



# Motion after-effect due to binocular sum of adaptation to linear motion

Alexander Grunewald <sup>a,\*</sup>, Ennio Mingolla <sup>b</sup>

<sup>a</sup> *Division of Biology, California Institute of Technology, Mail code 216-76, Pasadena, CA 91125, USA*

<sup>b</sup> *Department of Cognitive and Neural Systems, Boston University, 677 Beacon Street, Boston, MA 02215, USA*

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## Abstract

The motion after-effect (MAE) can be elicited by adapting observers to global motion of randomly distributed dots before they view a display containing dots moving in random directions, but no global motion. Experiments by others have shown that if the adaptation stimulus contains two directions of motion, the MAE points opposite to the vector sum of the adapting directions. The present study investigated whether such vector addition in the MAE could also occur if the two directions of motion were presented to separate eyes. Observers were adapted to different, but not opposite, directions of motion in the two eyes. Either the left eye, the right eye, or both eyes were tested. Observers reported the direction of perceived motion during the test. When they saw the test stimulus with both eyes, observers reported seeing motion in the direction opposite that of the vector sum of the adaptation directions. In the monocular test conditions observers reported MAE directions opposite to the corresponding monocular adaptation directions. In a second experiment we verified that subjects had interocular transfer of the MAE. Together these results are consistent with a model in which (1) addition of adaptation directions occurs at a binocular site; (2) directional adaptation occurs at a monocular site; and (3) monocular adaptation is able to change the threshold for obtaining an MAE at the binocular site, thus acting like binocular adaptation in interocular transfer of the MAE. © 1998 Elsevier Science Ltd. All rights reserved.

*Keywords:* Motion perception; Motion after-effect; Motion direction; Monocular motion after-effect; Binocular motion after-effect; Vector sum; Interocular transfer

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## 1. Introduction

Motion presented to one eye during an adaptation period leads to a motion after-effect (MAE), the perception of motion in the opposite direction, upon subsequent viewing of a stationary test stimulus in the same eye [1]. In the present report an MAE refers to an observer's perception of motion. It does not refer to a particular site of adaptation within the visual system. Thus, the MAE phenomenon is taken to result from motion adaptation at one or more of several motion representations. The interactions within the binocular motion representation can be studied by adapting observers binocularly to bivectorial motion, which is a motion display containing two different directions of motion [2–4]. Observers perceive motion opposite to the

vector sum of the two adaptation motions during testing, which is paradoxical, because during adaptation observers perceive transparent motion. Apparently some part of the visual motion processing system is able to distinguish between real motion and the MAE. When using stationary test patterns observers do not mistake the MAE for real motion, but when test displays are used which contain dynamic noise the MAE is indistinguishable from real motion [5,6]. Evidently at the motion detection stage the MAE is indistinguishable from real motion, while at the integration stage a clear distinction is made between MAE and real motion. Thus to explain the MAE one has to assume at least two stages: a motion detection stage, and a motion integration stage. Several models have been proposed to explain how the integration stage combines inputs from the detection stage. All models have in common the idea that motion detectors fatigue when they are stimulated with the same type of motion for a prolonged period of time.

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\* Corresponding author. Tel.: +1 626 3958337; fax: +1 626 7952397; e-mail: alex@vis.caltech.edu.

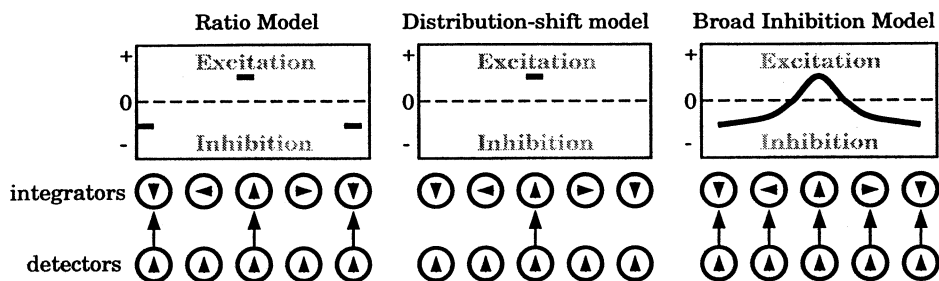


Fig. 1. Comparison of the net excitatory and inhibitory input from adaptable motion detectors to motion integrators in different MAE models. Left: ratio model; middle: distribution-shift model; right: broad inhibition model. The circles in the bottom half of each model denote direction selective units of preferred direction indicated by the arrows inside the circles. The bottom row of circles denotes motion detectors while the top row of circles denotes motion integrators. The arrows between circles indicate the connections that are postulated to exist in each model between motion detectors of a particular direction preference and motion integrators of all direction preferences. Analogous connections also exist for motion detectors of other motion preferences. The sign and strength of the connections between motion detectors and motion integrators are indicated by the graph at the top portion of each model description.

