

## Psychophysical evidence for interactions between visual motion and form processing at the level of motion integrating receptive fields

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### ABSTRACT

Recent physiological and psychophysical research has challenged the traditional view that motion and form information are processed in distinct, parallel pathways in the visual system. Rapid movement creates 'motion-streaks' parallel to the motion trajectory, which facilitate motion detection. Some motion-selective neurons in striate and extrastriate cortex are sensitive to motion parallel to their preferred orientation, a possible neural substrate of motion-streak effects. As a psychophysical test of the cortical site of motion–form interactions, four experiments measured the duration and direction of the motion after-effect (MAE) generated by drifting dot fields in the presence of either vertical, horizontal or oblique counter-phase pedestal gratings. In Experiment 1 a single, horizontally drifting dot field was used; motion streak interactions predict stronger after-effects for horizontal gratings. Experiment 2 employed two transparently drifting dot fields (obliquely upwards and downwards), which produce a horizontal MAE. If motion–form interactions depend only on individual dot field trajectory, there should be no effect of grating orientation on MAEs after bi-directional adaptation. MAEs from both uni-directional and bi-directional adaptation were stronger using horizontal gratings than using vertical gratings. Experiments 3 and 4 found that an oblique pedestal did not alter the apparent direction of the MAE from bi-directional motion, despite the fact that it reduced MAE duration compared to a parallel pedestal. These results provide new evidence that the strength of adaptation to motion is affected by simultaneously presented orientation signals, and implicate motion integrating receptive fields in extrastriate cortex as the likely neural locus of this motion–form interaction.

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### 1. Introduction

The established view of functional architecture in the primate visual system is that processing of form and motion is segregated in distinct and parallel neural pathways (DeYoe & Van Essen, 1988; Goodale & Milner, 1992; Ungerleider & Mishkin, 1982; Zeki, 1990). However, there is growing evidence from both physiological and psychophysical studies that motion and form processes interact in the visual system. Striking psychophysical evidence of the interaction is provided by the motion-induced position shift illusion: When observing a static window that contains a drifting grating (Gabor), the apparent position of the window is shifted in the direction of motion (Chung, Patel, Bedell, & Yilmaz, 2007; De Valois & De Valois, 1991; Fu, Shen, Gao, & Dan, 2004; Mather & Pavan, 2009; McGraw, Whitaker, Skillen, & Chung, 2002; McGraw, Walsh, & Barrett, 2004; Pavan & Mather, 2008; Whitney, 2002). The existence

of the illusion suggests that motion-processing mechanisms induce local distortions in the positional map of the stimulus which is derived by form-processing mechanisms (Chung et al., 2007; Tsui, Khoo, & Hayes, 2007). On the other hand it has recently been shown that form information can, in turn, affect the extraction of motion information. In particular, the form information made available by motion-streaks (i.e., speed lines) influences motion processing (Barlow & Olshausen, 2004; Edwards & Crane, 2007; Geisler, 1999; Geisler, Albrecht, Crane, & Stern, 2001). When a feature such as a dot moves fast enough its neural representation becomes smeared in space along its motion trajectory, owing to the temporal integration period of neurons in the visual system. This smear creates a spatial signal (i.e., a motion-streak or a speed line) that contains information about the orientation of the motion trajectory, and which has been shown to facilitate motion detection. From a computational perspective, the streak could be extracted by the static orientation system and combined multiplicatively with the output of perpendicularly oriented direction-selective motion sensors (Geisler, 1999). The combined signal would carry information about both the orientation and the direction of a motion trajectory. Motion-streaks

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influence the perceived direction and speed of moving stimuli (Burr & Ross, 2002; Krekelberg, Dannenberg, Hoffmann, Bremmer, & Ross, 2003; Ross, 2004) and can also induce a tilt aftereffect following adaptation to fast translational motion (Apthorp & Alais, 2009).

Motion-streak effects raise an important question about the architecture of visual processing: At what level of processing does the interaction between form and motion processing take place? Motion-selective neurons are present in several cortical areas, including striate cortical area V1 and extrastriate area MT. V1 neurons are thought to sense the motion of local contours, while MT neurons integrate this local information to solve the aperture problem (Pack & Born, 2001; Pack, Livingstone, Duffy, & Born, 2003). It has been shown that some neurons in the striate cortex of cats and monkeys are sensitive to motion-streak information, in the sense that they respond to motion parallel to the preferred spatial orientation of the receptive field rather than to motion orthogonal to the orientation of the receptive field (Geisler et al., 2001; Jancke, 2000). MT neurons are direction selective, speed tuned and also exhibit orientation tuning (Albright, 1984; Albright, Desimone, & Gross, 1984; Baker, Petersen, Newsome, & Allman, 1981; Born, 2000; DeAngelis & Newsome, 1999; Diogo, Soares, Koulakov, Albright, & Gattass, 2003; Felleman & Kaas, 1984; Kaskan, Dillenburger, Lu, Roe, & Kaas, 2010; Lagae, Raiguel, & Orban, 1993; Maunsell & van Essen, 1983; Rosa & Elston, 1998; Tanaka et al., 1986). Some MT neurons are sensitive to motion parallel to their preferred orientation (Albright, 1984; Maunsell & van Essen, 1983), while others are sensitive to orthogonal motion (Kaskan et al., 2010; Maunsell & van Essen, 1983).

