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SUMMATION OF ADAPTATION TO LINEAR MOTION**

Alexander Grunewald and Ennio Mingolla

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Motion aftereffects due to interocular summation of adaptation to linear motion

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Running head: Interocular motion aftereffect

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Abstract

The motion aftereffect (MAE) can be elicited by adapting observers to global motion before they view a display containing no global motion. Experiments by others have shown that if the left eye of an observer is adapted to motion going in one direction and the right eye is simultaneously adapted to motion going in the opposite direction, no MAE is reported during binocular testing. The present study investigated whether no binocular adaptation had occurred because the monocular motion signals cancelled each other during adaptation, or whether monocular adaptations cancelled each other during testing. Observers were adapted to different, but not opposite, directions of motion in the two eyes. Either both eyes, the left eye, or the right eye 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 opposite direction of the vectorial sum of the adaptation directions. In the monocular test conditions observers reported MAE directions about halfway between their binocular report and the direction opposite the corresponding monocular adaptation directions, indicating that both monocular and binocular sites had adapted. A decomposition of the observed MAEs based on two strictly monocular and one binocular representation of motion adaptation can account for the data.

Keywords: motion perception, motion aftereffect, motion direction, monocular motion aftereffect, binocular motion aftereffect, vector sum, interocular transfer

Introduction

Motion presented to one eye during an adaptation period leads to a motion aftereffect (MAE), the perception of motion in the opposite direction, upon subsequent viewing of a stationary test stimulus in the same eye. An MAE can also be measured in the other (unadapted) eye, indicating that there is interocular transfer (IOT) of the MAE (Lehmkuhle & Fox, 1975, 1976). 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 usual interpretation of IOT has been that the site at which the MAE was represented had to be binocular at least to some degree (Mitchell, Reardon, & Muir, 1975; Wade, 1976; Wolfe & Held, 1983). The present study investigates how binocular and monocular motion representations interact, and concludes that both binocular and monocular motion representations interact to yield an MAE, even during monocular testing.

There are other methods than IOT to investigate the binocularity of motion representations. One way is to adapt each eye to a different direction of motion, and to measure the extent to which the resulting MAE depends on which eye is viewing the test stimulus. This has been tested in the case of rotary adaptation motion, where one eye was adapted to clockwise, and the other to anticlockwise rotation (Anstis & Duncan, 1983; Jiao, Han, Jing, & Over, 1984). These studies reported that during monocular testing, rotary motion going opposite to the direction presented during adaptation to that particular eye was perceived. During binocular testing no motion was visible. These studies suggest that there are at least three representations that normally contribute to the perception of an MAE, two monocular and one binocular, and that the monocular ones are highly specific to the eye of origin. In

this report an MAE refers to the perception of motion an observer has. It does not refer to a particular site of adaptation within the visual system. Thus, the MAE phenomenon is taken to be the result of 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 two directions of motion (van Doorn, Koenderink, & van de Grind, 1985; Verstraten, Fredericksen, & van de Grind, 1994). Observers perceive motion opposite to the vector sum of the two adaptation motions during testing, which is paradoxical, because during adaptation observers did 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 does appear like real motion (Hiris & Blake, 1992; Raymond, 1993b). This has been taken as evidence that the MAE did not occur at the level of motion detecting units, but instead at or after a site which performs spatial pooling of motion signals. The ratio model states that the MAE is due to the fact that motion detectors for the direction of the adaptation stimulus fatigue, and therefore unmask activity in a competing detector coding motion in the opposite direction (Barlow & Hill, 1963). The distribution shift model asserts that the MAE is due to the fact that the activities within a motion representation shift due to adaptation (Mather, 1980). The ratio model is not compatible with the MAE of transparent motion (Verstraten et al., 1994), since it does not allow for interactions between motion detectors other than those in opposite directions. The distribution shift model on the other hand is compatible with this result, since it explicitly includes activities of all motion detectors in a motion representation. What this model does not address is how the monocular and binocular motion representation

interact to yield a single motion percept.