The ratio model states that motion detectors excite motion integrators of same direction preference and inhibit motion integrators of opposite direction preference [7]. This is illustrated in Fig. 1. Fatiguing of a motion detector for the stimulus direction un masks activity in a motion integrator coding motion in the opposite direction, thus causing the MAE. The distribution-shift model asserts that the MAE occurs because the distribution of activities within a motion representation changes due to adaptation [2]. There are no inhibitory interactions in this model, and thus the integration stage is just a (smoothed) copy of the detection stage (Fig. 1). Following adaptation motion detectors of the adaptation direction send below-baseline input to the motion integrators, thus causing (relatively) enhanced activity in the opposite direction. In the broad inhibition model motion detectors excite motion integrators of similar direction preference, and inhibit all motion integrators [8]. The strength of this inhibition peaks at units of opposite direction preference, and falls off gradually with a decrease in the angular difference between the direction preference of motion detectors and motion integrators. The net input of any motion integrator is the sum of its inhibitory and excitatory input. The model is set up such that the net input from motion detectors is excitatory for similar directions, and inhibitory for opposite directions, with a gradient between them. The MAE arises because the inhibition is peaked at the opposite direction of motion, and falls away following adaptation, leading to maximal activation at units having opposite direction preference. A schematic of this and a comparison with the ratio and the distribution-shift models is shown in Fig. 1.

The ratio model is not compatible with the observation that the direction of the MAE is less well defined than the direction of the adaptation stimulus [9]. Moreover the ratio model is not compatible with the MAE of transparent motion [4], since it would predict that

following adaptation to transparent motion, a transparent MAE would arise. The distribution-shift model predicts that the MAE following unidirectional adaptation is broad, since the activities underlying the MAE in this model are all activities except the one that adapted. However, the distribution-shift model cannot explain why transparent motion causes a non-transparent MAE. The broad inhibition model, on the other hand, was specifically developed to solve the seeming contradiction inherent in the non-transparency of the MAE following transparent motion adaptation. Perception of the motion stimulus is carried by directionally narrowly tuned excitatory connections between motion detectors and motion integrators. Thus bivectorial motion is seen as transparent motion. The MAE, on the other hand, is primarily due to broadly tuned disinhibition. Since inhibition is broadly tuned, so is the disinhibition following adaptation. Broad disinhibition smoothes the signals coming to the motion integration stage, thus causing a non-transparent MAE opposite to the vector average of the adaptation directions.

At present the broad inhibition model does not consider ocularity. There are two ways in which binocular effects could be introduced into the model. The first way focuses on effects of stereo disparity, while the second focuses on effects of ocularity. Research studying adaptation resulting from patterns that contained only disparity-defined motion showed that subjects see an MAE [10]. Thus there is an exclusively binocular component to the MAE. However, that type of motion differs in that it is not defined by luminance edges, but is second-order motion, which may exhibit very different properties. Related research, while not conclusive, suggests that the MAE is contingent on disparity [11]. In particular, following adaptation to a motion stimulus containing two different directions of motion at different disparities the MAE tends to be unidirectional if the test pattern is presented halfway (in terms of disparity) between the two adaptation disparities, while

it is bidirectional if two test patterns are presented at the adaptation disparities.

The ocularity of the MAE is an issue because after monocular adaptation an MAE can also be measured in the unadapted eye, indicating that there is interocular transfer (IOT) of the MAE [12,13]. The strength of IOT is usually measured as the ratio between the duration of the MAE of the unadapted eye and that of the adapted eye. The classic interpretation of IOT is that the site at which the MAE is represented has to be binocular at least to some degree [14–16]. However, IOT can also be studied by adapting each eye to a different direction of motion, and by measuring the extent to which the resulting MAE depends on which eye is viewing the test stimulus. In the case of rotary adaptation motion, where one eye is adapted to clockwise, and the other to anti-clockwise rotation, during monocular testing rotary motion going opposite to the direction presented during adaptation to that particular eye is perceived [17,18]. During binocular testing no motion is visible. This suggests that there are at least three representations that normally contribute to the perception of an MAE, two monocular and one binocular.

The intriguing question that arises from this analysis, and that will help resolve differences between ocular based and disparity based processing, is whether vector addition can also occur across the two eyes. The present study is designed to determine whether interactions between different directions of motion occur when motion stimuli are presented to different eyes. The experiments are aimed to guide the extension of the broad inhibition model to include monocular and binocular effects. Some preliminary experiments have previously been reported [19].