Thus there are potential neural substrates for motion-streak effects both at the level of motion sensors (V1) and at the level of motion integration (MT). The present study uses a psychophysical motion adaptation paradigm, namely the motion after-effect (MAE; see Mather, Pavan, Campana, & Casco, 2008 for review), to establish whether the stimulus dependency of motion-streak effects is consistent with an interaction at the level of motion sensing receptive fields or motion integrating receptive fields. In the first experiment we measured the duration of the MAE after adaptation to a dense spatial array of coherently drifting dots superimposed on a flickering grating (pedestal) oriented either parallel or orthogonal to the motion direction of the dots. The rationale was that if orientation information parallel to motion direction facilitates motion responses, as indicated by motion-streak effects, then MAE duration should be longer for parallel pedestals compared to orthogonal pedestals. A control condition was also included in which adapting dots were presented with no pedestal.

In the second experiment we measured the duration of the MAE after adaptation to two superimposed fields of transparently drifting dots, again in the presence of pedestal gratings, to determine whether orientation effects depend on the trajectory of the two component dot fields (coded by motion sensors such as those in V1) or on the combined direction of the two dot fields (coded by motion integrating receptive fields which have been found in MT). The two dot fields moved in orthogonal directions, one 45° above horizontal and the other 45° below horizontal, while the pedestal was presented either at a vertical or a horizontal orientation. Previous research has shown that orthogonally moving dot arrays are perceived as two clearly segregated and transparent dot fields during adaptation, but the perceived direction of the MAE is opposite the vector average (or vector sum) of the two motion components (Alais, Verstraten, & Burr, 2005; Mather, 1980; van der Smagt, Verstraten, & van de Grind, 1999; Verstraten, Fredericksen, & van de Grind, 1994; Verstraten, van der Smagt, Fredericksen, & van de Grind, 1999; von Grünau, 2002). The direction of the MAE from such bi-directional adaptation is usually attributed to processes operating at the level of motion integration (MT; e.g., Alais et al., 2005).

If the motion-form interaction also occurs at the motion integration stage, and if Experiment 1 finds that parallel pedestals produce longer MAEs than perpendicular pedestals using single dot fields, then the prediction for Experiment 2 is that the horizontally oriented pedestal should produce longer MAEs than the vertically oriented pedestal, because the horizontal pedestal is parallel to the vector-average MAE direction. On the other hand, if motion-form interactions occur at the level of motion sensors (e.g., V1), and are therefore tied to the trajectory of the component dot fields, then there should be no difference in MAE duration between horizontal and vertical pedestals, because in both cases the grating is 45° away from the component motion trajectories.

## 2. Experiments 1 and 2

### 2.1. Methods

#### 2.1.1. Participants

One author and nine naïve observers participated in the experiments. All participants had normal or corrected-to-normal visual acuity, participated voluntarily with no compensation and gave their informed consent prior to their inclusion in the experiment.

