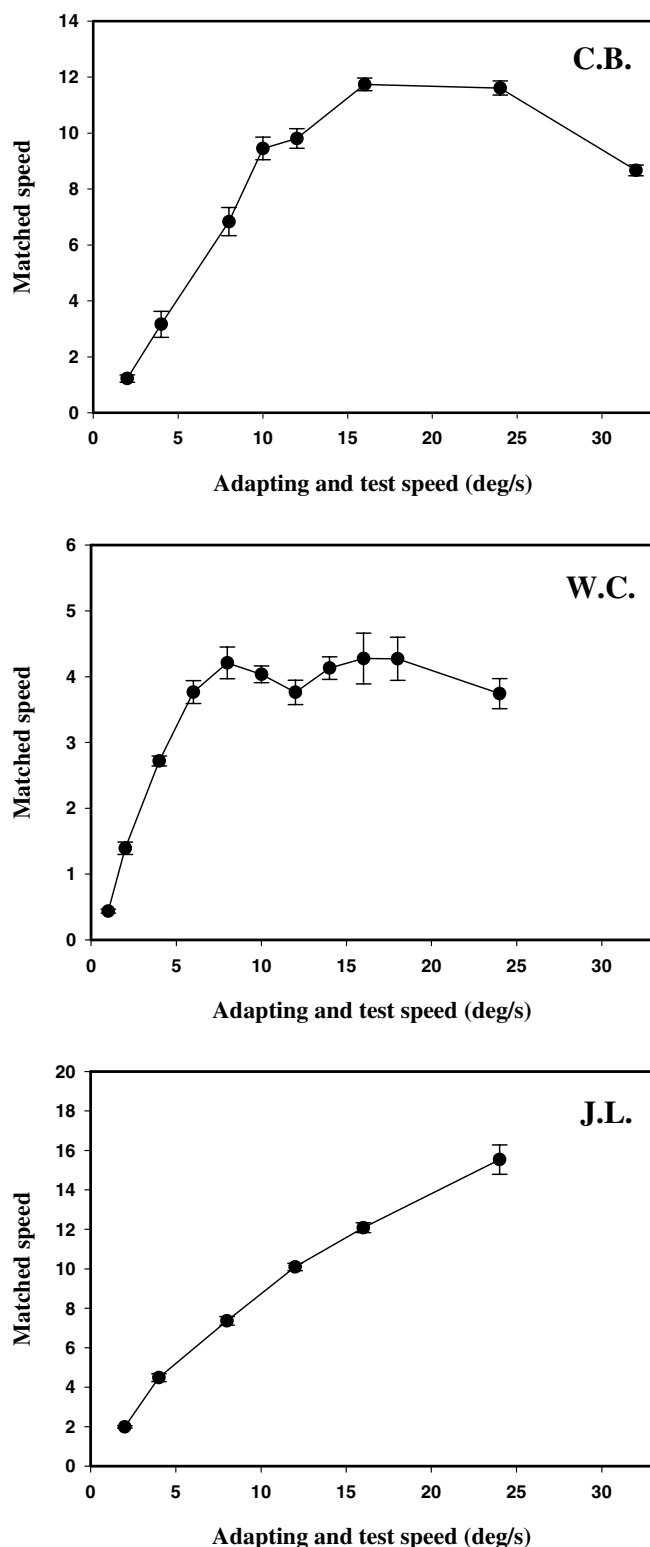


Fig. 2. Results from experiment one, in which the perceived speed of the dynamic MAE was measured as a function of co-varying local dot speed in both the adaptation and test stimuli. Each point is based on four PSEs (see Procedure) derived from 256 measurements (error bar: ± 1 SEM).

iment one. Data from the adaptor speed condition (test speed fixed while varying adaptor speed) contrast sharply with the former condition. For all observers, varying the

adaptor speed had little or no impact on the perceived speed of the dynamic MAE.

The results from our second experiment reveal that the perceived speed of the dynamic MAE in experiment one was largely determined by the local speed of the test stimulus. This leads to the following prediction. If, following motion adaptation, observers are presented with a test stimulus in which half the dots are assigned a slow speed and half are assigned a fast speed, then one should observe a transparent MAE with two dot sets appearing to move transparently in the same direction, but at different speeds.

We tested this prediction on a group of naïve observers. First of all observers were given a demonstration of the dynamic MAE with a single speed test stimulus. Those who reported experiencing a MAE² were then tested with a mixed speed test stimulus (2 and 10 deg/s) following adaptation to a single speed (4 deg/s). The observers were asked whether they saw one set of dots moving at the same speed, or two superimposed sets moving at different speeds. Nine of the ten observers tested reported seeing two superimposed dot sets—a slow set and a fast set—moving in the same direction. Having demonstrated the induction of a transparent MAE, we then measured the perceived speed of its two components. The adaptation pattern moved at 4 deg/s; half the dots in the test pattern moved at 2 deg/s, and half moved at 10 deg/s. Fig. 4 plots the perceived speed of the two transparent components. For both observers, particularly W.C., the perceived speeds of the slow and fast components are very similar to the MAE's apparent speed when all dots were either slow or fast (filled diamonds, taken from Experiment 1).