## 2. General methods

### 2.1. Apparatus

Observers were seated in front of a computer monitor. The screen was divided in two equal halves, left and right. Throughout the experiments each observer saw the left half of the screen only with the left eye, and the right half only with the right eye. A mirror haploscope was used to help observers fuse the two images. Matte black dividers ensured that observers could only see the screen through the mirrors. The path of the light from the screen to the eyes of the observers was about 80 cm long. Experiments were conducted in an illuminated room, but matte dividers surrounded the monitor to prevent reflections on the screen due to overhead illumination. The stimuli were generated using an Indigo 2 Silicon Graphics computer.

### 2.2. Stimuli

There were three phases in each experiment: adaptation, test, and inter-trial. Each trial alternated between adaptation and test phases, as explained in the procedure section. All stimuli appeared as though viewed through a circular aperture in a black foreground (luminance  $0.02 \text{ cd/m}^2$ ). The diameter of the aperture was 13 cm, which was equivalent to approximately 9.2 degrees of arc. The background viewed through the aperture appeared light grey (luminance  $16 \text{ cd/m}^2$ ). Motion was generated using random dot kinematograms, as explained below. All dots that were plotted had the same size (about 3.5 minutes of arc) and appeared black (luminance  $0.02 \text{ cd/m}^2$ ). In the middle of the aperture was a fixation mark, which was circular and had a diameter of 14 minutes of arc. That fixation mark was either red (luminance  $8 \text{ cd/m}^2$ ) during adaptation or green (luminance  $6 \text{ cd/m}^2$ ) during testing.

The frame rate at which stimuli were refreshed was 72 Hz during the adaptation phase, 36 Hz during the test phase, and 24 Hz during the inter trial phase. In pilot experiments we had found that this combination of frame rates yielded the strongest MAE, because it caused the strongest adaptation signal, but the testing signal did not rapidly wash out the after-effect. The reduced inter trial frame rate was used to help subjects be aware of the phase of the experiment they were in, which allowed them to relax (although subjects were asked to maintain fixation). Velocities were kept constant at  $20^\circ/\text{s}$  by using adjusted inter frame step sizes. Dot displacements were pregenerated, and dot positions were updated online. During the adaptation stimulus each population had the same displacement. During the test stimulus the displacements for each dot population were chosen at random, and then balanced, so that the sum of all the displacements amounted to a zero displacement.

The global direction of perceived motion could be determined independently for each eye. The global direction of motion can be specified as an angle measured counterclockwise from horizontal. By this scheme rightward motion corresponds to an angle of  $0^\circ$ , and upwards motion corresponds to an angle of  $90^\circ$ .

Initially the positions of all dots were chosen at random within a square region which contained the aperture, and whose side length was equal to the aperture's diameter. Dots were only visible if they were within the aperture. On each half of the screen either no dots, or 492 dots were drawn within the square. If dots were drawn, on average only about 80% of the dots were visible. This is equivalent to a mean dot density of about six dots per square degree of arc. Dots wrapped around the square if they crossed the boundary of the square and were randomly repositioned on the opposite

boundary. The dots drawn on the left half of the screen (and only visible to the left eye) will be referred to as 'left dots', the dots on the right half of the screen as 'right dots'. When the adaptation stimulus was presented, the fixation mark was red. During the test phase the fixation mark was green.

All test conditions were made up of dots moving randomly. At each frame a displacement of constant size, but of varying direction was randomly chosen for each dot. Hence no global direction of motion was displayed. Either left dots were presented alone, or right dots alone, or both left and right dots. Left and right dots, when displayed together in either adaptation or test phase were rivalrous, except in the binocular adaptation condition (Experiment 2).

### 2.3. Procedure

Throughout each trial, observers were instructed to look at the fixation mark; eye movements were not monitored. When observers initiated a new trial by pressing a button, they were presented with an adaptation stimulus for 1 min. Between adaptation and test phases the screen went black for 1 s, to avoid direct comparison between adaptation and test stimuli. During that period a warning tone told observers that a change of experiment phase was about to occur. Subsequent to that, a test stimulus appeared. In each trial only one condition was tested. Observers were instructed to adjust the direction of an arrow drawn outside the aperture extending radially away from the center of the aperture to the direction of global motion they perceived during the test phase. A mouse was used for that purpose. As observers moved the mouse horizontally to the right the arrow on the screen rotated clockwise, and similarly for leftwards mouse movements. The arrow was visible only during the test phase, and only then could observers adjust its direction. Initially the arrow was pointing upwards, to avoid biasing the observers. The arrow could be positioned with 1° accuracy. Observers adjusted rapidly to the use of a linear mouse trajectory to indicate circular directions in practice trials.

At the end of the test phase, which lasted 4 s, another warning tone indicated a second change in experiment phase. The screen went black again for 1 s. Then the adaptation stimulus reappeared again for 15 s. After the initial adaptation phase of 1 min, a 4 s test phase alternated with a 15 s adaptation phase. Alternations between 4 s test phase and 15 s adaptation phase continued until observers pressed a button during the test phase, indicating that they were satisfied that they had accurately matched the direction of the arrow with the direction of perceived motion. Between trials a pattern of randomly moving dots was presented for 30 s to eradicate any remaining MAE. Before the experi-

ment began observers were allowed 2–4 practice trials. During a single session observers were presented each condition six times, leading to a total of 30 trials. On average a session lasted for 1 h. Each observer participated in a single session for each experiment.