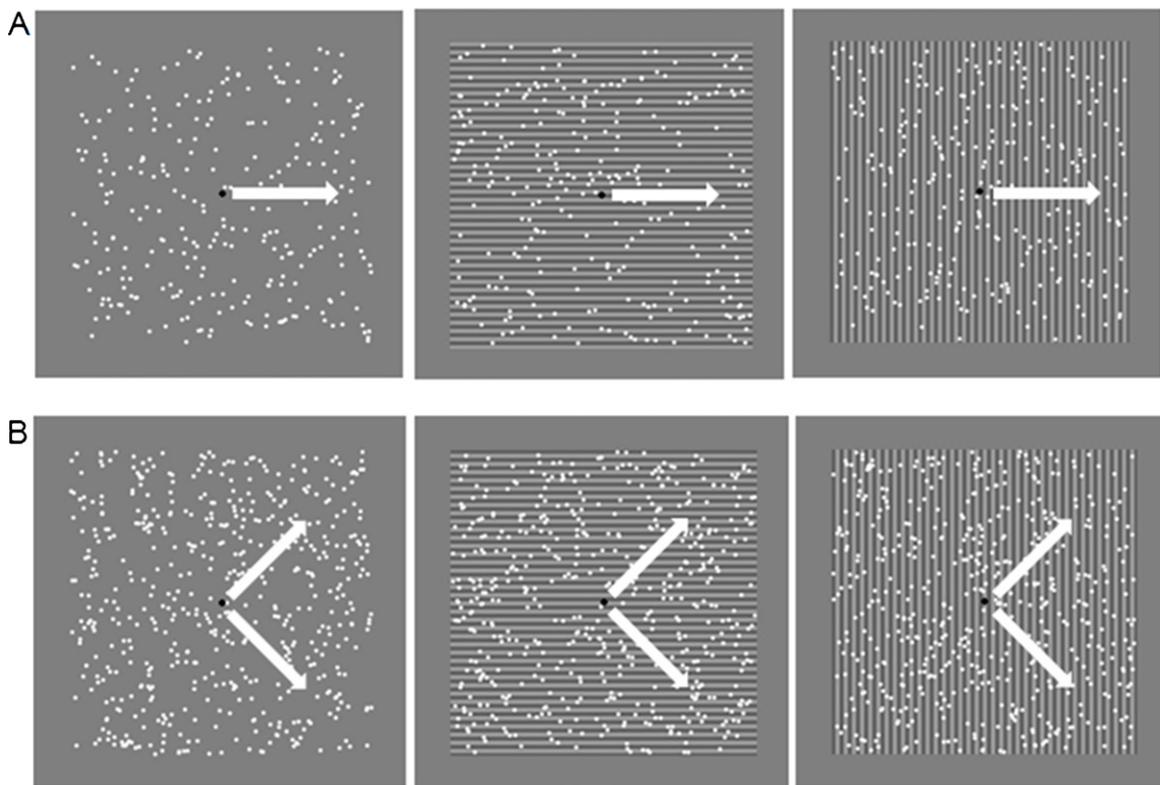
#### 2.1.2. Apparatus

Subjects sat in a dark room with their head resting on a chin rest fixed 57 cm from the display screen. Viewing was binocular. Stimuli were displayed on a 19 in. CTX CRT Trinitron monitor with a refresh rate of 75 Hz, and generated with Matlab Psychtoolbox (Brainard, 1997; Pelli, 1997). The screen resolution was 1280 × 1024 pixels. Each pixel subtended 182 arcmin. The mean luminance was 467 cd/m<sup>2</sup>, measured using a Minolta LS-100 photometer. Stimuli were generated using a gamma-corrected lookup table (LUT) to ensure display linearity.

### 2.2. Stimuli

Three different adapting stimuli were employed in Experiment 1: (i) a field of drifting dots; (ii) a field of drifting dots with superimposed pedestal grating oriented parallel to dot trajectory; (iii) a field of drifting dots with superimposed pedestal grating oriented orthogonal to dot trajectory. The dot field consisted of a dense spatial array of 266 coherently moving white dots (101 cd/m<sup>2</sup>) displayed within a square window (92 × 92°) at the center of the screen (density: 314 dot/deg<sup>2</sup>). The mean luminance of the background was set at 467 cd/m<sup>2</sup>. The diameter of each dot was 0.121° (4 pixels), and all dots moved at 91°/s in steps of 0.121° (4 pixels). This speed is associated with motion smear effects (Geisler, 1999), so should ensure activation of motion-sensitive neurons involved on motion-form interactions. Dots had a limited lifetime; that is, after 506 ms (448° path length, 37 steps) each dot vanished and was replaced by a new dot at a different randomly selected position within the square window. In addition, moving dots that traveled outside the window were wrapped around to the opposite edge. All dots moved either leftward or rightward.

The pedestal grating subtended 92 × 92° and overlapped with the window containing the dot field (Fig. 1A). The grating had a spatial frequency of 4 cpd (i.e., bar width matching the diameter of a dot) and was counter-phase flickered at 1 Hz to avoid the build-up of after-images. The Michelson contrast of the grating was set at 0.3. The same pedestal gratings were used in Experiment 2, but the dot field in this experiment consisted of two arrays of dots moving simultaneously and transparently in orthogonal directions (i.e., 45 and 315°, or 135 and 225°) (Fig. 1B). Adaptation to these bi-directional dot fields produced a single, apparently horizontally moving MAE. Pedestal grating orientation was either vertical or



**Fig. 1.** (A) Example of the adapting pattern in Experiment 1: 266 white dots (diameter  $0.125^\circ$ ) moving coherently either rightward (with arrow) or leftward (not shown). The left panel shows the condition with no pedestal grating, the middle panel shows rightward moving dots on a horizontal pedestal, and the right panel shows moving dots on a vertical pedestal. (B) Example of the adapting pattern in Experiment 2: 532 coherently moving dots, half of which moved at  $45^\circ$ , and half at  $315^\circ$  (white arrows) (we also used the opposite condition – not shown – in which half of the dots moved at  $135^\circ$  and the other half at  $225^\circ$ ).

horizontal, and therefore always  $45^\circ$  away from each dot field trajectory, but either parallel or orthogonal to the resulting MAE. Each dot array contained 266 dots, with all parameters matching those in Experiment 1.