Perceived translatory motion in one direction can be denoted by a vector, having a magnitude and a direction, and the MAE can also be decomposed in the same way (Wiesenfelder, 1993). For example, when observers are adapted to two different, but not opposite, directions of motion, and the speed of motion in one direction is varied, the direction of the MAE can be shown to depend on the variable adaptation speed (Verstraten et al., 1994). A simple model that explains how the magnitude of an observed MAE can be decomposed into the contributions from several monocular and binocular motion representations has been put forward (van Kruysbergen & de Weert, 1993). However, up to date there is no agreement on how to measure the magnitude of the MAE (Blake & Hiris, 1993; Raymond, 1993a; Wiesenfelder, 1993; Wolfe & Held, 1983). Moreover, the van Kruysbergen and de Weert (1993) model does not address the direction of the MAE observed in experiments.

As mentioned above, a few experiments have been conducted where each eye was adapted to a different direction of motion, and the direction of the MAE was reported as a function of the eyes that saw the test stimulus. Since in those experiments rotary motion was always used, observers could only reply by indicating that they perceived no MAE, or a clockwise or an anticlockwise MAE (Anstis & Duncan, 1983). Using linear motion instead, and asking observers to precisely indicate the direction of the MAE has the advantage that more information about the MAE as a vector is available. Moreover, it is possible that translation and rotation may be handled by entirely different mechanisms.

An experiment was conducted to address the issue of the dependence of the resulting MAE on test conditions. Each eye was adapted to a different direction of linear motion and it was found that during binocular viewing of the test stimulus the MAE pointed in the

direction of the vector sum of the expected individual MAEs. When the test stimulus was viewed monocularly, the expected MAE was opposite to the direction of adaptation for the eye in question. However, it was found that *neither monocular MAE pointed in the direction opposite to the direction of motion that was presented to that eye*, i.e. there always was an interaction between the directions of motion signals derived from the two eyes.

Methods

Observers

Five observers participated in the experiment (four male, one female). All were graduate students between 26 and 30 years of age. All observers had normal or corrected-to-normal vision. Observers were naive about the purpose of the experiment, and three of them had had some experience in psychophysical experiments. They were paid \$5 for a session that lasted about half an hour.

Apparatus

Observers were seated in front of a TV screen. The screen was divided in two equal halves, left and right. Throughout the experiment observers saw the left half of the screen only with their left eye, and the right half only with the right eye. Prisms and mirrors were used to help observers fuse the two images. Matte black dividers ensured that observers could only see the screen through the prisms and thus the left half of the screen was only seen by the left eye, and the right half only by the right eye. The path of the light from the screen to the eyes of the observers was about 1m long. Experiments were conducted in an illuminated

room. Stimuli were generated using an INDIGO Silicon Graphics computer.

Stimuli

There were two phases in the experiment: adaptation and test. Each trial alternated between adaptation and test phases, as explained in the procedure section. The luminances and sizes are given below as measured through the prisms. All stimuli appeared as though viewed through a circular aperture in a black foreground (luminance 0.83 ft-L). The diameter of the aperture was 15cm, which was equivalent to approximately 8.6 degrees of arc. The background viewed through the aperture appeared light grey (luminance 4.0 ft-L). Motion was generated using random dot kinematograms, as explained below. All dots that were plotted had the same size (3 minutes of arc) and appeared black (luminance 0.83 ft-L). In the middle of the aperture was a fixation mark, which was circular and subtended 20 minutes of arc. That fixation mark was either blue (luminance 1.3 ft-L) during adaptation or red (luminance 1.9 ft-L) during testing.

The frame rate at which stimuli were refreshed was 60 Hz. Between subsequent frames dots were displaced by 20 minutes of arc, thus resulting in a speed of 20 deg/sec. All dots in all displays moved with the same speed, but their direction of motion varied. Two factors influenced the direction of motion of individual dots: the global direction of motion and the level of coherence. The global direction of 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 degrees, and upwards motion corresponds to an angle of 90 degrees (see figure 1). The coherence indicates the probability that a dot will move in the global direction. If it does not move in the global

direction its direction was chosen at random from all possible directions (0 to 360 degrees). 0% coherence means that although each dot's displacement between screens is the same size, its direction is chosen randomly. 95% coherence means that with 95% probability a dot was moving in the global direction of motion for the eye in question, while with 5% probability it was moving in a direction chosen at random.