### 2.4. Data analysis

Data was first analyzed by using ANOVA. Since all main effects were statistically significant, more detailed comparisons between individual conditions were performed. Outliers were detected when a single response was more than two standard deviations outside the range of the responses for the identical condition, and when the standard deviation of the remaining five responses was at least three times smaller. When an outlier was detected, the entire block of trials in which the outlier occurred was removed. This procedure had to be applied only in one subject, and then only once (subject BB, Experiment 2, condition 1e/1e).

## 3. Experiment 1

The first experiment was designed to test whether adaptation to different directions can sum binocularly, and whether the eye or eyes that are being stimulated during testing influence the direction of the MAE following rivalrous adaptation.

### 3.1. Methods

#### 3.1.1. Observers

Four male observers participated in the experiment. All were between 26 and 39 years of age. All observers had normal or corrected-to-normal vision. Observers were naive about the purpose of the experiment, and all of them had had some experience in psychophysical experiments.

#### 3.1.2. Stimuli

There were five stimulus conditions. During the adaptation phase either left dots were presented alone, or right dots alone, or left and right dots. Left and right dots always were single populations of dots, moving at an angle of 45 and 135°, respectively. During the test phase one of three possible stimuli was presented to the observers. Either left dots were presented alone, or right dots alone, or both left and right dots. Not all combinations of adaptation and test stimuli were used. The following stimuli combinations were used: adaptation to both left and right dots, followed by test with left alone, right alone, and both; adaptation to right dots and test with right dots, and adaptation to left dots, and test with left dots. Fig. 2 summarizes all the stimulus combinations used in this experiment.

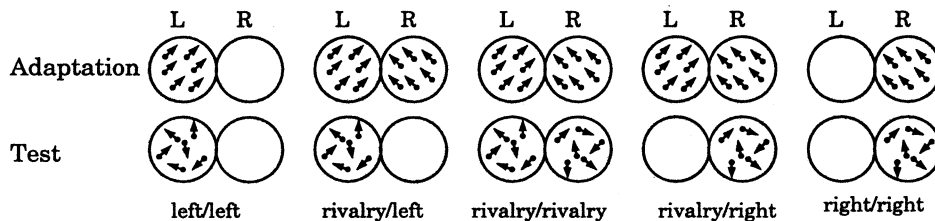


Fig. 2. Schematic of the stimuli used in Experiment 1.

### 3.2. Results

The adaptation stimuli that were only presented to one eye were perceived as unidirectional motion by the observers. When the adaptation stimulus contained two populations of dots, observers reported that during the adaptation phase they saw two groups of dots that were overlapping and moving in different directions. All observers reported that at times they could only see one group of dots moving, i.e. they were experiencing binocular rivalry. During debriefing the observers reported that during the test phase they always saw only one direction of motion. Most observers needed only two to three repetitions of the test phase to complete a trial. A one-way ANOVA showed that there was a highly significant difference between the conditions ( $P < 0.001$ ). Following rivalrous adaptation, the binocular test stimulus lead to the response that the MAE was going downward ( $270^\circ$ ); furthermore, monocular testing lead to a significant deviation from a downward MAE ( $t$ -test,  $P < 0.001$ ). Comparing the response to monocular adaptation in the left eye with binocular adaptation and test in the left eye revealed no statistically significant differences ( $t$ -test,  $P > 0.1$ ). This was also true for the right eye. A summary of these results is shown in Fig. 3. Following the experiment subjects reported that the after-effect was weakest in the 'downwards case', which corresponds to the binocular adaptation and test condition. This is reflected in most subjects in the tendency towards bigger standard deviation in that condition, although that did not reach significance using the  $F$ -Max test.

### 3.3. Discussion

Following rivalrous adaptation and rivalrous testing a single MAE ensued, pointing opposite to the vector sum of the adaptation directions. This suggests that the result of motion adaptation interacts between the two eyes to yield a single MAE. On the other hand, following rivalrous adaptation and monocular testing, the MAE did not differ from the MAE following monocular adaptation. In other words, if there is a binocular site of adaptation, it did not measurably change the direction of the MAE in the monocular test conditions (by tilting the MAE downwards).

Interocular transfer of the MAE has always been assumed to be occurring due to a binocular site of adaptation. If indeed no binocular site contributed to the MAE in Experiment 1, we would predict that no IOT of the MAE would occur. This stands in stark contrast to a solid body of research indicating that IOT does occur [12–15,20,21]. Unlike previous studies using dot adaptation stimuli [20,21] the motion stimuli used in the present study were rather fast ( $20^\circ/\text{s}$ ), and it is possible that at higher speeds no IOT occurs. To test this we ran a second experiment, in which we specifically compared the direct MAE and the interocular MAE.