For Experiment 1 The test stimulus consisted of a static dot array at the same density as the adapting stimulus (266 dots in Experiment 1, 532 dots in Experiment 2, both  $92 \times 92^\circ$ ) without a pedestal grating.

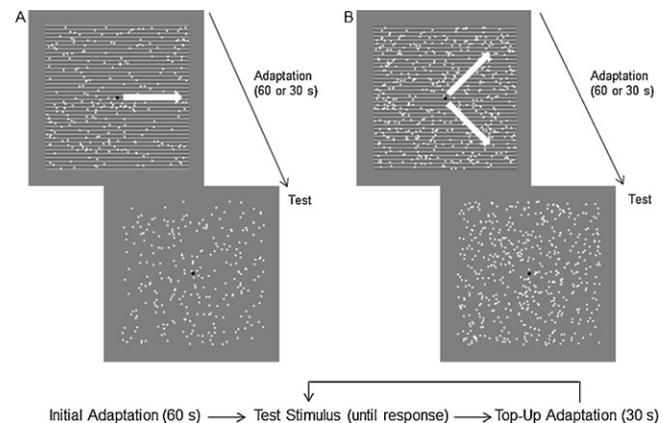
### 2.3. Procedure

Participants were instructed to fixate on a black spot ( $0.2^\circ$ ,  $0.21 \text{ cd/m}^2$ ) positioned at the center of the screen and were given initial training to familiarize them with the stimuli and the task. In Experiment 1 each experimental session began with an initial adaptation period of 60 s, followed immediately by the test stimulus that lasted until the participant's response. Participants were instructed to maintain fixation on the central black spot and to press the spacebar when any motion aftereffect they saw in the test pattern ceased. Then, after a one-second pause, adaptation periods of 30 s alternated with test presentations and MAE measures (Fig. 2A). Experimental conditions were blocked; the direction of adaptation and, if present, grating orientation were kept constant within each block. Experiment 1 involved 6 blocks: 3 pedestal conditions (i.e., no pedestal, parallel pedestal and orthogonal pedestal)  $\times$  2 motion directions (i.e., leftward and rightward). Each block contained 11 trials. The procedure for Experiment 2 was the same as Experiment 1, 6 blocks were presented: 3 pedestal conditions (i.e., no pedestal, pedestal parallel to MAE direction, and pedestal orthogonal to MAE direction)  $\times$  2 MAE directions. A leftward MAE was obtained following adaptation to the  $45$  and  $315^\circ$  components and a rightward MAE following adaptation to the  $135$  and  $225^\circ$  components.

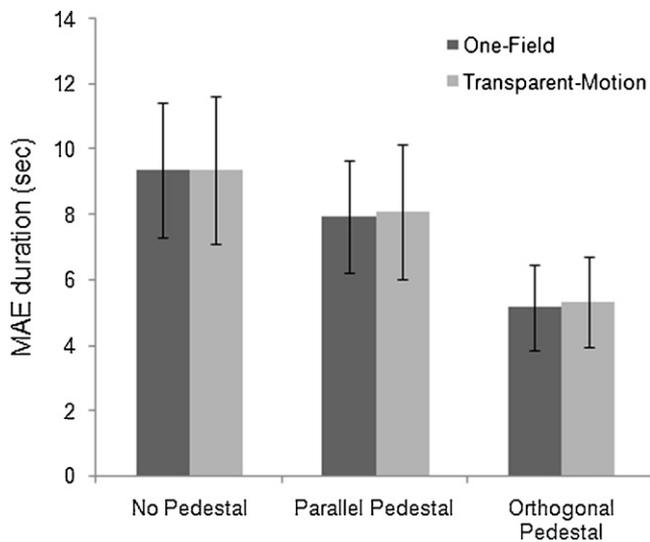
## 3. Results

### 3.1. Duration data

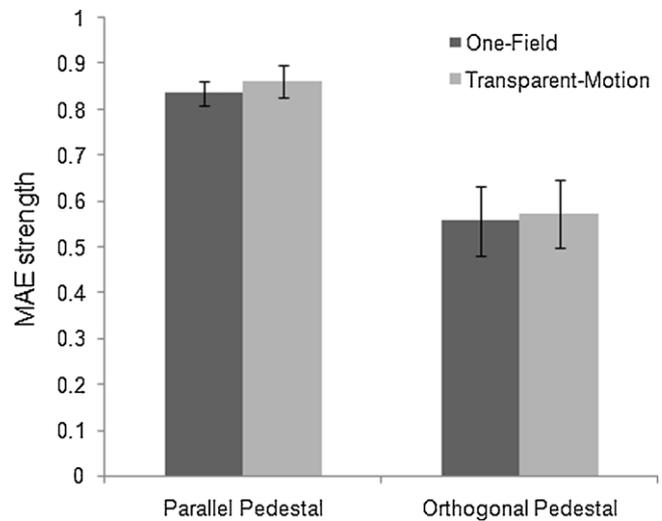
There was no difference between results for leftward and rightward adapting directions, so data were collapsed across adapting direction. Fig. 3 shows mean MAE duration in all the conditions across the two experiments. A two-factor repeated measures ANOVA was conducted, including Motion Type (uni-directional vs.