4. Discussion

The results from these experiments, in which perceived speed was used as a measure of the dynamic MAE, demonstrate a number of points. First, we have shown that the dynamic MAE is speed tuned. Second, we demonstrate that, while the dynamic MAE is necessarily induced by a moving adaptation pattern, the speed of the adaptation pattern appears to have little or no bearing on the perceived speed of the dynamic MAE. Rather, the apparent speed of the MAE appears to be determined solely by the local speed of the dynamic test pattern. Third, this dependence of apparent MAE speed on the speed characteristics of the test pattern correctly predicts that, if one uses a test stimulus containing slow and fast moving dots, a single speed adaptation pattern can induce a transparent MAE. This latter finding is reminiscent of the transparent MAE reported by van der Smagt et al. (1999), with some key differences; most notably, while van der Smagt et al. used a transparently moving adaptation pattern containing two speeds our adaptation pattern contained just the one speed. While the dot density of our stimuli was quite high (64 dots/

² Two observers did not experience a motion aftereffect when presented with a single-speed test stimulus and, therefore, were not tested with the two-speed test pattern.

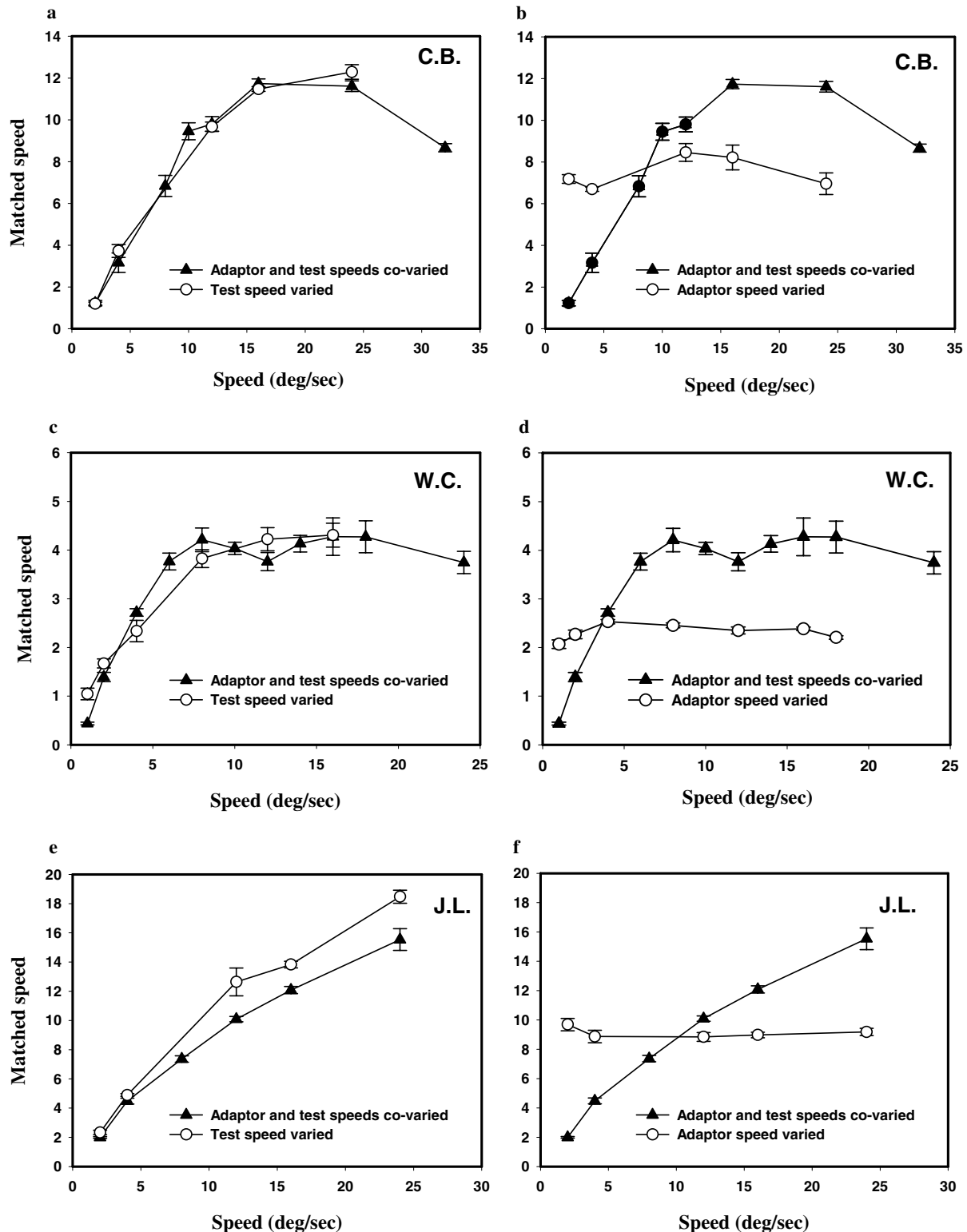


Fig. 3. Perceived speed of the dynamic MAE is plotted as a function of varying dot speed in the test stimulus (a, c, and e) and the adaptation stimulus (b, d, and f). The speed tuning functions from experiment one are included for comparison purposes (filled triangles). One can immediately see that the tuning functions generated when varying the test stimulus speed are practically indistinguishable from the original speed tuning functions. Varying the adaptation stimulus speed, on the other hand, has no noticeable effect on the apparent speed of the dynamic MAE.

deg²), it is considerably sparser than the dense random pixel arrays used by van der Smagt et al. It could be that the transparent MAE reported here is simply a consequence of

the relatively sparse dot density. However, informal viewing by the authors shows the effect to persist over a fourfold increase in dot density (256 dots/deg²).

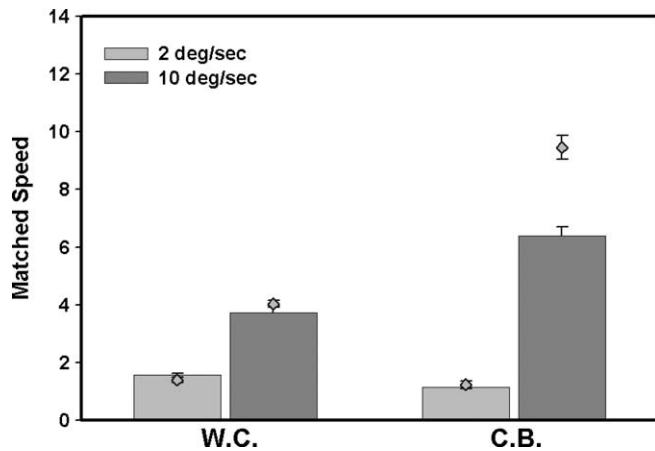


Fig. 4. The light grey and dark grey bars plot observers' perceived speed of the slow (2 deg/s) and fast (10 deg/s) components of the transparent motion aftereffect, respectively. Filled diamonds (taken from Experiment 1) plot perceived MAE speed when either test speed is used in isolation.