## 4. Experiment 2

In a second experiment we wished to determine whether any IOT could occur in our experimental paradigm. To test this we adapted subjects in one eye, and tested in the same, or the other eye.

### 4.1. Methods

#### 4.1.1. Observers

The same four observers as before participated in this experiment. Because the observers had not been informed as to the purpose and outcome of the first experiment they were still naive with respect to the goals of the experiment.

#### 4.1.2. Stimuli

There were five stimulus conditions. During the adaptation phase either left dots were presented alone, or right dots alone, as before. An additional adaptation display was introduced in which binocular dots were presented, i.e. dots were at corresponding positions on the two halves of the screen. In this display on the two halves of the screen two populations of 246 dots each were displayed. One population of dots moved at an angle of  $45^\circ$ , and the other at  $135^\circ$ . The purpose of this stimulus was to show that in the present paradigm summation of binocular motion directions could occur. While Experiment 1 strongly suggests this, it is conceivable that it might not. We also introduced this stimulus to prevent subjects from categorizing stimuli into only

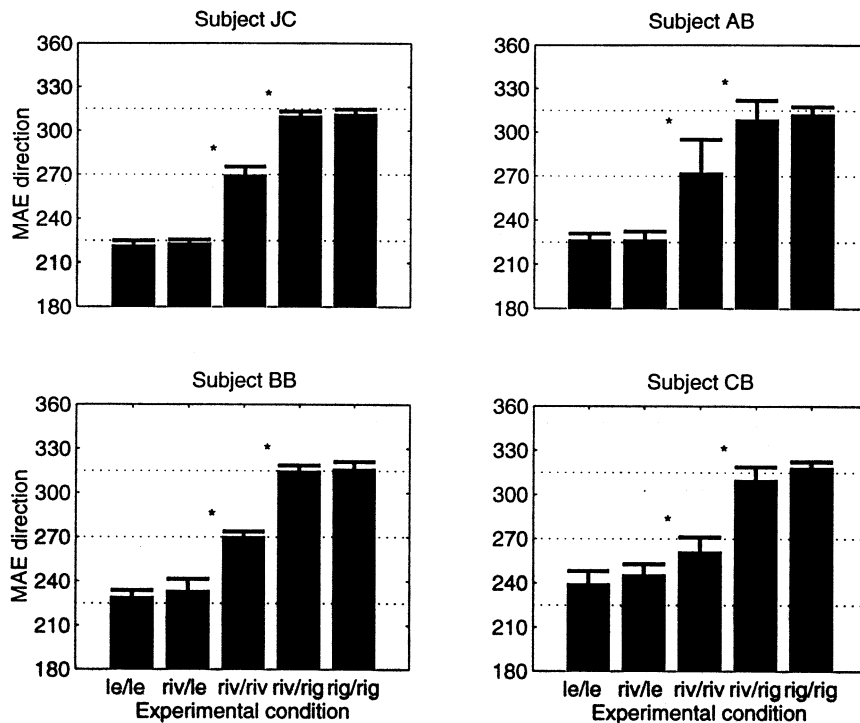


Fig. 3. MAE directions reported by subjects in Experiment 1. The dotted lines indicate the expected MAE due to monocular adaptation only (225 and 315°), and due to vector sum of MAEs due to binocular addition (270°). A \* indicates a significant difference between neighboring columns ( $P < 0.01$ ). Error bars indicate one standard deviation.

two classes, and responding accordingly. The final reason for this stimulus was to maintain as much consistency to the previous experiment, so that from the subjects' point of view they were performing the same task twice, although they were told that this was a different experiment. The test stimuli were the same as those of the first experiment. Not all combinations of adaptation and test stimuli were used. All combinations of monocular adaptation and monocular test stimuli were used (i.e. left/left, left/right, right/left, right/right), and the binocular adaptation stimulus followed by the rivalrous test stimulus. Fig. 4 summarizes all the stimulus combinations used in this experiment.

#### 4.2. Results

Subjects again could always report motion in the test display. The directions of the MAE due to IOT tended to agree with the directions of the direct MAE, indicating that IOT was taking place, although this did not reach significance in one subject. These results are summarized in Fig. 5. During debriefing observers indicated that some trials 'were a lot harder than others'. This statement is reflected in a difference of variance across all conditions ( $F$ -Max test,  $P < 0.01$ ) in all but one subject, but the conditions at which the variances were most extreme were not consistent across subjects. Following binocular adaptation the after-effect was

unidirectional and downward, that is the MAE was opposite to the sum of the adaptation directions.