**Fig. 2.** Adapting procedure. (A) Experiment 1: subjects adapted to a field of 266 coherently moving dots (either leftward or rightward). Panel A shows the condition in which dots move rightward on a parallel pedestal grating. The test pattern was a field of 266 stationary dots and lasted until a participant's response. (B) Experiment 2: subjects adapted to two fields of transparently moving dots (each field of 266 dots). Panel B shows the condition in which one field moved at  $45^\circ$  and the other at  $315^\circ$ . The test pattern was a field of 532 stationary dots. Following 60 s of adaptation (the first trial) or 30 s of top-up adaptation, a stationary test pattern was presented.



**Fig. 3.** Mean MAE duration (s) after adaptation to either a single field of moving dots or two fields of transparently moving dots, with no pedestal and with pedestal oriented either parallel (horizontal) or orthogonal (vertical) with respect to the direction of uni-directional dots or to the vector average direction of bi-directional dots. Error bars  $\pm$  SEM.



**Fig. 4.** Normalized data. Normalization was calculated as the ratio between the duration of the MAE in each pedestal condition and the duration in the no pedestal condition. Error bars  $\pm$  SEM.

bi-directional motion), and Pedestal Condition (no pedestal, parallel pedestal and orthogonal pedestal) as factors. There was a highly significant effect of Pedestal ( $F(2,18)=959$ ,  $p=0.001$ ,  $\eta^2=0.52$ ), but no significant effect of Motion Type and no significant interaction between Motion Type and Pedestal ( $F(1,9)=0.031$ ,  $p=0.86$ ,  $\eta^2=0.003$  and  $F(2,18)=0.04$ ,  $p=0.96$ ,  $\eta^2=0.004$ , respectively). Simple and repeated contrasts revealed significant differences between the no pedestal condition and the parallel pedestal condition ( $F(1,9)=1364$ ,  $p=0.005$ ,  $\eta^2=0.6$ ), the no pedestal condition and the orthogonal pedestal condition ( $F(1,9)=10.62$ ,  $p=0.01$ ,  $\eta^2=0.54$ ), and the parallel pedestal condition and the orthogonal pedestal condition ( $F(1,9)=751$ ,  $p=0.023$ ,  $\eta^2=0.45$ ). In addition, the repeated measures ANOVA reported a significant effect of the Subjects factor ( $F(1,9)=1928$ ,  $p=0.002$ ,  $\eta^2=0.68$ ).

### 3.2. Normalized data

We calculated the ratios of the duration of the MAE in the parallel and orthogonal pedestal conditions with respect to the duration of the MAE in the no pedestal condition (Fig. 4), as a measure of the relative strength of adaptation in the two pedestal conditions. A repeated measures ANOVA treating Motion Type and Pedestal Orientation as factors found a significant effect of pedestal orientation ( $F(1,9)=1765$ ,  $p=0.002$ ,  $\eta^2=0.66$ ), but no significant effect of Motion Type ( $F(1,9)=0.32$ ,  $p=0.58$ ,  $\eta^2=0.034$ ). Simple contrasts revealed a significant difference between the parallel pedestal condition and the orthogonal pedestal condition ( $F(1,9)=1765$ ,  $p=0.002$ ,  $\eta^2=0.66$ ). The ANOVA reported a significant effect of the Subjects factor ( $F(1,9)>100$ ,  $p=0.0001$ ,  $\eta^2=0.97$ ).

## 4. Discussion

The results of the first experiment showed that addition of a grating pedestal to a single drifting dot field significantly reduced the duration of the MAE relative to control conditions without a pedestal, regardless of pedestal orientation. Importantly, the reduction was much greater (44%) using a pedestal oriented orthogonally to the direction of the single dot field than when using a parallel pedestal (16%). The longer MAE duration obtained with parallel versus orthogonal pedestals is consistent with a motion-form interaction which favours orientation signals parallel

to the motion trajectory (usually provided by motion-streaks). Most importantly, we obtained virtually identical effects of pedestals on MAE duration using bi-directionally transparent adapting motion, with reductions of 43% and 13% in orthogonal and parallel conditions respectively. This latter result supports the view that the underlying motion-form interaction occurs after the point at which the two component motions are integrated into a single motion trajectory which corresponds to the axis of apparent motion seen in the MAE, most likely in extrastriate area MT.