–FIGURE 1 ABOUT HERE–

Initially all dots were chosen at random within a square region which contained the aperture, and whose sidelength 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 300 dots were drawn within the square. If dots were drawn, on average only about 80% of the dots (about 236 dots) were visible. This is equivalent to a mean dot density of about 1 dot per square degree of arc. Dots wrapped around the square if they crossed the boundary of the square. The dots drawn on the left half of the screen 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 was blue. Left dots and right dots were presented, moving with 95% coherence. This level of coherence was chosen during adaptation (instead of 100%) to avoid moving constellations on the screen that might distract observers. The left dots were moving in direction 30 deg, the right dots were moving in direction 150 deg. The same adaptation stimulus was used for all observers in all trials.

During the test phase one of three possible stimuli was presented to the observers. During the test phase the fixation mark was red. All test conditions were made up of dots moving with 0% coherence. Hence no global direction of motion was displayed. In the left eye condition only left dots were displayed, but no right dots. In the right eye condition only

right dots were displayed, but no left dots. In the binocular condition both left dots and right dots were displayed. Figure 2 summarizes all the stimuli used in the experiment.

–FIGURE 2 ABOUT HERE–

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 the adaptation stimulus for one minute. Between adaptation phase and test phase the screen went black for 1 second, 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, one of the three possible test stimuli appeared. In each trial only one condition was tested. Observers were instructed to adjust the direction of an arrow drawn outside the aperture to the direction of motion they perceived during the test phase. An analog dial was used for that purpose. As observers rotated the dial the arrow on the screen rotated in the same way. 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 degree accuracy.

After 4 seconds another warning tone indicated a second change in experiment phase. The screen went black again for one second. Then the adaptation stimulus reappeared again for 16 seconds. After the initial adaptation phase of one minute a 4 second test phase alternated with a 16 second adaptation phase. Alternations 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 observers

were allowed to take a rest if they wanted. Before the experiment began observers were allowed 3-4 practice trials. During a single session observers were presented each condition (left, right and binocular test stimulus) five times, leading to a total of 15 trials. On average a session lasted for 30 minutes. Each observer participated in a single session.

Results

Observers reported that during the adaptation phase they saw two groups of dots that were overlapping and moving in different directions. Some observers reported that at times they could only see one group of dots moving, i.e. they were experiencing binocular rivalry. During the test phase observers reported seeing only one type of motion. Most observers needed only 2-3 repetitions of the test phase to complete a trial. The results of the measurements for each observer are given in the first three columns of table 1, and are graphically shown in figure 3. In summary, the binocular test stimulus lead to the response that the MAE was going downward (270 deg). The monocular test stimuli lead to the response that the MAE was deviating from downwards motion. In the case of the left eye test stimulus, the direction of the MAE deviated leftward from the vertical, while the direction of the right eye MAE deviated rightward from the vertical. A oneway ANOVA shows that the differences between these conditions were highly significant ($F(2, 12) > 20, p < 0.001$ for each observer). Moreover, a regression analysis revealed that in four observers at least 89% of the variance could be explained by the stimulus conditions. In the fifth observer (MA) 78% could be explained.

–FIGURE 3 ABOUT HERE–

If the three motion representations did not interact with each other, then each monocular test condition recalled activities only from the appropriate monocular motion representation. In that case the expected direction of the MAE was downwards in the binocular test case, and opposite to the monocular directions of adaptation in the monocular test cases. The direction of the MAE in the binocular case pointed in the expected direction. However, a comparison between the expected directions of motion in the monocular MAEs and the observed direction of the MAEs (one-sided t -test) shows that the difference is significant ($p < 0.05$), except in one condition in one observer (MA, right eye), where they did not differ ($p > 0.2$). Also, the directions of both monocular MAEs differed significantly from downwards motion (one-sided t -test, $p < 0.05$). Thus the monocular MAEs pointed in a direction between downwards and the expected (i.e. opposite to the adapting direction) monocular MAE.

Discussion

The results indicate that, in general, observers never experienced motion going in the opposite direction to the motion to which they monocularly adapted. Moreover, the perceived direction of motion depended very strongly on the test condition. In particular, during binocular testing a MAE was experienced which was in the opposite direction to the vector sum of the two adaptation directions when the adaptation stimuli had equal speeds.

Interactions between motion representations

One way to explain differences between MAE directions dependent on the eye that saw the test stimulus is to assume that in each condition the eye that is stimulated during testing the appropriate representation is recalled, and that there is no interaction between those representations (Anstis & Duncan, 1983). If that is so, then the motion representations are adapted in the same direction in which the MAE is observed. Why then do the monocular MAEs not point opposite to the monocular adaptation directions?