#### 4.3. Discussion

The condition of binocular adaptation followed by rivalrous test essentially replicates the previous findings of Verstraten et al. [4]. The other conditions of Experiment 2 show that there was IOT of motion adaptation in our paradigm.

### 5. General discussion

Following adaptation to bidirectional motion, a unidirectional MAE occurs [4], a finding that we have replicated. But how does the visual system beyond the site of motion adaptation 'decide' to segregate the two directions of motion during the adaptation phase, and to integrate them into one direction of motion during the test phase? This puzzle was first posed by Verstraten et al. [4] in the context of binocular adaptation and testing. While the broad inhibition model accounts for integration of motion adaptation [8], it remains silent about monocular and binocular effects. Further psychophysical work showed that integration of motion directions is disparity contingent [11]. This suggests that the sites of motion adaptation are disparity selective,

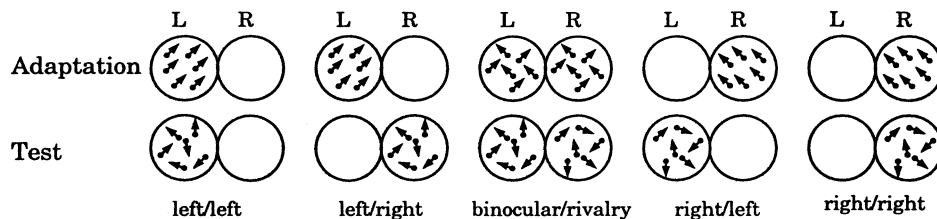


Fig. 4. Schematic of the stimuli used in Experiment 2.

and that motion integration only occurs if the appropriate adaptation sites are being activated.

The present experiments were aimed at understanding whether ocularity follows the same pattern, or not. In parallel to the findings where disparity was systematically varied, we find that integration of motion adaptations from each eye only occurs if both eyes are tested. In contrast to the disparity contingent findings we find that following rivalrous adaptation the untested eye had no influence at all on the direction of the resulting MAE. In other words, in the disparity study the same motion components contributed to all motion percepts; the test pattern affected only whether components were integrated or not. In the present ocularity study, on the other hand, the test pattern influenced which components contributed to the motion percept. This suggests that disparity and ocularity are not processed analogously. Since ocular information is by necessity available before disparity information, the present experiments suggest that ocularity should have primacy in the extension of the broad inhibition model. But even along those lines, the model can be extended in several ways. First, one could assume that the motion detection stage could be two monocular sites and the motion integration stage one binocular site. We refer to this model as the M-B model. Alternatively, it could be that the motion detection stage is comprised of one binocular and two monocular sites, which combine in a single binocular integration stage. We refer to this model as the MB-B model. A schematic of these models is shown in Fig. 6.

To further develop our model we designed the present experiments. The results from Experiment 1 show that, following rivalrous adaptation with a rivalrous test, subjects perceive a MAE in the direction opposite to the vector sum of the adaptation directions. This suggests that the motion integration stage is binocular. Experiment 1 suggests that no binocular representation contributed to the binocular addition of monocular motion components, thus favoring the M-B model. The second experiment suggests that interocular transfer of the MAE took place. Traditionally IOT has been viewed as reflecting the existence of a binocular site of adaptation. Thus Experiment 2 argues for the MB-B model. How can the results from the two experiments be reconciled? We propose that neither the

MB-B nor the M-B models are correct, and instead suggest two further alternative models that are elaborations of these models to explain the seeming contradiction between Experiment 1 and Experiment 2.

First, note that IOT is usually measured by looking at the magnitude of the MAE, ignoring the direction of the MAE. In the present experiments subjects were asked to indicate the direction of the MAE. If direction and magnitude of the MAE arise based on different adaptation sites, it is possible that while the MAE magnitude is due to adaptation at monocular and binocular sites, the MAE direction is due to adaptation only at monocular sites, which subsequently add at a binocular site. We will refer to this model as magMB-dirM model. It is diagrammed in Fig. 7. Binocular summation of adaptation vectors when stimulated with a rivalrous stimulus then leads to the summing of the monocular MAE components. Lack of interference from the untested eye following rivalrous adaptation would be due to lack of activation due to a test stimulus. In the traditional IOT experiments, the magnitude of the MAE would be determined by the binocular representation of magnitude, and in the non-transferred MAE the magnitude would be determined by both monocular and binocular representations of magnitude. But IOT of MAE is not directionless, as demonstrated in Experiment 2, which suggests that the adapted monocular direction representation can contribute a (possibly small) motion component to the MAE. Indeed our results suggest that the observers' certainty of the MAE direction was poor. In this view the lack of IOT in Experiment 1 when adapting to a rivalrous stimulus, and testing with a monocular stimulus arises because the motion representation stimulated by the test stimulus is able to 'drown out' the motion representation that is not stimulated with a test display. But how could magnitude and direction of the MAE be determined separately?