Experiments 3 and 4 provided additional tests of the hypothesis that motion-form interactions occur after motion integration. Both experiments employed only bi-directionally transparent adapting fields, as used in the second experiment, but examined the effects of an obliquely oriented pedestal that matched the motion axis of one of the adapting components. Experiment 3 measured the direction of the MAE following bi-directional motion with or without an oblique pedestal. In the absence of a pedestal the MAE from our bi-directional stimulus should appear to move horizontally, as stated earlier. If the effect of the oblique pedestal occurs at the component level, the results of Experiment 1 show that it should favour the signal generated by the parallel component relative to that generated by the orthogonal component, and should thus bias the direction of the resulting MAE towards the direction of the parallel component in the bi-directional adapter. On the other hand, if the motion-form interaction occurs after the point at which component signals are integrated to compute a combined direction, then there should be no shift in apparent MAE direction following adaptation containing an oblique pedestal; the MAE from bi-directional adaptation should appear to move horizontally both with and without the oblique pedestal. However, since the pedestal does not match the combined (horizontal) direction of the bi-directional stimulus, it should produce a shorter MAE than that obtained using a parallel pedestal. Experiment 4 tested this prediction by measuring MAE duration following bi-directional adaptation involving parallel, orthogonal and oblique pedestals (a partial replication of Experiment 2).

## 5. Experiment 3

### 5.1. Method

#### 5.1.1. Participants

Two authors and eight naïve observers participated in Experiment 3. All participants had normal or corrected-to-normal visual

acuity, participated voluntarily with no compensation and gave their informed consent prior to their inclusion in the experiment.

### 5.1.2. Apparatus

The apparatus was the same used in the previous experiments.

### 5.2. Stimuli

Bi-directional adapting stimuli and stationary test stimuli were the same as those employed in Experiments 1 and 2, with the following exceptions. Only two stimulus conditions were used, a control condition containing no pedestal and an experimental condition containing an obliquely oriented pedestal (45 or 135°) which matched the motion axis of one component in the bi-directional dot field. A black fixation dot was continuously present at the center of the stimulus, as before. A second black dot (diameter 0.2°) appeared during testing, positioned around the circumference of a virtual circle (radius 56°) centered on the fixation spot. The position of this spot around the virtual circle was under the control of the participant.

### 5.3. Procedure

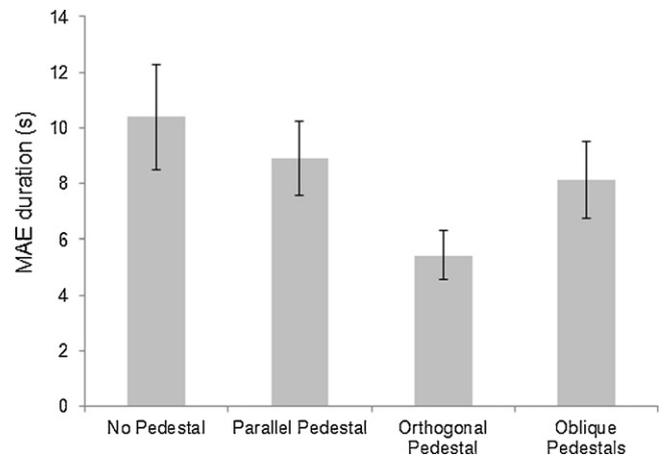
Participants were instructed to fixate the central black spot at all times. Each experimental session began with an initial adaptation period of 60 s, followed immediately by the test stimulus that lasted until the participant made a response. Then, after a one-second pause, adaptation periods of 30 s alternated with subsequent test presentations. After each adaptation period participants were instructed to set the circumferential position of the black dot relative to fixation so that it matched the direction of the MAE. The position of the dot was adjusted using the left and right arrows of the computer keyboard. Its initial position at the start of a trial varied randomly from trial to trial. Participants indicated that a direction setting had been made by pressing the keyboard's SPACE bar. The experiment consisted in 6 blocks: 3 pedestal conditions (i.e., no pedestal, 45° pedestal and 135° pedestal) × 2 MAE directions. Each block consisted of 11 trials. The direction of adaptation and, if present, the orientation of the pedestal were varied between blocks.