There is substantial evidence pointing to the existence of two partially overlapping speed channels, one which processes low speeds and one which processes high speeds (Snowden, 1990; Verstraten et al., 1996; Edwards, Badcock, & Smith, 1998). This proposed existence of two speed channels has been strengthened by a number of MAE studies (Verstraten et al., 1998, 1999; van der Smagt et al., 1999). Our finding of a transparent motion aftereffect is consistent with the notion of two overlapping speed-tuned channels. Whilst our mid-speed adaptor would presumably cause adaptation in both channels, the dual channel nature of the system would only be made perceptually evident through the presentation of our dual speed test stimulus.

Our main finding, that perceived speed of the dynamic MAE is determined by the motion characteristics of the test stimulus, adds to the debate on the mechanisms underlying direction and speed coding. Much of the evidence to date suggests that speed and direction are not encoded independently. For example, performance in speed and direction discrimination tasks is impaired following damage to macaque MT (Newsome & Paré, 1988; Orban, Saunders, & Vandenbussche, 1995). There is also psychophysical evidence that performance in both types of task is similarly affected by analogous stimulus manipulation. Thus a random dot stimulus containing a range of either mixed directions or mixed speeds drawn from a band-limited distribution is perceived as moving in the vector average direction (Williams & Sekuler, 1984) or the vector average speed (Watamaniuk & Duchon, 1992), respectively. In addition, co-variation of speed and direction discrimination has been reported (Festa & Welch, 1997), suggesting that they depend on the same underlying motion mechanisms.

There is, however, a small but growing body of evidence that speed and direction processing may not be as tightly linked as the above studies suggest. Matthews, Luber, Qian, and Lisanby (2001, 1999) report evidence of a double dissociation between direction and speed discrimination. On the one

hand direction discrimination is vulnerable to the 'oblique effect', while speed discrimination is not (Matthews & Qian, 1999). Conversely the medial application of transcranial magnetic stimulation results in a significant impairment of speed, but not direction, discrimination (Matthews et al., 2001). The data from our experiments reveal that, while its perceived direction is dependent on the motion direction of the adaptation stimulus, perceived speed of the dynamic MAE is largely independent of adaptation speed and remains constant across a range of adaptation speeds. The local speed of the dynamic test stimulus, on the other hand, determines the perceived speed of the MAE. This observed dissociation of speed and direction of the dynamic MAE provides additional evidence for a degree of independence between speed and direction processing by the visual system.

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