One way to explain this would be to claim that the monocular representations interact with each other during adaptation, therefore leading to activity within those representations which is shifted towards the direction of motion in the other eye. A consequence of this would be that during adaptation the real (monocular) direction of motion would not be perceived, but rather one shifted towards the vertical, which is not what observers reported. However, it could be that adaptation of a site closer to the vertical could occur despite the perception of the correct motion. That is, adaptation and perception of motion might be to some degree independent of each other. A difficulty with this explanation is that it is usually assumed that the MAE is due to adaptation at a site that was active during adaptation (Barlow & Hill, 1963; Mather, 1980). This implies that within a single motion representation the effect of adaptation to motion and the resulting MAE should be at the same site. This indicates that the monocular MAEs were due to the interaction of several motion representations that had adapted, and that the test conditions could selectively recall some of these representations.

Another question that is raised is why the binocular MAE pointed in the direction opposite to the direction of vector sum of the adaptation directions. A first explanation would

be that there is no binocular adaptation, but only monocular adaptation, and that they combine during binocular testing. This leaves unanswered, however, why during adaptation observers see two distinct directions of motion, while they see only one direction of motion during testing. This rules out that a purely monocular process is responsible for the binocular MAE.

An alternative explanation would be that the two directions of motion present during adaptation stimulated binocular cells, and that these cells responded ideally to downwards motion, but also a bit to the two different directions of adaptation motion. A problem with this is that it suggests that during adaptation three directions of motion should be perceived: the two real directions, and their vector sum. However, that is not the case. Therefore, the directions might compete, or a later stage might pool activities (Verstraten et al., 1994).

The foregoing observations suggest that the observed MAEs are due to the interactions between separate monocular and binocular representations. During adaptation all of these representations adapted, and during testing some or all of these representations could be recalled, depending on the test stimulus. Suggestions for how pooling of activities can reduce uncertainty of motion representations has been described in recent models (Bischof & Di Lollo, 1990; Grossberg & Mingolla, 1993; Hugh R, Ferrera, & Yo, 1992). A binocular extension of these models may also be able to explain the interactions between the motion representations discussed here.

Decomposition of the observed MAEs

Assuming that adaptation at each motion representation amounts to the instantiation of an adaptation vector at those representations, it is possible to consider how the motion rep-

representations interact to yield the observed MAEs. A simple scheme is to assume that the binocular motion representation is recalled whenever a test stimulus is presented. What varies, however, is which monocular representations are recalled. In the following it is assumed that a representation is either recalled completely, or not at all. Moreover, it is assumed that recalling a representation amounts to adding into a vector sum the adaptation vector corresponding to that representation. Thus the observed MAE in the left eye test is the sum of the adaptation vectors from the left and the binocular motion representations. The appendix shows how this leads to a system of 6 non-linear equations with 6 variables. This system can be solved using the directions for the observed MAEs. Table 1 summarizes the solutions found for each observer. It can be seen that in general the estimated strengths of the two monocular representations were about the same ($\hat{R}_l = \hat{R}_r$). The estimated direction of the binocular representation ($\hat{\rho}_b$) is generally downward (observers DB, JV, NAM), but it can be shifted from downward when the 3 MAEs indicate a bias in one direction (observers MA and NML).

This decomposition gives an estimate for the magnitude of the MAEs, without any magnitude estimation asked by observers. The binocular MAE is slightly stronger than the monocular MAEs, a result that could be compared with existing measures of the MAE in further experiments. Our decomposition indicates that, at least for adaptation motions of equal speed (cf. Verstraten et al. (1994)) the observed MAEs can be fully explained as the weighted vector sum of three independent motion representations at which adaptation occurred.

–TABLE 1 ABOUT HERE–

This analysis can also be used to predict the interocular transfer (IOT) of the MAE.

According to the values from Table 1, IOT should be about 44% (the mean value across observers), which is significantly below the value reported in the literature, which is closer to 70%. The most likely explanation is that in the present experiment the binocular representation was activated less during adaptation than the monocular representations. Consequently the contribution of the binocular representation to the MAE would be weaker than that of the monocular contributions. The reason for the lower activation of the binocular representation could be that in the monocular representations the site coding the adaptation stimulus was activated maximally. However, in the binocular representation, the site coding the vector sum of the adaptation direction was activated maximally. Motion detectors have a limited directional bandwidth (Levinson & Sekuler, 1976; Raymond, 1993b), and so the site that was most active in the binocular representation was activated significantly less (since neither of the directions pointed in its optimal direction) than the maximally activated sites in the monocular representations. It is important to note that this means that the present experiment shows that the binocular representation was probably adapted less, but not that the binocular representation in general contributes less to the MAE. On the other hand the results of the decomposition can make predictions about variations in the ocularity of the observers.