## 6. Results

Each participant's direction setting was averaged across their repeated observations in each condition, and then the group average direction setting was calculated. For rightwards moving bi-directional dot fields (combined direction at zero°) the group mean directional setting was 1799° (SE 0.74°) in the control condition (no pedestal), and 1791° (SE 0.6°) in the experimental condition (oblique pedestal). For leftwards moving adapters (combined direction 0°), average MAE directions were -0.054° (SE 0.73°) in the control condition and -0.96° (SE 113°) in the experimental condition. A repeated measures ANOVA found no significant difference between control and experimental settings (Rightward:  $F(1,9) = 117$ ,  $p = 0.31$ ,  $\eta^2 = 0.12$ ; leftward:  $F(1,9) = 192$ ,  $p = 0.2$ ,  $\eta^2 = 0.18$ ). In addition, the repeated measures ANOVA found a significant effect of the Subject factor for leftwards moving adapters but not for rightwards adapters (Leftward:  $F(1,9) > 100$ ,  $p = 0.0001$ ,  $\eta^2 = 0.99$ ; rightward:  $F(1,9) = 0.35$ ,  $p = 0.57$ ,  $\eta^2 = 0.037$ ).

## 7. Discussion

As predicted by the hypothesis that motion-form interactions occur after motion integration, oblique pedestals had no effect on the direction of the MAE produced by bi-directional adaptation.



**Fig. 5.** Mean MAE duration (s) after adaptation to two fields of transparently moving dots, with either no pedestal, with pedestal oriented parallel or orthogonal to the vector average (or vector sum) of the two moving components, and with oblique pedestals oriented parallel to one moving component. Error bars  $\pm$  SEM.

Such pedestals should nevertheless modulate MAE duration, producing an after-effect that is intermediate between those obtained with pedestals parallel and orthogonal to the integrated direction of the bi-directional stimulus. The final experiment tested whether that the oblique adapter used in Experiment 3 does indeed modulate MAE duration between the extreme values produced by parallel and orthogonal pedestals.

## 8. Experiment 4

### 8.1. Methods

#### 8.1.1. Participants

Two authors and eight naïve observers participated. All participants had normal or corrected-to-normal visual acuity, participated voluntarily with no compensation and gave their informed consent prior to their inclusion in the experiment.

#### 8.1.2. Apparatus

The apparatus was the same as in the previous Experiments.

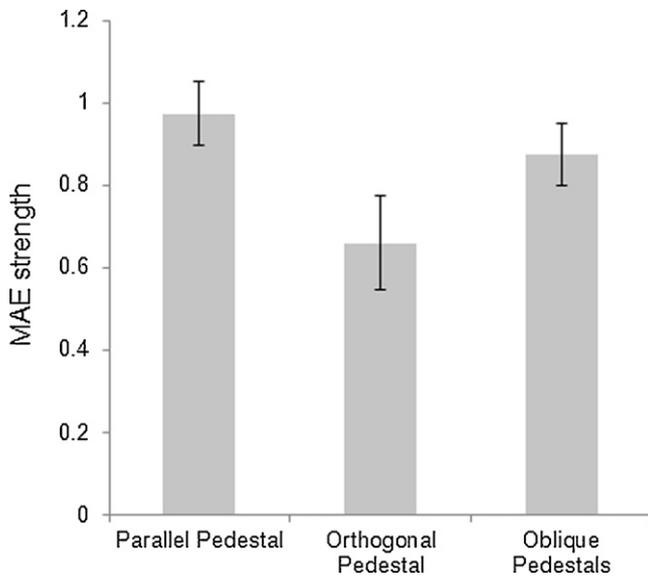
### 8.2. Stimuli and procedure

Adapting stimuli were a sub-set of the bi-directional stimuli used in previous experiments. Test stimuli were the same as those used in previous bi-directional experiments. Four different adapting conditions were employed, all involved bi-directional dot fields and differed in terms of the pedestal: (i) no pedestal (i.e., control condition); (ii) horizontal pedestal (i.e., parallel to MAE direction); (iii) vertical pedestal (i.e., orthogonal to MAE direction); (iv) oblique pedestal (i.e., parallel to one motion component and orthogonal to the other, 45 or 135°). The procedure for Experiment 4 was the same as in Experiments 1 and 2 10 blocks were presented, five pedestal conditions (as above; two oblique orientations) × 2 MAE directions.

## 9. Results

### 9.1. Duration data

There was no significant difference between results for leftward and rightward adapting directions, or for the two oblique pedestals, so data were collapsed across these conditions. Fig. 5 shows mean MAE duration in each pedestal condition. MAEs were longest in the control condition (mean 10.38 s) and shortest in the orthogonal



**Fig. 6.** Normalized data. Normalization was calculated as the ratio between the duration of the MAE in the pedestal conditions and the duration in the no pedestal condition. Error bars  $\pm$  SEM.

condition (543 s). Parallel pedestals generated a MAE of 892 s. The oblique pedestals generated MAEs that were intermediate between those in the parallel and orthogonal conditions (812 s). The effect of stimulus condition was highly significant according to a repeated measures ANOVA ( $F(3,27) = 858, p = 0.0001, \eta^2 = 0.49$ ). Importantly for the predictions above, paired contrasts revealed that the intermediate MAE obtained for the oblique pedestal was significantly different from the MAEs obtained in both other pedestal conditions (oblique pedestals vs. parallel pedestal:  $F(1,9) = 648, p = 0.031, \eta^2 = 0.42$ ; oblique pedestals vs. orthogonal pedestal:  $F(1,9) = 783, p = 0.021, \eta^2 = 0.47$ ). The repeated measures ANOVA also reported a significant effect of the Subjects factor ( $F(1,9) = 4599, p = 0.0001, \eta^2 = 0.84$ ).