The magnitude of the MAE may be dominated by the overall (non-directionally tuned) level of activation of a set of neurons, while the direction of the MAE may be dominated by specific direction-tuned cells that adapt. The overall activation may adapt in an untuned way within the stimulated region of visual space, and would therefore be both monocular and binocular. On the other hand, adapting motion detectors may be

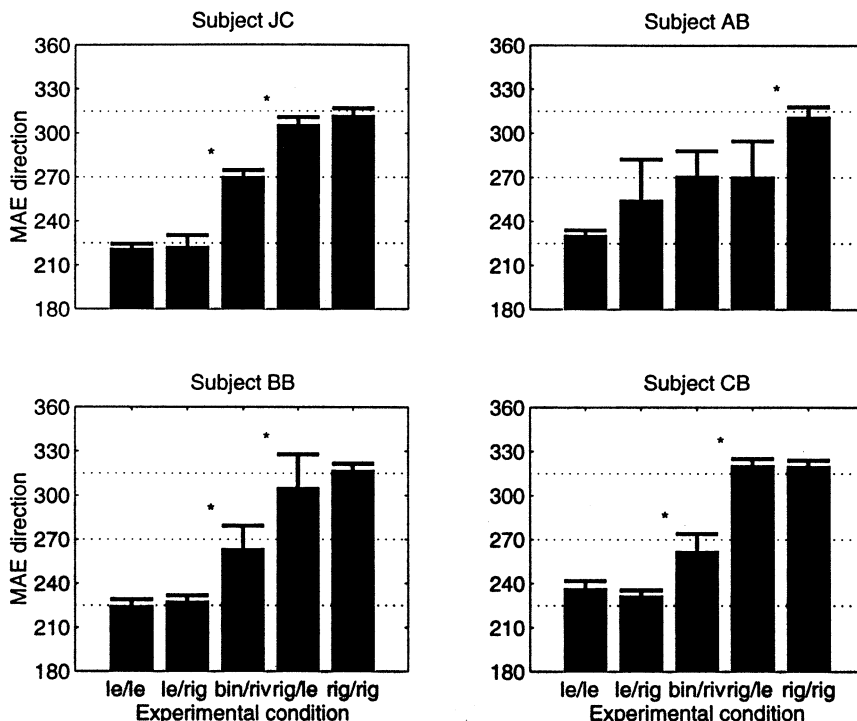


Fig. 5. MAE directions reported by subjects in Experiment 2. Plotting conventions are as in Fig. 3.

primarily monocular, and thus only those activated by the stimulus adapt. In support of this idea several models have argued that orientationally untuned normalization at different levels in the visual system plays an important role in visual processing [22,23], and there is some evidence supporting the existence of monocular motion detectors [24], although there also seem to be many binocular cells.

An alternative interpretation is that the magnitude and direction components of the MAE arise at the same site. But instead of adaptation occurring at a site that is in itself binocular, it is happening between the monocular inputs and the binocular site itself. We refer to this model as the MthreshB model. A schematic of this model is shown in Fig. 7. Monocular inputs following adaptation are only able to drive the binocular site if they are activated by a test pattern in the adapted eye, whereas a test pattern in the unadapted eye only

changes the threshold of the binocular site. Via this mechanism a monocular test stimulus could activate a monocular representation and thereby the corresponding binocular representation, whereas the untested representation would not contribute to the resulting MAE. IOT, on the other hand, would occur because adaptation changes the threshold, but still requires activation through a test pattern, even if it originates in the non-adapted eye. This decrease of threshold would have to be quite substantial to cause the MAE due to IOT as has been reported. At the present time our data are consistent with both the magMB-dirM and the MthreshB models, but we favor this latter explanation because it appears simpler. Further experiments will be necessary to shed light on these issues.

Since our stimuli contained zero disparity, we cannot generalize any implications from the disparity study [11] to our results. On the other hand, it is interesting to

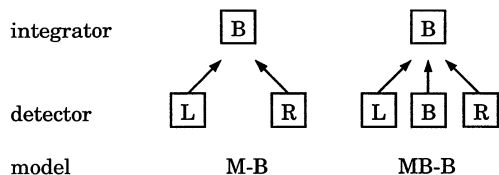


Fig. 6. Two simple models to explain monocular and binocular effects in the MAE. The boxes represent motion representations. The bottom and top rows give the proposed detector and integrator stages, respectively. The letter inside each box indicates whether a representation is monocular (L-left, R-right) or binocular (B).