This decomposition is also consistent with the physiology that is thought to underlie motion perception. It is known that a good proportion of cells in cortical area V1 are direction selective (Snowden, Treue, & Andersen, 1992). Some of those neurons are binocular, but there also many monocular neurons (Hubel & Wiesel, 1968). V1 projects to area MT which is known to contain a large population of mostly binocular direction selective cells (Felleman & Kaas, 1984). Neurons in area MT have big receptive fields. It is possible that the three

motion representations discussed in this study are located in V1, and that the interactions between the motion representations occur in the convergence onto neurons in area MT. Very little is known about this convergence, in particular how inputs from V1 are weighted in the sum. Future physiological and psychophysical research will have to address how motion representations are weighted when they interact.

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Appendix

As discussed above, three sites likely contributed to the MAEs reported, two monocular sites, and one binocular site. If it is assumed that the reported MAEs are the weighted vector sum of each of those sites, it is possible to write down the following expressions linking the reported MAEs to the motion representations:

$$M_l \vec{m}_l = R_l \vec{r}_l + R_b \vec{r}_b$$

$$M_r \vec{m}_r = R_r \vec{r}_r + R_b \vec{r}_b$$

$$M_b \vec{m}_b = R_l \vec{r}_l + R_r \vec{r}_r + R_b \vec{r}_b$$

where M_l and \vec{m}_l are the magnitude and the unit vector pointing in the direction of the MAE observed respectively in the left eye condition. Similarly for the right (M_r and \vec{m}_r) and the binocular (M_b and \vec{m}_b) MAEs. R_l and \vec{r}_l are the magnitude and the unit vector pointing in the direction of the left monocular motion representation respectively. Similarly for the right monocular (R_r and \vec{r}_r) and binocular (R_b and \vec{r}_b) motion representations. It is possible to write each MAE unit vector as

$$\vec{m}_i = \begin{pmatrix} \cos(\mu_i) \\ \sin(\mu_i) \end{pmatrix}$$

where $i = l, r$ or b . μ_i is the measured direction of the MAE. Similarly for the motion representations:

$$\vec{r}_i = \begin{pmatrix} \cos(\rho_i) \\ \sin(\rho_i) \end{pmatrix}$$

ρ_i ($i = l, r$ or b) is the direction of a given motion representation that adapted.

Since each vector is 2-dimensional, the above system has 6 equations. Assuming that the monocular motion representations during testing point in the opposite direction than the monocular adaptation stimulus for that eye ($\rho_l = 210$ and $\rho_r = 330$) means that there are 7 unknowns in the system. Only relative strengths are of interest here so R_b can be set to one without loss of generality. By doing this all magnitudes will be relative to the binocular representation, and there are only six variables left. This non-linear system can be solved for each observer. The solutions are estimates to the real variables, and are denoted by the same symbol with a hat. For example the real direction of the binocular adaptation is ρ_b and the estimated direction is $\hat{\rho}_b$. The solutions are shown in table 1.

Figure Captions

Figure 1: The frame of reference employed throughout this report.

Figure 2: The stimuli employed in the experiment. There was one adaptation stimulus, and three different test stimuli.

Figure 3: The direction of the MAEs as reported by the observers. The dashed arrows indicate the directions of the adaptation stimulus. The thin solid arrows give the expected directions of motion if the motion representations are independent. The thick solid arrows indicate the mean directions of the observed MAEs. The grey segments indicate one standard deviation from each mean.

The left eye was adapted with motion going rightward and up (dashed arrow pointing right and up), and the right eye with motion going leftward and up. If the direction of the MAE measured in the left eye had been independent from the right adaptation, then the expected direction of the MAE had been opposite to the direction in which the left eye adapted, i.e. leftward and down (thin arrow pointing left and down). Similarly the expected MAE for the right eye was rightwards and to the right. The expected direction in the binocular case was downwards, as was the measured MAE. The observed MAE in the left eye test case pointed leftward and down (thick arrow pointing left and down), and in the right eye test case it pointed rightward and down. In the binocular case it pointed downward.