### 9.2. Normalized data

We calculated the ratios of the duration of the MAE in the parallel, orthogonal and oblique pedestal conditions with respect to the duration of the MAE in the no pedestal condition (Fig. 6), as a measure of the relative strength of adaptation in the pedestal conditions. Results for the parallel and orthogonal pedestals replicated those obtained in Experiment 2, with reductions of 141% and 476% respectively (135% and 431% in Experiment 2, respectively). The reduction in MAE duration using oblique pedestals was 218%, intermediate between the effects in the other two conditions. The repeated measures ANOVA also reported a significant effect of the Subjects factor ( $F(1,9) = 9635, p = 0.0001, \eta^2 = 0.92$ ).

## 10. Discussion

The results of Experiment 4 confirm that oblique pedestals do modulate the resulting MAE duration, producing an effect intermediate between those obtained with parallel and orthogonal pedestals. Thus the lack of an effect of oblique pedestals on MAE direction obtained in Experiment 3 cannot be due to the fact that oblique pedestals behave in a way which is equivalent to either parallel or orthogonal pedestals. The lack of an effect of apparent direction, paired with a significant effect on MAE duration, supports the hypothesis that pedestal effects represent motion–form interactions occurring after motion integration.

## 11. General discussion

Data from a series of four experiments indicate that pedestal gratings modulate motion adaptation in a way that is consistent with the motion–form interactions which underlie motion streak effects, namely boosting motion responses parallel to contour orientation compared to responses orthogonal to orientation. Furthermore, this interaction occurs after the stage at which local motion signals are integrated to compute pattern motion, probably in extrastriate area MT. The crucial evidence bearing on the latter point comes from two results. First, orientation tuned pedestal effects depend on the combined direction of a bi-directional adapting stimulus, not on the directions of its components. Second, pedestals do not alter the apparent direction of the MAE from bi-directional motion. It makes good computational sense for the motion–form interaction underlying motion streaks to occur at motion integration, because only at this stage can the interaction augment responses to actual pattern motion, rather than the unstable responses to individual motion components. Indeed, motion streak interactions can serve to disambiguate local motion signals and so help to solve the aperture problem, but only if they are applied at the motion integration stage (see Albright, 1984; Geisler, 1999; Pack & Born, 2001). By their very nature, motion streaks always point in the direction of pattern motion.

Although parallel pedestals produce longer adaptation than orthogonal pedestals, consistent with motion–streak facilitation, both kinds of pedestal reduce MAE duration compared to control conditions with no pedestal. This effect is consistent with a gain control or normalizing mechanism in which the outputs of motion sensors are suppressed by activity in neighbouring receptive fields. This normalization may be the mechanism that produces the adaptation itself (van de Grind, Verstraten, & van der Smagt, 2003; van de Grind, van der Smagt, & Verstraten, 2004). There is both physiological and psychophysical evidence for such response normalization (e.g., Georgeson & Scott-Samuel, 1999; Heeger, 1992; Rainville, Scott-Samuel, & Makous, 2002). Rainville et al. (2002) measured motion discrimination thresholds for drifting gratings as a function of the orientation and spatial frequency of simultaneously presented counter-phase flickering mask gratings. They found that suppression, as measured by threshold elevation, was maximal for masks at the same orientation as the drifting grating and minimal at the orthogonal orientation. Rainville et al. (2002) identified area MT as the principle cortical area involved in such normalization (c.f., Heeger, Boynton, Demb, Seidemann, & Newsome, 1999).

In conclusion, a growing body of research now supports the view that motion and form signals interact extensively during visual processing. Previous psychophysical research has shown that orientation signals generated by motion streaks can affect detection thresholds for moving stimuli (Burr & Ross, 2002; Edwards & Crane, 2007; Geisler, 1999). Perceived position can in turn be affected by prior adaptation to motion (McGraw et al., 2002). Results presented here provide new evidence that the strength of adaptation to motion is affected by simultaneously presented orientation signals, and implicates motion integrating receptive fields in extrastriate cortex as the likely neural locus of this interaction. A plausible function of the interaction is to facilitate motion responses that identify the direction of object motion, and hence solve the aperture problem.

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