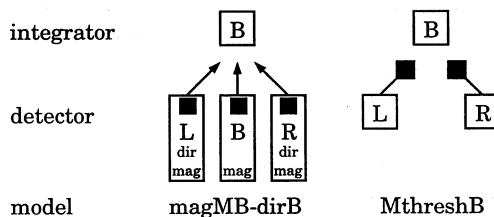


Fig. 7. Two models that can account for the data from Experiments 1 and 2. Conventions are as in Fig. 6. In addition a black square indicates a site of adaptation, 'mag' denotes the magnitude of the MAE, while 'dir' denotes the direction of the MAE.

note that in that study both disparity and ocularity cues were present. Based on our results we have to conclude that monocular adaptation must have taken place in addition to the reported disparity contingent effects. And according to our data the monocular adaptation should have interacted, yielding an integration MAE. In some of their stimulus conditions the ocularity based MAE, and the disparity based MAE make different predictions about the ensuing percept. Presumably they trade off against each other. We believe this to be reason for the variability in their results. Some subjects reported seeing an integrated MAE: in this case the integration of monocular cues dominated the final motion percept. Other subjects reported seeing a non-integrated MAE: in that case the disparity contingent MAE dominated the motion percept. It will be interesting to further study the relative strengths, and the interactions between these two types of motion adaptations.

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### References

- [1] Wohlgenuth A. On the after effect of seen movement. *B J Psychol (Monogr Suppl)* 1911;1:1–117.
- [2] Mather G. The movement after-effect and a distribution-shift model for coding the direction of visual movement. *Perception* 1980;9:379–92.
- [3] van Doorn AJ, Koenderink JJ, van de Grind WA. Perception of movement and correlation in stroboscopically presented noise patterns. *Perception* 1985;14:209–24.
- [4] Verstraten FAJ, Fredericksen RE, van de Grind WA. Movement after-effect of bi-vectorial transparent motion. *Vis Res* 1994;34(3):349–58.
- [5] Hiris E, Blake R. Another perspective in the visual motion after-effect. *Proc Natl Acad Sci USA* 1992;89:9025–8.
- [6] Raymond JE. Movement direction analysers: independence and bandwidth. *Vis Res* 1993;33(5/6):767–75.
- [7] Barlow HB, Hill RM. Evidence for a physiological explanation of the waterfall phenomenon and figural after-effects. *Nature* 1963;200:1345–7.
- [8] Grunewald A, Lankheet MJM. Orthogonal motion after-effect illusion predicted by a model of cortical motion processing. *Nature* 1996;384:358–60.
- [9] Levinson E, Sekuler R. A two dimensional analysis of direction-specific adaptation. *Vis Res* 1980;20:103–7.
- [10] Patterson R, Bowd C, Phinney R, Pohndorf R, Barton-Howard WJ, Anzilotta M. Properties of the stereoscopic (cyclopean) motion after-effect. *Vis Res* 1994;34(a):1139–47.
- [11] Verstraten FAJ, Verlinde R, Fredericksen RE, van de Grind WA. A transparent motion after-effect contingent on binocular disparity. *Perception* 1994;23:1181–8.
- [12] Lehmkuhle SW, Fox R. Effect of binocular rivalry suppression on the motion after-effect. *Vis Res* 1975;15:855–9.
- [13] Lehmkuhle SW, Fox R. On measuring interocular transfer. *Vis Res* 1976;16:428–30.
- [14] Mitchell DE, Reardon J, Muir DW. Interocular transfer of the motion after-effect in normal and stereoblind observers. *Exp Brain Res* 1975;22:163–73.
- [15] Wade NJ. On interocular transfer of the movement after-effect in individuals with and without normal binocular vision. *Perception* 1976;5:113–8.
- [16] Wolfe JM, Held R. Shared characteristics of stereopsis and the purely binocular process. *Vis Res* 1983;23(3):217–27.
- [17] Anstis S, Duncan K. Separate motion after-effects from each eye and from both eyes. *Vis Res* 1983;23(2):161–9.
- [18] Jiao SL, Han C, Jing QC, Over R. Monocular-contingent and binocular-contingent after-effects. *Percept Psychophys* 1984;35(2):105–10.
- [19] Mingolla E, Grunewald A. Motion after-effects due to interocular summation of adaptation to linear motion. *Invest Ophthalmol Vis Sci* 1995;36(4):54.
- [20] Raymond JE. Complete interocular transfer of motion adaptation effects on motion coherence thresholds. *Vis Res* 1993;33(13):1865–70.
- [21] Nishida S, Ashida H, Sato T. Complete interocular transfer of motion after-effect with flickering test. *Vis Res* 1994;34(20):2707–16.
- [22] Grossberg S, Mingolla E. Neural dynamics of form perception: boundary completion, illusory figures, and neon color spreading. *Psychol Rev* 1985;92:173–211.
- [23] Heeger DJ. Normalization of cell responses in cat striate cortex. *Vis Neurosci* 1992;9:181–97.
- [24] Hubel DH, Wiesel TN. Receptive fields and functional architecture of monkey striate cortex. *J Physiol (Lond)* 1968;195:215–43.