Table Caption

Table 1: The mean directions measured for each of the observers, and the solutions of

the system of equations given in the appendix. $\hat{\rho}_b$ is the estimated direction in which the binocular motion adapted. \hat{R}_l and \hat{R}_r are the strengths of the left and the right monocular motion representations respectively (R_b is assumed to be 1, see Appendix). \hat{M}_l , \hat{M}_b , and \hat{M}_r are the estimated magnitudes of the left, binocular, and right MAEs respectively.

Observer	Measured MAEs			Parameters of Decomposition						predicted IOT
	left eye	binocular	right eye	$\hat{\rho}_b$	\hat{R}_l	\hat{R}_r	\hat{M}_l	\hat{M}_b	\hat{M}_r	
DB	238.8	279.6	312.8	283.0	1.5	1.7	2.0	2.6	2.5	40%
JV	250.0	279.8	300.0	273.3	0.6	0.9	1.4	1.8	1.7	56%
MA	245.4	283.6	324.0	315.6	1.6	1.4	1.7	2.3	2.4	40%
NAM	229.0	270.0	312.8	274.3	2.2	2.1	2.8	3.1	2.8	32%
NML	235.0	276.0	293.6	248.5	0.6	1.2	1.5	1.8	1.7	53%

Table 1:

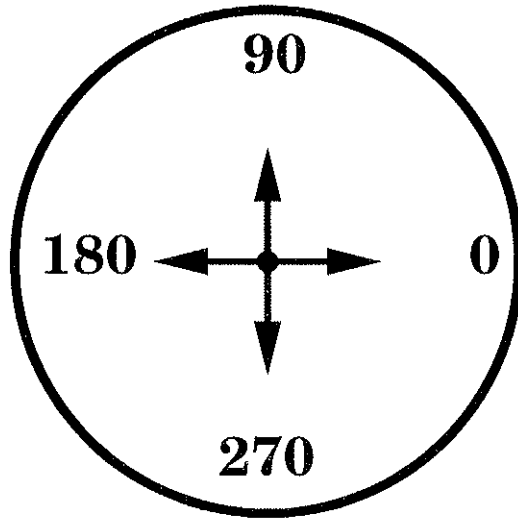


Figure 1:

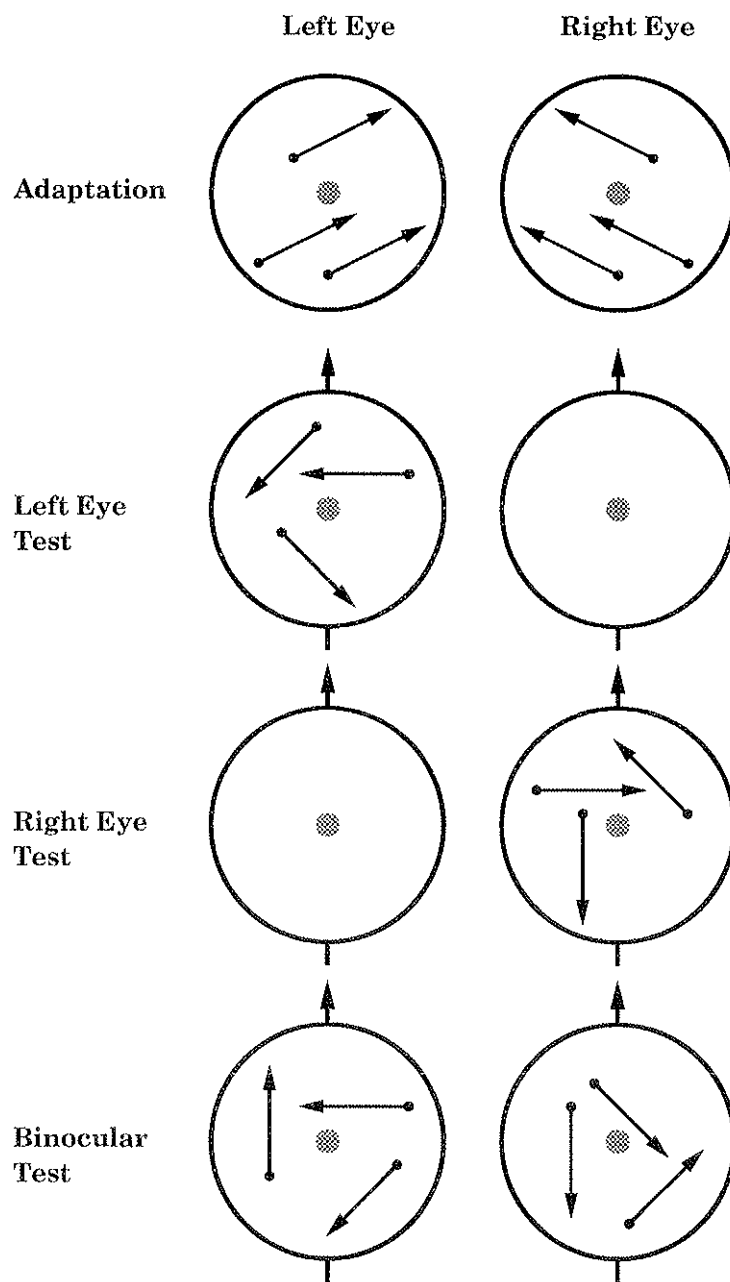


Figure 2:

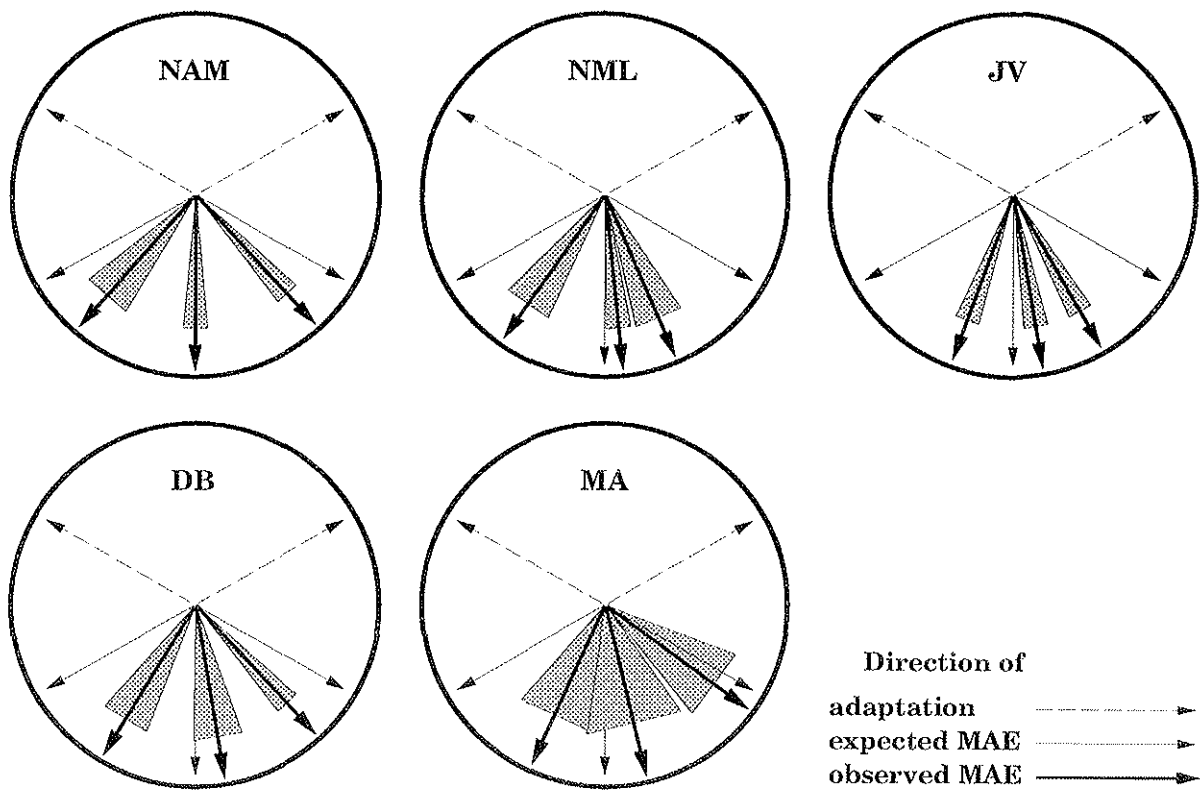


Figure 3: