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STORAGE OF AND RECOVERY FROM THE MOTION AFTEREFFECT: EVIDENCE FOR A DUAL PROCESS INVOLVING FATIGUE AND RECALIBRATION

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A Thesis
in
the Department
of
Psychology

Presented in Partial Fulfillment of the Requirements
for the Degree of Doctor of Philosophy at
Concordia University
Montréal, Québec, Canada

September 1999

0-612-43575-X

ABSTRACT

Storage of and Recovery from the Motion Aftereffect: Evidence for a Dual Process Involving Fatigue and Recalibration

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Concordia University, 1999

After prolonged inspection of motion in a particular direction, subsequent viewing of a stationary stimulus induces the perception of motion opposite to adaptation. This is the historical waterfall illusion, today referred to as the motion aftereffect (MAE). The purpose of this dissertation was to posit a functional theory which better explains the underlying neuropsychological mechanism responsible for the production of the motion aftereffect. A psychophysical approach was employed to test the predictions which stem from the traditional fatigue and the recalibration models. To investigate this question, this series of experiments examined the most difficult challenge to the conventional fatigue interpretation, that is, the storage of the motion aftereffect. In Experiment 1, MAE duration was recorded for variable adaptation durations and the decay of the MAE was tracked. In Experiment 2, MAE duration was measured following uninterrupted- versus interrupted-adaptation to test for storage via summation across adaptation episodes. Experiment 3 examined the effect of the intervening visual environment on the long-term storage of the MAE. Finally, Experiments 4a and 4b investigated the time course of immediate and long-term MAEs which were induced in opposite directions to each other. All experiments yielded evidence of MAE storage. The time course for recovery from adaptation illustrated a fast component, independent of the visual environment, like that postulated by traditional fatigue models. As well, a slower mechanism was evident from the data, which did depend on one's visual experience, and hence is consistent with the notion of visual recalibration.

ACKNOWLEDGMENTS

A doctoral thesis is anything but individual, rather it is a project influenced by many people. It would not be possible without the constant intellectual guidance and motivational support from my supervisor, Dr. Michael von Grünau. Thank you sincerely meim Doktorvater, you have taught me so much throughout my graduate studies. In you, I have found a mentor, and a dear friend.

I would also like to express my gratitude to Drs. Rick Gurnsey and Michael Bross. Your guidance, expertise, and valuable insight was appreciated throughout all stages of this thesis. Our many discussions together were both interesting and challenging, and have been integral to my intellectual growth. Thank you also to committee members Drs. Keith Humphrey and Reginald Storms for offering your time and expertise in the evaluation of this dissertation.

Thank you kindly to all of the participants. Your dedication to the many hours of testing was greatly appreciated.

I greatly appreciate the support from Fonds pour la Formation de Chercheur et l'Aide à la Recherche (FCAR), as well as from Concordia University that I received during my graduate studies.

While working is possible in any environment, successful and enjoyable research is a direct result of the laboratory family. The continuous support, patience, motivation, and good friendships which were established in our lab was an important contribution to my education and this thesis. Thank you and I have enjoyed working with you all: Stéphane Dubé, Marta Iordanova, Lyne Racette, Armando Bertone, Peter April, and of course Michael von Grünau.

The love from my family made the good times better and the not so good times bearable. Thank you to my family, especially to my mother and father for encouraging my education despite the consequence of the many miles between us. Your love and airmiles have been much appreciated over these years.

I would like to express my sincere gratitude to my colleague, friend, and husband, Dr. Stéphane Dubé. When I was frantic, you were calm. When I was impatient, you were tolerant. When I was exhausted, you were motivational. In all that you are, you continue to inspire me to be all which I can. I admire your accomplishments and I love you.

The unconditional love from a child is indeed the greatest inspiration of all. Thank you Céleste and Estelle for filling my heart with more love than I could have imagined. Your giggles and dancing make life's stresses seem frivolous and life's challenges seem more attainable.

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GENERAL INTRODUCTION

1.1 MOTION AS A NARRATOR

The way our perceptual system operates is somewhat analogous to a parent reading a storybook to her young child.

> *You see, this is the sun, it is bright yellow. It is a circle. In fact, it is round, like a ball. In the morning it rises and at night time it sets.*

This parent has described most elements of vision simply by describing the sun to her attentive child. For instance, the shape or pattern (circle), the color (yellow), the luminance (bright), the 3-D depth component (round like a ball), as well as, the motion (rises and sets) of the object are all illustrated. The parent may not even realize the richness of visual information she is providing by these simple words. All visual attributes are important in our visual experience, however, each offers a different kind of information about our environment. Color, luminance, shape, depth, and texture can be thought to provide a context for objects or scenes, while motion information narrates the story. In the above illustrative story, for example, the child may *see* that the sun has a particular shape, color, brightness, and dimensionality, but the child may not *understand* the meaning of this object until mummy tells her (i.e. provides a motion or action for the object) or until the child detects a change in position of the object in reference to the visual scene. One could possibly remove any one of the visual parameters other than motion and although the richness would be reduced, the story would remain intact and meaningful. For instance the book could be printed in black and white, or the sun may be slightly distorted in shape, or the brightness of the sun may be reduced. If, however, the motion is removed from the object, then the meaning or purpose of the object or scene is lost. Imagine a world where the sun does not rise or set (for those societies which use this as a cue to day/night); cars do not move; people do not walk; balls that do not bounce; water does not flow; movies do not play; children do not skip. The story of life would lose its [typical] narration without the action given to our visual scenes via motion information. There are, unfortunately, some people who experience this motionless visual life as a result of damage to the area of the brain responsible for motion processing (Zihl, von Cramon, & Mai, 1983). Motion, thus, in addition to providing information utilized by the visual system for detection of an object, segregation of an object from its background, definition of an object's shape, and guidance of limb and eye movement, also provides something that all other visual attributes cannot: an object's purpose or action (Michotte, 1963). It is in this way that motion narrates the story of our visual environment.

1.2 THE MOTION AFTEREFFECT

It was just outlined how important motion information is for the proper understanding and interpretation of one's visual experience. The grave consequences of failing to detect the information provided by motion in the environment were discussed. What about the reverse motion abnormality? Can our motion system fail us by reporting motion that is not really in the visual field? Indeed, this *crying wolf* scenario does not require cerebral damage and is, in fact, an integral part of normal vision in that everyone probably has or will experience this motion phenomenon.

1.2.1 The Phenomenon and its History

Following prolonged viewing of motion in a given direction, a stationary object or pattern appears to drift in the opposite direction. Indeed, this is a well known and well-documented visual phenomenon, which, in present day, is generally referred to as the *motion aftereffect*, or MAE. Throughout history, this illusory motion effect has also been variously called the aftereffect of seen movement, the movement aftereffect, successive motion contrast, and the waterfall illusion. For over a century, however, this peculiar optical illusion was best known as *the waterfall illusion.*

Extensive historical overviews of the motion aftereffect have been published by Wade (1994) and more recently by Wade and Verstraten (1998). In the next few paragraphs some of the ancient reports they have discussed at length will be briefly outlined as well as in the subsequent discussion of stimuli and MAE measurement. They report that the MAE was probably first described by Aristotle in his book of dreams (ca 330 B.C.), where he wrote: "when persons turn away from looking at objects in motion, e.g., rivers, and especially those which flow very rapidly, they find that the visual stimulations still present themselves, for the things really at rest are then seen moving" (Ross, 1931, p. 459b). There has been much debate over whether Aristotle reported the incorrect direction of the MAE, however, after comparison of a number of different Greek translations, Verstraten (1996) claims that Aristotle did not report a MAE direction.

The first person to describe the direction of the MAE was, likely three centuries later, Lucretius ca 56 B.C. (Verstraten, 1996). His report again depicted the MAE in reference to flowing water: "when our spirited horse has stuck fast in the middle of a river, and we have looked down upon the swift waters of the stream, while the horse stands there a force seems to carry his body sideways and pushing it violently against the stream, and, wherever we turn our eyes, all seems to be rushing and flowing in the same way as we are" (Book IV, p. 309).

Wade and Verstraten (1998) state that MAE was not rediscovered until the nineteenth century in other naturalistic settings. Purkinje, for instance, in an article discussing vertigo, described the MAE as "Another form of eye dizziness (which) can be demonstrated if one observes a passing sequence of spatially distinct objects for a long time, e.g. a long parade of cavalry, overlapping waves, the spokes of a wheel that is not rotating too fast. When the actual movement of the objects stops there is a similar apparent motion in the opposite direction" (1820, p. 96-97). Five years later, he wrote of his visual experience: "One time I observed a cavalry parade for more than an hour, and then when the parade had passed, the houses directly opposite appeared to me to move in the reversed direction to the parade" (1825, p. 60), and it is this statement in reference to the MAE which is commonly quoted from him.

Nine years later Addams wrote his landmark paper about his illusory experience with a waterfall, and consequently the term "waterfall illusion" came into common use. His full article was reproduced in Swanston and Wade (1994). While observing the Falls of Foyer in northern Scotland, Addams wrote: "Having steadfastly looked for a few seconds at a particular part of the cascade, admiring the confluence and decussation of the currents forming the liquid drapery of waters, and then suddenly directed my eyes to the left, to observe the vertical face of the sombre age-worn rock immediately contiguous to the water-fall, I saw the rocky face as if in motion upwards, and with an apparent velocity equal to that of the descending water". The MAE was rediscovered independently several times since then and has typically been discussed in reference to flowing water. Thompson (1877) made reference to Addams' article and was probably the first to refer to the phenomenon as the waterfall illusion (see Wade & Verstraten, 1998). Verstraten (1994), however, states that historically "the river illusion" would have been a more suitable term because the first, and majority of the subsequent descriptions of the MAE were in reference to rivers, not waterfalls, because rivers were much more frequently encountered in the environment. Despite Verstraten's arguments, it was suggested by Wade (1994) that the MAE may have been coined *the waterfall illusion* due to the ease of inducing it with descending water. Psychophysically, there is evidence for a more compelling effect for descending water over flowing water. To illustrate, Mather (1980) found MAEs for vertical motion to be stronger than for oblique or horizontal motion, with the weakest of the three being the horizontally induced MAE. Thus "waterfall illusion" was perhaps a warranted title. Today, however, it is generally more accepted and appropriate to coin this visual illusion as the motion aftereffect due to the numerous inducing stimuli, water-related or not, natural or artificial, which induce it.

Wohlgemuth (1911 cited in Wade & Verstraten, 1998) reviewed the aforementioned reports of the MAE and conducted 34 of his own MAE investigations for his doctor of science at the University of London (discussed in section 1.2.2). Thereafter, approximately 9 studies on the MAE were published from 1911 to 1950, which grew to 79 studies from 1950 to 1963 (see Holland, 1965 for a review). In his more current review of the literature, Wade (1994) reported that most studies in the mid-twentieth century used the MAE as a tool for assessing personality characteristics, arousal, and brain pathology. In addition, he identified approximately 400 MAE studies between 1963 and 1993. This incredible number of papers was no doubt stimulated by technological advances which facilitated the study of the MAE (e.g. computerized displays, stimuli, and programming). Today, the study of the motion aftereffect remains of great theoretical interest, and is investigated both psychophysically and/or physiologically. The focus from the 1960's to the present time has shifted back to the stimulus determinants of the MAE in addition to its underlying mechanisms and functional aspects.

1.2.2 Stimuli used to Generate MAEs

Prior to formal experimentation with the MAE, the most common inducing stimuli were environmental motions such as rivers, streams, waterfalls, cavalry, or trains. In modern times, with our improved technology, other forms of rapid and continuous motion in our environment like, for instance, moving vehicles, movie credits, and subway trains, provide additional "natural" candidates for inducing an MAE. In the laboratory, however, scientists employ artificial stimuli such as mechanical wheels and infinite bands and more recently, computer generated stimuli, which permit the investigation of the properties of the motion aftereffect with a greater degree of stimulus control. Even these stimuli have undergone immense change over the years with advanced methods of stimulus generation and an increased understanding and interest in the MAE.

Wade (1994) describes how in the middle of the nineteenth century Plateau (1849) was the first to report a motion aftereffect induced by a non natural stimulus, a stroboscopic disc (a.k.a. the phenakistoscope). Like many discoveries in science, Plateau's discovery was somewhat accidental and occurred while he was studying the perceptual effects of rotating patterns. Following prolonged exposure to a rotating pattern seen through the phenakistoscope, stationary objects appeared in motion (i.e. the classic MAE). His experience motivated him to design what became known as the *Plateau spiral*, a black disc with a white Archimedes spiral on it. This was the first intentionally and artificially designed MAE stimulus. Specifically, Plateau observed that if one fixates on the disc rotating in a counter-clockwise direction, then subsequently shifts one's gaze to another object, for example, the face of a person, the object appears to shrink for some time. If, on the other hand, the disc is rotated in the opposite direction (i.e. clockwise) then the adaptation effect is also the opposite: the object seems to expand.

In his review of the historical MAE stimuli, Wade (1994) indicates that the Plateau spiral or some variant of it, like concentric, counter-rotating spirals, rotating sectored discs was the most popular and widely used stimulus in the second half of the nineteenth century and even throughout the early part of this century. It remains one of, if not the, most powerful artificial inducing stimulus to date. Due to the complexities in the resulting perceptual effects and in the generated motion vectors (Broerse, Dodwell, & Crassini, 1992), however, most contemporary researchers tend to employ simpler stimuli, so as to attain a better comprehension of the mechanisms involved in MAE production.

Wade and Verstraten (1998) found that Oppel (1856), on the other hand, conducted MAE experiments with linear motion of parallel stripes, which Bowditch and Hall (1881) modified by the addition of a stationary surround. Wade and Verstraten also describe how Exner (1887), and Borschke and Hescheles (1902) investigated MAEs following adaptation to two simultaneous and superimposed linear motion directions. This type of motion stimulus was later coined a *plaid* by Adelson and Movshon in 1982 and today are composed of two superimposed drifting sine-wave, square-wave, or rectangular-wave gratings. These stimuli have been widely used to study MAEs since their re-introduction in 1982 (e.g. Mather, 1980; van Doorn, Koenderink, & van de Grind, 1985; Wenderoth, Bray, & Johnstone, 1988; von Grünau & Dubé, 1992, 1993; Kwas, von Grünau, & Dubé, 1995, in revision).

A current issue concerns the study of MAEs induced by first- and second-order motion stimuli (Mather, 1991; McCarthy, 1993; Nishida, Ashida, & Sato, 1994; Ledgeway, 1994; Ledgeway & Smith, 1994a, b; Bertone & von Grünau, 1998). First-order stimuli (stimuli described thus far) are defined by spatio-temporal variations in luminance and/or color, whereas, second-order stimuli are defined instead by relative motion, texture, and/or contrast variations. Researchers have either utilized these characteristics in either single vector or multi-vector displays as previously outlined.

Random dot kinematograms, typically consisting of an array of say 100 computer generated dots, have also been adapted for use in MAE studies (Hiris & Blake, 1992; Blake & Hiris, 1993; Raymond, 1993a, b, 1994, 1996, 1998; Steiner, Blake, & Rose, 1994; Wist, Gross, & Niedeggen, 1994; Lankheet & Verstraten, 1995; Verstraten, Fredericksen, van Wezel, Lankheet, & van de Grind, 1996). These displays, unlike the spirals or gratings, can be adjusted in the percent coherence of moving dots in particular directions.

Finally, color has also been incorporated in the study of MAEs. Two color related manipulations have been traditionally employed. The first consists of a modified McCollough effect, making color and motion mutually contingent (Hepler, 1968; Favreau, Emerson, & Corballis, 1972; Mayhew & Anstis, 1972) and the second via the use of isoluminant stimuli (Mullen & Baker, 1985; Cavanagh & Favreau, 1985).

This brief review reveals that over the last century a wide variety of motion stimuli, real or computer generated, have been used in the ongoing investigation of the motion aftereffect. Since the mid-1970's, however, the favored MAE inducer has been some variant of a drifting sine-wave grating (Pantle, 1974; Keck, Palella, & Pantle, 1976; Keck & Pentz, 1977; Cameron, Baker, & Boulton, 1992).

1.2.3 Measurement of MAEs

The oldest and most commonly used measure of the motion aftereffect is how long it lasts; i.e., its *duration*. Though this technique was first employed by Oppel (1856) in the mid-nineteenth century (Wade, 1994), it remains the most common MAE measure to the present day. In addition, the technique has evolved minimally. Early studies relied on verbal records (e.g., subject verbalizes response to experimenter "the motion has stopped") and/or qualitative responses (e.g., MAE or no MAE). Current studies measure the duration of MAE in a quantitative and precise manner (e.g., computer records duration).

Intensity of the MAE (i.e., how strong or vivid) was and remains a qualitative measure of the MAE and traditionally involves a verbal response by subjects (Wade, 1994). Likewise, the speed of the MAE was historically measured via verbal statements (Wade, 1994), and by manipulating a lever on a kymograph (Basler, 1909 as cited by Wade, 1994). Current MAE speed measurements are made with nulling methods. The speed of the MAE is estimated by the amount of real motion to just cancel the effect.

As previously introduced, the common method of MAE measurement today is the *nulling* technique. In addition to speed estimates, this method is additionally used to quantitatively measure contrast and direction. Nulling techniques are employed with a multitude of motion stimuli including single gratings, counterphasing grating, plaids, or RDKs. For single gratings, counterphasing gratings, and plaids, the amount of contrast change necessary to cancel the MAE provides a measure of the illusory movement's contrast. Likewise, the orientation of these gratings and plaids which just cancels the MAE indicates the perceived direction of the illusory motion. In the case of RDKs, the percent of coherently moving dots required to cancel the MAE provides an estimate of the illusory motion's strength, contrast, and direction.

A related measurement technique is *direction-specific threshold elevation*, that is, adaptation to a particular direction raises the threshold for motion in the same direction, but not for other motion directions (Pantle & Sekuler, 1969; McCarthy, 1993; Raymond, 1993a, b). This method yields quantitative measures of the change in and recovery of direction thresholds.

1.2.4 General Characteristics of MAEs

Some of the more general and accepted characteristics of MAEs were reported in a review by Wade (1994) in which he discusses Wohlgemuth's (1911) review of early works, and his findings. The former includes general findings such as: the MAE requires motion across the retina; is more marked with fixation; is restricted to the adapted retinal area; is stimulated by prior motion; immediately follows adapting motion; improves with practice; can be produced in each eye independently; binocularly combines different monocular adaptations; can be produced by a wide range of speeds; transfers between eyes; can be produced by stroboscopic motion; and can be seen with the eyes closed.

In addition to these parameters, Wohlgemuth himself observed that the MAE is more readily visible in the objective than in the subjective field (eyes closed); can be revived briefly by blinking; and if the eyes remained closed for a long period of time then the MAE would still be seen upon opening the eyes. In other words, the MAE is *stored* (the topic of present interest). He also noticed that the MAE is more marked with well-illuminated stimuli; occurs with indistinct moving contours; increases with spatio-temporal frequency; is related to the velocity of the adapting motion; is better for square-wave than rectangular-wave gratings; is additive to real motion; has a velocity comparable to that of the adapting motion; occurs with light- or dark-adapted eyes; has different characteristics in the central and peripheral portions of the retina; does not occur with motion of the whole visual field; occurs for motion over very small visual angles; is the resultant of MAEs after opposite simultaneous or successive motions over the same retinal area; is restricted to the orientation of lateral motion; does not require attention; and does not occur for touch. As apparent from this summary, Wohlgemuth's observations were plentiful and have since been re-observed and investigated in more depth (discussions to follow throughout this paper). In addition to proposing neural mechanisms responsible for the production of the motion aftereffect (see sections 1.4 and 1.5), the focus of many studies has been to determine the probable site of the MAE (low- versus high-level). In the next section some of the general characteristics just mentioned will be further discussed with respect to the possible site(s) of MAE production.

1.3 SITE OF THE MAE

Many of the studies reviewed so far support the idea that the MAE results from the effects that the adapting stimulus has on low-level motion selective mechanisms. In recent times, however, numerous investigations have been undertaken in attempts to examine the role of higher-level mechanisms in the generation of MAEs and to test the hypothesis that the site responsible for MAEs is perhaps much higher in the visual cortical stream than traditionally postulated. The following sections summarize this current work.

1.3.1 Interocular Transfer Studies

Measuring the extent to which adaptation of one eye produces an aftereffect in the other eye, i.e. measuring interocular transfer (IOT), is a technique widely employed to determine where in the visual processing stream adaptation occurs. In typical experimental procedures, an adaptation stimulus is presented to one eye, followed by a test stimulus to the other eye. Physiological studies suggest that binocular integration increases as signals move from LGN to striate cortex (V1) to extrastriate areas like MT (Hubel & Wiesel, 1968; Zeki, 1978; Maunsell & van Essen, 1983). Therefore, absence of interocular transfer would suggest that adaptation occurs at a relatively early stage of visual processing. Conversely, complete interocular transfer may suggest that adaptation is occurring at a higher level, where binocular signals are completely integrated and eye-of-origin information is lost.

Steiner, Blake, and Rose (1994) compared the IOT of MAEs generated from expanding, rotating, and translating dynamic random dot patterns. The amount of coherence in a random dot motion display required to null the MAE was used to measure the strength of the MAE. Partial IOT was observed for all patterns, however the degree of IOT was found to be greater for expansion and rotation than for translatory motion. Complex motion signals, like expansion and rotation, are analyzed by motion sensors in higher visual areas like MST and 7a (Snowden, Treue, & Andersen, 1992; Sereno, 1993; Graziano, Andersen, & Snowden, 1994). That the IOT is greater for MAEs generated by these complex motion patterns and that higher level areas process these displays, together suggest the involvement of higher visual areas in MAEs to complex animation sequences.

At the same time, Nishida, Ashida, and Sato (1994) examined interocular transfer of static and flicker MAEs produced by both first- and second-order motion stimuli. Subjects adapted to either a drifting luminance grating (first-order motion) or a drifting grating defined by a flicker or texture difference (second-order motion) and indicated the subsequent duration of the MAE seen with either a static or counterphasing luminance grating test. Results indicated that the static MAE transferred partially, whereas the transfer of flicker MAE was nearly perfect. The findings implicate a higher level of processing for flicker MAE than for static MAE.

The IOT of MAE to relative motion displays was extensively examined by Wade, Swanston, and de Weert (1993). Interestingly, they measured MAE to illusory rather than to real motion. Their setup consisted of three areas; a central square-wave grating (2.3 degrees high by 2.5 degrees wide), with upper and lower gratings of similar dimensions, each separated by 0.2 degrees. During adaptation, the upper and lower gratings drifted in the same direction but the central grating remained stationary. Due to induced motion, however, observers perceived the central grating to be drifting in a direction opposite to the surround gratings. Thus, in the test phase, when all three gratings were stationary, observers reported a central MAE which moved opposite to the central grating's illusory direction. It is not clear, however, whether this central MAE was indeed an MAE to the induced motion during the adaptation phase or whether the illusory central motion was again induced motion via the surround MAEs. In general, they did report some IOT of these relative MAEs (30%), but this transfer was somewhat smaller than that from retinal MAEs (average of 50%).

Symons, Pearson, and Timney (1996) found no IOT with relative motion displays. They observed that the MAE was strongest after viewing a moving field embedded in a stationary patterned surround, which suggested that relative motion is an important signal for MAE generation. The contribution of relative motion to binocular aspects of the MAE was not clear however. Subjects viewed a uniformly moving set of random dots surrounded by a stationary random-dot annulus. These displays could be presented in a variety of combinations to each eye separately or to both eyes during adaptation and test. Although the presence of relative motion during adaptation significantly extended the duration of the monocular motion aftereffect, it did not augment IOT. The presence of stationary surround contours in the nonadapting eye did not influence the aftereffect in the adapting eye. They found that the enhancement provided by stationary surround contours is largely dependent on their presence during adaptation. The presence or absence of surround contours during the test phase did not influence the duration of the aftereffect. They therefore proposed that the motion aftereffect is, in part, the result of adaptation to relative motion that occurs relatively early in the visual pathway, before binocular integration.

Lehmkuhle and Fox (1976) reported that IOT of a translational motion aftereffect was greater if the non-adapting eye viewed an equiluminant field than if it viewed a dark field. Timney, Symons, Wilcox, and O'Shea (1996) tested this proposal in three experiments. First, they assessed IOT with equiluminant and dark occlusion for three different aftereffects (MAE, tilt aftereffect, and contrast threshold elevation). Transfer of MAE was greater with equiluminant occlusion than dark occlusion; there was no significant difference in the amount of transfer for the tilt aftereffect or the contrast threshold elevation effect. Second, they tested the hypothesis that spuriously large IOT could be the result of an aftereffect induced from tracking eye movements in the non-adapting eye. When potential tracking movements were reduced by using rotating spokes, a rotating spiral, or contracting concentric circles, there was a reduction in the occlusion-dependent transfer of the MAE. Third, they found that luminance shifts had no influence on the amount of transfer when all contours were eliminated from the non-adapting eye. They concluded that the type of occlusion used for measuring IOT of the translational MAE is important only when visible contours in the non-adapting eye contribute to the adapting process.

Nishida and Ashida (1998) investigated the conflicting findings on the amount of IOT for flicker versus static MAEs (section 1.3.4). They conducted an exhaustive study involving MAE measurement methods (duration versus nulling, see section 1.2.3), eccentricity (central versus 4.2 degrees in the periphery), attention-distracting task (section 1.3.5), as well as first- versus second-order motions (section 1.3.2). They found that there is perfect interocular transfer of the flicker MAE for duration but only partial transfer for nulling (via contrast modulation of counterphasing gratings). In addition, there was complete IOT for central presentations but incomplete IOT for peripheral fields. Partial IOT was observed following conditions involving an attention-distracting task during adaptation (digit detection in a letter stream). Finally, following adaptation to a stimulus in which first- and second-order structures were drifting in opposite directions, IOT was over 100% with a first-order dynamic test (luminance modulated counterphase grating), in that surprisingly, the MAE duration was longer for the unadapted eye than for the adapted eye.

The type of stimulus is important in the degree of IOT of the MAE. In general, there is greater IOT when the stimulus characteristics warrant a higher level of visual processing (e.g. expansion, secord-order motion, dynamic tests).

1.3.2 First- and Second-Order Studies

First-order motion is thought to be predominantly processed by a quasi-linear motion pathway that contains luminance-based motion detectors, whereas, second-order motion is dominantly processed by a non-linear pathway that involves highly non-linear preprocessing prior to motion extraction. The outputs from these two pathways are possibly integrated at a higher level (e.g. MT) where a final motion percept is determined (Kim & Wilson, 1993). The assumption that the quasi-linear pathway responsible for first-order motion is a low-level motion system (e.g. V1) and the non-linear pathway for processing second-order motion signals is a relatively high-level motion system (e.g. V2), is the basis for determining the locus of motion adaptation. Second-order MAEs would thus suggest a higher level influence, whereas, lack of second-order MAEs (MAEs found only with first-order stimuli) would imply a lower level mechanism. Incidentally, cross-adaptation MAEs would suggest an even higher level of influence (i.e. MT) following the integration of different motion signals.

The magnitude of flicker MAE following adaptation and cross-adaptation with first- and second-order motion has been measured using both a nulling method (Ledgeway, 1994) and MAE duration (Ledgeway & Smith, 1994b). The second-order motion adaptation stimulus was composed of contrast-modulated noise produced by multiplying two-dimensional random noise by a drifting vertical sinewave grating. The first-order adaptation stimulus was composed of luminance-modulated noise produced by adding the sinewave grating to the noise field. The test stimuli were directionally ambiguous first- or second-order motion patterns composed of either two opposite drifting sinewave gratings added to static noise or its contrast-modulated equivalent. Results revealed similar MAEs for first- and second-order motion for both the same- and cross-adaptation conditions. These data therefore imply that MAEs are generated at a high level site where integration of first- and second-order motion signals takes place, such as MT (Wilson, Ferrera & Yo, 1992).

In the report previously described in section 1.3.1 (on IOT), Nishida et al. (1994) examined static and flicker MAEs produced by both first- and second-order motion stimuli. Again, subjects adapted to either a first-order motion or second-order motion and indicated the duration of their subsequent MAE with either a static or counterphasing luminance grating test. Both first- and second-order motion stimuli produced aftereffects, however, static MAEs were produced only by first-order motion, thus implicating a higher level of processing (V2) for the second-order stimuli.

Drift direction, spatial frequency, and stimulus type (first- or second-order) of adaptation and test stimuli were systematically manipulated and direction-identification thresholds were measured by Nishida, Ledgeway, and Edwards (1997). They reported robust elevations of direction-identification thresholds when adaptation and test stimuli were either both first-order or second-order gratings. Interestingly, these effects exhibited both direction and spatial frequency selectivity. Cross-adaptation between type of stimulus (first- versus second-order) were present but weak in comparison to the matched conditions. They argued that these findings give direct support for the existence of multiple-scale processing for first- and second-order motion and that they are initially processed by different mechanisms.

Cropper and Hammett (1997), contrary to many recent psychophysical studies on MAE, did not observe MAEs following second-order motion adaptation. They claim that the spatial frequency and orientation content of the first-order (luminance) carrier is very important in determining the properties of a second-order (contrast) modulation of that carrier. In light of this they examined whether there was any evidence for a motion aftereffect in one-dimensional second-order patterns containing only two sinusoidal luminance components (i.e. a spatial beat). Their stimuli consisted of either one cycle per degree (cpd) luminance sinusoids or one cpd luminance beats modulating a carrier sinusoid of five cpd. MAE magnitude was measured for all combinations of first and second-order test and adapting patterns. Both static and dynamic test stimuli were utilized. MAEs were only induced by first-order adapting stimuli, and likewise, were only measurable in first-order test stimuli, regardless of whether the test was counterphased or otherwise. They concluded that the induction of a motion aftereffect for second-order stimuli is not a general result and is critically dependent upon (amongst other things) the local properties of the stimulus, including the spatial frequency and orientation content of the first-order carrier.

Their findings support a low-level MAE mechanism perhaps in area V1, prior to the analysis of second-order motion signals.

As discussed in section 1.4.3.3, a static grating surrounded by drifting (inducer) gratings is perceived to drift in the direction opposite that of the inducers. The subsequent MAE is consequently opposite to the illusory central motion perceived in adaptation (i.e. same direction as the surrounding inducers during adaptation). To yield a better understanding of first- and second-order MAEs, Nishida, Edwards, and Sato (1997) investigated simultaneous motion contrast differences for first- and second-order stimuli with static and counterphasing central gratings (not a MAE study per se). When the central grating was static, the second-order surround stimuli induced little motion contrast (i.e. poor induced motion) whereas the first-order surround stimuli produced clear motion contrast. If the central grating was instead dynamic (counterphase flicker), first- and second-order surround stimuli produced equally effective motion contrast. The type of stimulus employed in the study of relative motion aftereffects is thus important in that, if the induced motion seen in adaptation is weak to begin with, the subsequent MAE will necessarily be weak, if present at all.

Bertone and von Grünau (1998) extended the investigation of first- and second-order MAEs to compare central with peripheral fields of view. They adapted participants to first- and second-order motion stimuli in central and peripheral visual fields followed by subsequent testing of MAEs via static and counterphasing (dynamic) test gratings. Dynamic MAEs were equal in duration across eccentricities for both first- and second-order motion adaptation. Static MAEs, conversely, were observed for both types of adaptation in the periphery, but a central static MAE was found only following first-order motion adaptation. The authors interpreted the central MAE to be a special case of motion aftereffect, perhaps mediated by a low-level mechanism, consistent with previously reported data.

Some studies reviewed in this section support an MAE generated by second-order motion and hence support a higher level influence. Other studies did not observe MAEs following second-order motion and thus support a low-level mechanism. One important aspect of this inconsistency may be, as Cropper and Hammett (1997) argue, that there are fundamental differences in what researchers are considering to be *pure* second-order motion stimuli.

1.3.3 Coherent Motion Studies

While the majority of cells in area MT are thought to process one-dimensional motion signals, some also seem capable of combining different motion signals to create a coherent motion percept. Areas lower than this (i.e. V1), on the other hand, are thought to process only one-dimensional motion signals (Movshon, Adelson, Gizzi & Newsome, 1985; Rodman & Albright, 1989; Snowden, Treue, Erickson & Anderson, 1991). Motion aftereffects induced by a stimulus which contain two component motions (i.e. plaid stimulus) have been investigated to determine if their characteristics imply pre- or post-integration of motion signals. Two MAEs, opposite to the two component directions might implicate a low-level influence on motion adaptation, like area V1. One MAE, in the direction opposite to the resultant, on the other hand, might suggest that a higher level (e.g. MT) is involved either in the production of MAE following motion signal integration, or in the integration of the two MAEs thus resulting in only one MAE direction. In any case, one resultant MAE would be evidence implicating higher level processes in the motion aftereffect.

After adaptation to two superimposed simultaneously (Marshak & Sekuler, 1979; Mather & Moulden, 1980; van Doorn, Koenderink, & van de Grind, 1985) or successively (Levinson & Sekuler, 1976) drifting gratings (i.e. a plaid), result in one coherent MAE opposite to the vector sum of the inducing components (Riggs & Day, 1980; Movshon et al., 1985). More recently, these findings have been replicated with two simultaneously (Verstraten, Fredericksen, & van de Grind, 1994) or successively (Verstraten, Fredericksen, Grüsser, & van de Grind, 1994) moving random-pixel arrays. These displays yield the percept of two sheets of dots transparently drifting over one another. The data again illustrated that although two directions are perceived simultaneously during adaptation, the MAE is unidirectional, opposite to the vector sum direction (i.e. the coherent percept direction) during induction. These findings thus support the notion that MAEs are formed following the integration of individual motion signals and hence implies a high-level influence.

The above results indicated that coherent motion perception is involved in the production of the motion aftereffect. To test this , Raymond (1993a) had subjects adapt to a unidirectionally moving random dot kinematogram (RDK with 100% coherence), and subsequently tested their direction sensitivity to global motion in a noisy RDK (<100% coherence) was measured. Global motion sensitivity is assessed by measuring motion coherence thresholds (i.e. the percentage of coherently moving dots needed to correctly identify the direction of movement). Following motion adaptation, coherence thresholds were elevated in the adapted direction while thresholds in the opposite direction (i.e. the direction of the traditionally measured MAE) were unaffected. Raymond suggested an extrastriate mediation of motion integration based on her data. It is believed that MAEs (at least those from RDKs) are likely due to the depressed ability to detect coherent motion, and because area MT is thought to be responsible for integrating motion signals, it follows that these data support a high site of adaptation. Note also that Raymond demonstrated 100% IOT of this effect (Raymond, 1993b), again suggesting high level involvement.

Additional evidence which suggests that perception of coherent motion can be reduced via adaptation is provided by von Grünau and Dubé (1993). Different from Raymond, these authors employed plaids in their investigation which could be manipulated in their transparency/coherence percept. Specifically, temporal and/or spatial characteristics can be modified to create plaids which yield either the percept of two gratings moving in their respective directions or that of a plaid which moves in a novel direction consistent with vector summation (Adelson & Movshon, 1982; Adelson & Movshon, 1984; Stoner, Ramachandran, & Albright, 1990; Krauskopf & Farell, 1990; Vallortigara & Bressan, 1991; Trueswell & Hayhoe, 1993; Kwas, von Grünau, & Dubé, 1995, in revision). von Grünau and Dubé found that subjects who adapt to coherence or transparency subsequently perceive an ambiguous test plaid as less coherent or less transparent, respectively, suggesting that the processes for the two percepts are quite independent. These processes are proposed to be identified with both low-level mechanisms (i.e. direction selective units in V1) for transparency, and high-level mechanisms (i.e. pattern sensitive cells in MT) for coherence (Movshon et al., 1985; Snowden et al., 1991).

It is important to note that although this line of evidence seems to imply a role for direction- and pattern-selective mechanisms, there is evidence that MAEs for the component motions may not exist as such, but rather that the MAE is formed at or after the site where components become integrated. Verstraten, Fredericksen, Grüsser et al. (1994), for instance, demonstrated that adaptation to unidirectional motion is stored and used in combination with adaptation to subsequent orthogonal motion. Other studies related to coherent versus transparent MAEs typically report similar findings (Wenderoth et al., 1988;

Burke & Wenderoth, 1993; Alais, Wenderoth, & Burke, 1994; Alais, Burke, & Wenderoth, 1996; van Wezel, Lankheet, Verstraten, Marée, & van de Grind, 1996).

The coherent motion studies reviewed in this section support an extrastriate contribution to the motion aftereffect. The final perception of the motion aftereffect is singular and whether it follows the integration of multiple MAEs or of multiple motion signals, the region whose properties most resemble the percept is high level, at least in area MT where motion signal integration is thought to occur.

1.3.4 Static versus Dynamic Test Stimuli Studies

The nature of the patterns used to test for the MAE are important because they are generally thought to reveal different sites of adaptation along the path of visual motion processing. A static MAE is simply a motion aftereffect observed with a stationary test pattern. A dynamic MAE (synonymous to flicker MAE), on the other hand, is a motion aftereffect seen with a non stationary test stimulus (examples include RDKs and counterphase flicker patterns). It is believed that a static MAE indicates the adaptation of a low-level motion-mechanism responsible for the processing of first-order motion and a flicker MAE reflects motion processing at a higher level responsible for the processing of second-order motion (Nishida & Sato, 1995).

Nishida et al. (1994) examined the interocular transfer of static and flicker MAE produced by both first- and second-order motion stimuli (previously discussed in sections 1.3.1 and 1.3.2). They reported that static MAEs were induced only by first-order motion and IOT was partial. For flicker (dynamic) MAEs IOT was nearly complete with either first- or second-order adaptation stimuli. The findings implicate a higher level of processing for the flicker MAE than for the static MAE.

Nishida and Sato (1995) had subjects adapt to a stimulus with both first- and second-order structures that moved in different directions. Their subjects reported static MAEs in the direction opposite to the first-order component in the adaptation stimulus, and flicker MAEs in the direction opposite to the second-order component. These observed differences in MAE may implicate higher level processing for dynamic MAEs.

The temporal tuning properties of dynamic MAE (flickering test stimuli) was examined using sinusoidal gratings of several spatial frequencies (Ashida & Osaka, 1995). The MAE duration was measured for various adapting temporal frequencies. Unlike the static MAE, the flicker MAE did not depend on temporal frequency, but did depend on its velocity. They took this as further support for the idea that the two kinds of MAE have different origins and suggest a higher origin for the flicker MAE, perhaps in area MT or MST.

Using random-dot kinematograms, Verstraten et al. (1996) investigated different characteristics of storage (see section 1.6) of MAEs obtained with stationary test patterns versus dynamic test patterns. The static MAE was almost completely stored when the static test was preceded by a dynamic test while the dynamic MAE was not stored when dynamic testing was preceded by a static test pattern. Their results support different characteristics of the static and dynamic MAEs and thus they too posit higher level influences responsible for dynamic tests. Recently, however, van der Smagt, Verstraten, and van de Grind (1998) found that dynamic MAEs could be stored when preceded by the static test pattern, if adapting motion was high speed (11.28 to 14.10 degrees/second, individually adjusted).

These results, they argue, also yield support for differential sites of static versus dynamic MAEs in that each has preferential speeds.

Previously the study by Nishida, Edwards, et al. (1997) was discussed in reference to its first- and second-order parameters (section 1.3.2). The study also investigated the differences between static and dynamic tests. Although they do not examine the motion aftereffect, they do offer pertinent information in regard to stimulus characteristics in motion perception. To better understand first- and second-order MAEs, they investigated simultaneous motion contrast differences for first- and second-order stimuli with static and counterphasing central gratings. When the central grating was static, the second-order surround stimuli induced little motion contrast (i.e. poor induced motion) while the first-order surround stimuli produced clear motion contrast. If the central grating was instead dynamic (counterphase flicker), first- and second-order surround stimuli produced equally effective motion contrast. Their study illustrates the complexity in the first- and second-order motion interactions. Their findings perhaps support differential sites of adaptation dependent upon whether the central motion was first- or second-order.

The effects of adaptation and test contrasts on the duration of the static and dynamic MAEs were examined by Nishida, Ashida, and Sato (1997). The effects of contrast on the duration of static and flicker MAEs were quite similar. MAE duration increased with increasing adaptation contrast and this was observed for all of their test contrasts. For example, when the test contrast was low, MAE duration increased rapidly with increasing adaptation contrast, and saturated at a low level. When the test contrast was high, MAE duration also increased but did so over a wider range of adaptation contrasts. Finally, MAE duration decreased steadily with increasing test contrast (i.e., when adaptation contrast was held constant). In contrast with other studies, their findings reveal a functional similarity between the static and dynamic motion aftereffect and because dynamic

MAEs are thought to be processed by higher levels in the visual stream, their data imply similarly high level influences for both types of MAEs.

Likewise, Hess, Demanins, and Bex (1997) demonstrate similar behavior between static and dynamic MAEs. The motion aftereffect was measured using both static and dynamic test stimuli in a group of normal observers and a group of strabismic amblyopes. Amblyopes exhibited a reduced aftereffect for both static and dynamic stimuli and only two of the eight amblyopes exhibited any measurable interocular transfer for either test stimulus. Interestingly, these results suggested a motion deficit in amblyopia affecting both the static and dynamic motion aftereffects in a comparable manner, suggesting that both low- and high-level influences may be affected.

As already discussed (section 1.3.2), Bertone and von Grünau (1998) examined first- and second-order MAEs to compare central with peripheral fields with both static and dynamic test gratings. To recap, dynamic MAEs were equal in duration across eccentricities for both first- and second-order motion adaptation. Static MAEs, on the other hand, were observed for both types of adaptation in the periphery, but a central static MAE was found only following first-order motion adaptation. The authors interpreted the central MAE to be a special case of motion aftereffect, perhaps mediated by a low-level mechanism (only the first-order motion was able to drive the static MAE in central field of view).

The conclusions based on static and dynamic MAEs are somewhat like those drawn from the first- and second-order MAEs and likely share the same explanation. All the studies which investigate the static versus dynamic tests employ first- and second-order motion stimuli and hence the inconsistencies may again be related to the fact that researchers may not be using comparably "pure" second-order motion stimuli. However, the evidence does generally support some high level input into the motion aftereffect with these types of displays.

1.3.5 Attention Based Studies

If attention has a modulatory effect on the motion aftereffect then this can also be used as a tool for pinpointing the locus of MAE. Little effect of attention has been demonstrated in the primary visual cortex (Haenny & Schiller, 1988), whereas several studies have shown that spatial attention gates the responses in V4 and IT (Desimone, Wessinger, Thomas, & Schneider, 1990). Large modulatory effects were found for cells in area MST and 7a with a match-to-sample cognitive task (Ferrera & Maunsell, 1992). Thus if attention has an effect on MAE then we may assume that the site at which they interact is somewhat higher level, i.e. at least beyond area V1.

Chaudhuri (1990) measured MAEs induced by a translating texture background when subjects were simultaneously engaged in a separate discrimination task during the adaptation period (both with or without a fixation point). The task consisted of striking a key when a numeral, as opposed to an alphabetical character, appeared within a small window located at fixation. Observers reported significantly weaker MAEs with reduced length for conditions involving the attentional task. Likewise, in another experiment, when the task was to indicate presence of an alphanumeric character presented centrally in the motion display (while fixation was on or lateral to character presentation), the subsequent MAE was considerably reduced. When the attentional task was to indicate when the motion display itself was a particular color (i.e. red), however, the MAE was not depressed. Chaudhuri interpreted these results as support for the idea that the MAE is susceptible to attentional mechanisms, and because physiological studies reveal attentional modulation of neuronal activity mainly at sites beyond striate cortex, these data support an extrastriate contribution to the MAE.

Similarly, Takeuchi and Kita (1994) examined the effects of a concurrent alphanumeric discrimination task on the duration of MAEs following adaptation to sinusoidal luminance patterns of translational, expansion/contraction, and rotational motion. They found that attentional effects depended on the type of adapting motion and the size of the adapting stimulus. The MAE of translation motion, for instance, was attenuated by the attentional task, whereas, the MAEs following the more complex motions were unaffected by the attention. In addition, larger motion stimuli are less susceptible to the effect of attention. Contrary to the physiological data mentioned earlier, their results suggested that low-level motion processing is modulated by attentional processes, whereas, high-level motion detectors are less affected by these same attentional influences. In other words, the MAE cannot always be switched off (Braddick, 1990) as some have suggested.

The studies reviewed above investigated the detrimental influence of a non-motion distractor task on the motion aftereffect. The reverse has likewise been examined. Lankheet and Verstraten (1995) studied the effects of voluntary attention on the amount of coherence in a random dot motion display required to null the MAE induced by dynamic random dot patterns having 100% coherence. While adapting, observers paid attention to one of two transparently displayed random dot patterns, moving concurrently in opposite directions. Without selective attention to one component this stimulus display does not cause an MAE (Verstraten, Verlinde, Fredericksen, & van de Grind, 1994). Selective attention was found to modulate the susceptibility to motion adaptation. Attending to the rightward drifting grating induced a leftward MAE, and vice versa. They concluded that attention can differentiate between spatially superimposed motion vectors and that attention modulated the activity of motion mechanisms before or at the level where adaptation gives rise to MAEs. Motion sensitive units in areas V4 (Wilson, Ferrera, & Yo, 1992), MST, and 7a show large modulatory effects, thus suggesting extrastriate contribution to MAEs.

Similar attentional influences have been observed with a bivectorial stimulus that could be seen as first-order motion in one direction or second-order motion in another (Iordanova, Riscaldino, Gurnsey, & von Grünau, 1996). Participants adapted to the bivectorial pattern and were instructed to attend to either the first- or second-order component. Flicker MAEs were longer for the attended direction and likewise shorter for the unattended direction in comparison to passive viewing conditions (no instruction to direct attention), illustrating the higher level influence of attention on MAE production.

Bertone, von Grünau, and Pakneshan (1997) replicated Lankheet and Verstraten's (1995) finding with a slightly modified experimental procedure. Subjects either passively adapted to a plaid or actively attended to one of the moving components and were later tested with both counterphase flickering and a stationary plaid. Following the non-attending condition, subjects reported MAEs opposite to the adapted plaid direction. After attending to a component during adaptation, on the other hand, MAEs were maximally opposite to the attended component direction with flicker and static tests. With subsequent viewing of a static test, however, perceived direction eventually shifted opposite to the plaid direction. These data indicated a time limit for attentional modulation particular to static test stimuli.

The modulatory influences of attention are thus threefold. Distracting attention away from motion adaptation can cancel an MAE; directing attention to the adapting motion can strengthen the MAE; and finally, directing attention to the adapting motion can even produce an otherwise absent MAE. The site of adaptation, however, is less clear. Physiological data indicate that attention has little if any effect on the primary visual area.

Combined with the evidence reviewed in this section supporting the effect of attention of the MAE, it would seem that the site must be higher than area V1. The psychophysical data from Takeuchi and Kita (1994), demonstrating attentional influences on translational motion which can be analyzed by V1 cells, complicates this theory a little.

1.3.6 Functional Magnetic Resonance Imaging (fMRI)

Tootell, Reppas, Dale, Look, Sereno, Malach, Brady, and Rosen (1995) used fMRI to measure local haemodynamic changes (reflecting activity) in human visual cortex during production of the MAE. They demonstrate a clear increase in activity in V5 when subjects experienced an MAE following adaptation to stimuli moving in a single local direction. Two gratings moving in reversing opposed directions, produced neither a perceptual motion aftereffect nor elevated blood flow levels post-adaptation. The time course of the motion aftereffect (measured in concurrent psychophysical tests) was essentially identical to the time course of the fMRI motion aftereffect. Tootell et al. claim that because the motion aftereffect is direction specific, this is indicative that cells in human area V5 are also direction specific. In addition, they recorded in five other retinotopically defined cortical areas and report that similar motion-specific aftereffects were either absent or when present, were smaller than those in V5.

Employing fMRI, Rees, Frith, and Lavie (1997) examined cortical activity in motion areas of the brain during motion adaptation. They tested Lavie's theory of attention, which proposes that the processing load in a relevant task determines the extent to which irrelevant distractors are processed. Participants were required to perform linguistic tasks of low or high load while ignoring irrelevant visual motion in the periphery of the display. Although task and distractor were unrelated, both functional imaging of motion-related activity in cortical area V5 (i.e. equivalent to MT in monkey) and psychophysical measures of the motion aftereffect were reduced during the high load linguistic task. They argue that these findings are consistent with the prediction that perception of irrelevant distractors depends on the relevant processing load. This is an elegant study which yields physiological support for the psychophysical findings (outlined in the previous section), illustrating attentional modulation of motion perception and hence the subsequent motion aftereffect.

Likewise, Uusitalo, Virsu, Salenius, Nasanen, and Hari (1997) recorded magnetoencephalographic responses from seven adults during the presentation of stationary and rotating radial gratings. Rotations lasting one second evoked movement-specific sustained activity in the parieto-occipitotemporal border area, in agreement with the activation of the V5 complex specialized for the analysis of movement. The source areas of the movement-specific sustained fields were transiently active 100-130 milliseconds (ms) after the onsets of both rotating and stationary stimuli, suggesting that movement-related cortical areas respond to any transient changes in the visual environment. Transients were evoked also in other brain areas 60-200 ms after onsets of both stimuli. Four subjects displayed additional motion-related sustained activity in the rolandic area. Sustained activity continued after the stimulus movement in several subjects during perception of the movement aftereffect. The authors concluded that the transient activity may evoke visual attention while sustained activity of the V5 complex may be related to the conscious perception of movement (and hence the MAE).

A close correlation between activity in MT/V5+ and perception of the MAE was observed in a fMRI study by He, Cohen, and Hu (1998). Activity was high during adaptation and experience of the MAE, but low during a blank interval (storage interval). In their second experiment, subjects experienced MAEs and their MT/V5+ activity was high when they fixated the same location as adaptation. MAEs were not observed, and MT/V5+ activity was correspondingly low, when subjects fixated a remote location. They interpret their findings to be indicative of MT/V5+ cells involved in the production of the MAE.

In a similar fMRI study, Culham, Dukelow, Vilis, Hassard, Gati, Menon, and Goodale (1999) demonstrated comparable results. Again, activity in area MT+ was high during adaptation, dropped during the storage interval (pitch black), and was again enhanced thereafter during the test period when the subjects experienced their MAEs.

1.3.7 Conclusions

Currently, not much is known about the site of generation of the motion aftereffect. Conclusive neural imaging evidence is only beginning to emerge. Based on the aforementioned studies on IOT, first- and second-order MAEs, coherent motion, static versus dynamic tests, the role of attention, and fMRIs, it may be postulated that the site of MAE production depends on the type of adaptation and test conditions. In addition to investigating the probable site of MAE, researchers have been proposing different theoretical interpretations of the mechanism underlying the motion aftereffect. As will be discussed in the following sections, neural fatigue cannot thoroughly account for this aftereffect and hence it is understandable that research has not been successful at converging on a single adaptation site based on the characteristics of typical cell responses particular to the visual areas. The ensemble(s) of cells that is (are) most responsible for the processing of the differential characteristics of adapt and/or test patterns may feed their analyses to some processor that uses the information to calibrate and recalibrate the visual system (discussed in section 1.5).

1.4 TRADITIONAL MODELS OF THE MOTION AFTEREFFECT

With the fascination of observing the motion aftereffect came the scientific desire to fully understand its physiological substrate. Theories of the MAE have evolved with our growing comprehension of visual circuitry and neuroanatomy. This next section will examine several theories of the MAE and their historical evolution.

1.4.1 Eye-Movement Model

The earliest theoretical account for the motion aftereffect suggested that residual *eye movements* are responsible for the illusory motion (Purkinje, 1820; Addams, 1834; Classen, 1863; Helmholtz, 1865; Exner, 1894; Wohlgemuth, 1911; see Wade, 1994 for a review). Addams (1834), for instance, explained the motion aftereffect in the following manner: "I conceive the effect to be owing to an involuntary and unconscious muscular movement of the eyeball, and thus occasioning a displacement of the images on the retina" (p.373). He suggests that following several brief periods of tracking the descending water (periodic contraction of the eye muscles) and thereafter gazing at a stationary surface (e.g. rock), the eye muscles will invariably continue to drift in the tracking direction (pursuit afternystagmus) yielding the perception of the still surface to flow upward. Some researchers have found that tracking uni-directional motion over time can indeed elicit an MAE and explain this effect in reference to eye movements (Mack, Goodwin, Thordarsen, Benjamin, Palumbo, & Hill, 1987; Mack, Hill, & Kahn, 1989; Chaudhuri, 1991; Timney, Symons, Wilcox, & O'Shea, 1996). There is also strong evidence which suggests that eye movements are neither necessary nor sufficient to explain MAEs in general. Wade (1994) states that even as early as 1875, Mach rejected the eye movement theory because it failed to account for motion seen in the spiral MAE. Three years later, experimental evidence supported Mach's view when Kleiner (1878 as cited in Wade, 1994) observed that following adaptation to a display in which one central sectored disc rotated in a direction opposite to two adjacent ones, subjects experienced three different MAEs simultaneously (i.e. opposite MAEs for adjacent versus central areas). Likewise, eye movements were discounted due to the fact that the MAE occurs with stabilized retinal images (Sekuler & Ganz, 1963; Drysdale, 1975).

Even if eye movements are sufficient to induce aftereffects under particular conditions, they are not necessary to produce MAEs. Furthermore, eye rotations are not correlated with the rotary MAE (Seidman, Leigh, & Thomas, 1992). Due to the substantial evidence against the eye movement interpretation, and to increased comprehension of the visual system and its physiological underpinnings, a revised theory was required to explain the motion aftereffect.

1.4.2 Ratio Model

Despite the need, the next theoretical model of the motion aftereffect was not generated until approximately a century after the eye-movement theory. Sutherland (1961), proposed that MAEs may result from the temporary imbalance of the maintained discharges of cells responsive to motion in different directions. This widely referenced *ratio model* was based on the then new and exciting evidence from Hubel and Wiesel (1959) demonstrating that cells are differentially responsive to motion direction. Their model thus attempts to account for the motion aftereffect in the following manner. When contours are not in motion, all direction-selective cells, regardless of their preferred direction, generate approximately equal levels of spontaneous baseline activity. Following prolonged exposure to a particular motion, say downward, cells preferring downward motion will have virtually no spontaneous activity. This produces a biased distribution of spontaneous activity. Cells responsive to downward motion now show little if any spontaneous activity, while cells responsive to upward motion show a normal level of spontaneous activity. This biased distribution of spontaneous activity produced following adaptation is similar to the activity distribution evoked by actual motion upward--hence the illusory upward motion. In other words, this biased distribution of spontaneous activity could produce the motion aftereffect.

Later Barlow and Hill (1963) measured responses from rabbit retinal ganglion cells, and their results corroborated Sutherland's model. Barlow and Hill specified, however, that MAEs result from the temporary imbalance of the maintained discharges of cells responsive to opposite directions (opponent-process) not simply different directions. Figure 1.1 provides a schematic illustration of the ideas put forth by both Sutherland (1961) and Barlow and Hill (1963).

Much research, unfortunately, has accumulated against the elegant simplicity of the ratio model, the strongest of which are MAEs from multivectorial transparent motion. The ratio model suggests that cells tuned to a particular direction and those tuned to the opposite, interact with each other only and not with other groups of cells. A bi-directional MAE following adaptation to non-opponent transparent motion is thus a prediction of the ratio model. Each adapting motion should theoretically cause an imbalance of firing between cells tuned to, and opposite to, the motion direction. This would produce two simultaneous MAEs. After adaptation to two superimposed simultaneously (Marshak & Sekuler, 1979; Mather & Moulden, 1980; van Doorn et al., 1985) or successively (Levinson & Sekuler, 1976) drifting gratings (i.e. a plaid), which yield the transparency

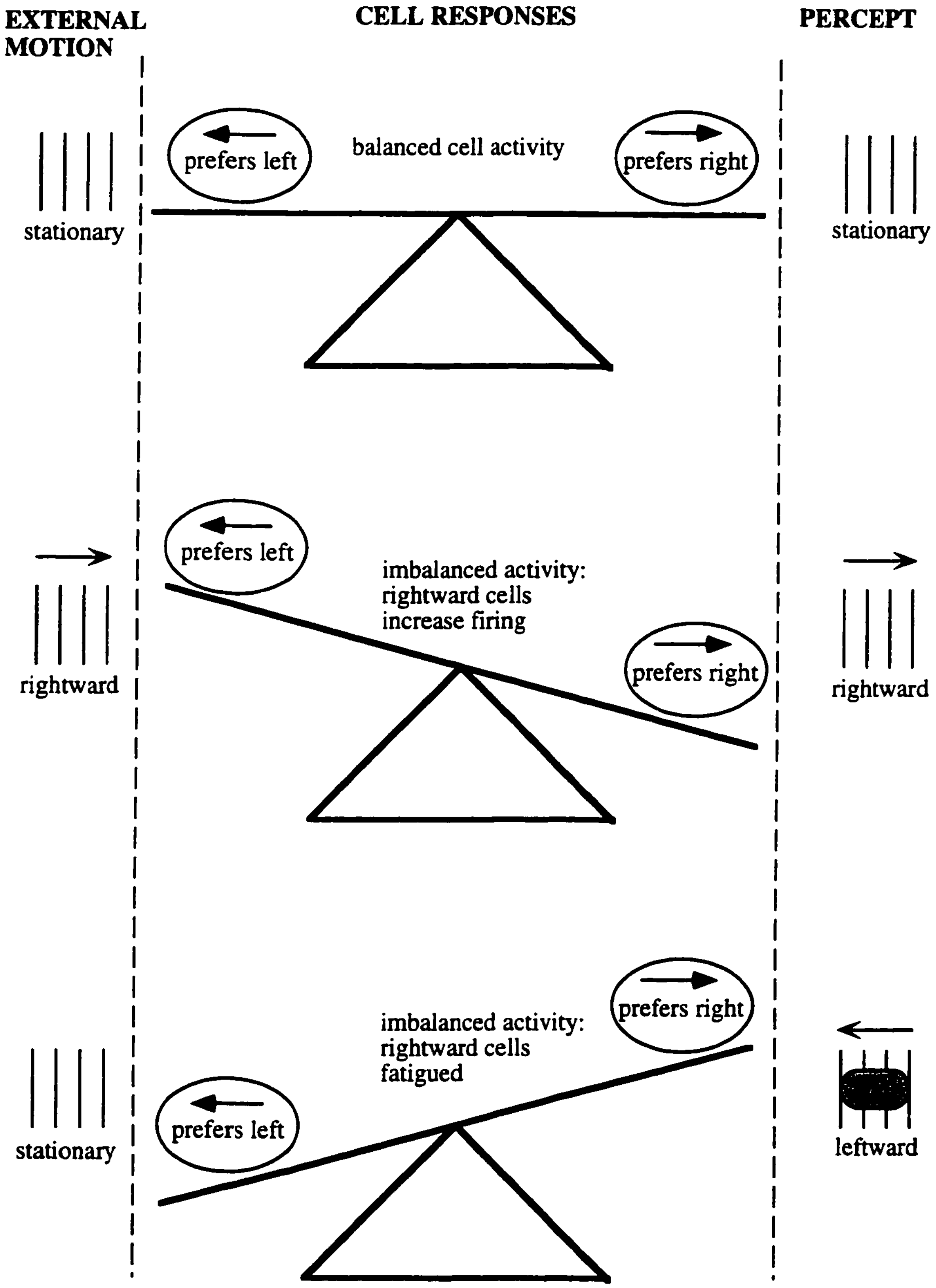

Figure 1.1. A schematic representation of the ratio model of Sutherland (1961) and of Barlow and Hill (1963).

percept during adaptation, result in one coherent MAE opposite to the vector sum of the inducing components.

Raymond (1993a) designed an elegant test of the ratio model of the MAE. Subjects adapted to a coherent unidirectionally moving RDK and subsequently their motion coherence thresholds for motion in the four cardinal directions (up, down, left, right) in a noisy RDK were measured. A noisy RDK is produced when a percentage of dots move coherently in one direction while the remaining dots are moving in random directions. Coherence thresholds are assessed by measuring the percentage of dots needed to cohere for the subject to correctly identify the direction. Following motion adaptation, coherence thresholds were elevated an impressive 0.64 log units in the adapted direction while thresholds in the other three directions (including the direction of the traditionally measured MAE) remained unchanged. Raymond refers to this as the incoherence aftereffect, in that MAEs, at least those from RDKs, are due to decreased ability to detect coherent motion. This, she argues, demonstrated that global movement analyzers operate independently, rather than in an opponent manner. The ratio model would instead predict enhanced sensitivity after adaptation in the direction opposite that of adaptation. Raymond's finding is consistent with the next model.

1.4.3 Distribution-Shift Model

A non-opponent model was first suggested by Levinson and Sekuler (1976) to account for data from a study in which they recorded the perceived direction of a vertically drifting random-dot display after adaptation to a similar pattern moving in various directions. They observed 10 degree shifts in perceived direction of the upward moving test pattern away from the adaptation direction when the test and adaptation directions differed by as much as 65 degrees in either direction. Although the ratio model provides a sufficient account for their data they suggested that a non-opponent model was more parsimonious in explaining the MAE. They posit a multiple analyzer model with independence among analyzers. Adaptation thus fatigued the analyzer(s) sensitive to the adapting direction(s) and consequently the shift in perceived direction of the test stimulus was due to a shift in the weighted average activity of *all* the direction sensors.

Subsequently, Mather (1980) independently proposed the same modification to the ratio (opponent) model into what he terms a *distribution-shift model* (non-opponent). His justification was based on the studies, as previously described, which demonstrated that adaptation to two non-opponent direction results in an MAE that is opposite direction to the resultant. Similarly to Levinson and Sekuler (1976), his model does not simply consider the ratio between the output of motion-sensor pairs tuned to opposite directions, but rather incorporates all direction selective cells into the process of imbalance. This theory is not without critical weaknesses however.

1.4.3.1 Problems with the Distribution-shift Model

The major limitation of this MAE model is the dichotomy of the percept during the adaptation phase versus the test phase. When observers view a "transparent" plaid during adaptation they clearly perceive two separate motion directions, yet during the test phase the MAE is definitely uni-directional. If our direction perception is determined by a distribution of cell responses as Mather suggests, then this model must predict a uni-directional adaptation direction as well. Alais, van der Smagt, Verstraten, and van de Grind (1995) found additional evidence that the percept during adaptation does not coincide with the direction of the subsequent MAE. They employed square-wave luminance gratings with an array of small random dots covering the high-luminance regions. Owing to the texture, the direction of these gratings, when seen through a circular aperture, is disambiguated because the visual system is provided with an unambiguous motion energy. Thus, the direction of textured gratings can be varied independently of grating orientation. They reported that when subjects were required to judge the direction of textured gratings moving obliquely relative to their orientation, they can do so accurately. This is of interest because most studies of one-dimensional motion perception have involved (textureless) luminance-defined sine-wave or square-wave gratings, and the perceived direction of these gratings is orthogonal to their orientation due to the aperture problem (Wohlgemuth, 1911). Interestingly, when subjects are required to judge the direction of an obliquely moving textured grating during a period of adaptation and then the direction of the motion aftereffect (MAE) immediately following adaptation, these two directions were not found to be directly opposite each other. MAE directions were always more orthogonal to the orientation of the adapting grating than the corresponding direction judgments during adaptation (by as much as 25 degrees). These results are not readily explained by the distribution-shift model.

As will be illustrated in sections to follow, much evidence has accumulated which shows a mismatch between the behavior of the proposed ensemble of cells and the characteristics of the MAE. For instance, a study (discussed at length in section 1.3.4) reported an interaction between adaptation and test contrasts which simply does not reflect that of the sensitivity function of motion detecting mechanisms (Nishida, Ashida, et al., 1997). Additional studies, as will be outlined in the next sections, likewise offer some challenges to this working hypothesis of MAEs.

1.4.3.2 The Incoherence Aftereffect

Recently, Raymond and Isaak (1998) employed similar experimental stimuli and procedures to Raymond (1993a) and found evidence that coherence thresholds for RDKs were elevated for adapting directions (subthreshold) and lowered for opposite directions (suprathreshold). Their previously reported finding was that there is no facilitatory effect in detecting coherent motion in the direction opposite to adaptation, which supported the distribution-shift model. These data do not seem to support the independence of motion analyers and thus may be more consistent with the opponent process of the ratio model.

1.4.3.3 Center/Surround MAEs

Murakami and Shimojo (1995) examined the effect of surround motion on the MAE elicited in the center. Their display consisted of a central sinusoidal grating which drifted within a circular aperture (approximately 3 degrees in diameter) and was surrounded by another sinusoidal grating which drifted within a rectangular aperture (approximately 24 degrees wide by 18 degrees high). The duration of MAE in the center after adaptation was measured for various surround velocities and directions. MAE was stronger when the surround moved in a direction opposite to the center than when center and surround moved in the same direction. They interpret their findings as inconsistent with a distribution-shift model for MAEs as this interpretation does not account for the influence of the surrounding loci on induced MAEs in the central region (i.e. such models are based on unidirectional motion sensitive mechanisms). Instead, they suggest that this is evidence for higher level *motion contrast detectors*, possibly located in area MT. Physiological evidence by von Grünau and Frost (1983) supports this type of double-opponent process mechanism. As such, these types of sensors would be maximally excited by opposing motion signals in central versus surround regions. Murakami and Shimojo extend the argument by adding that these motion contrast mechanisms would maximally fatigue following adaptation to contrast motions, yielding strong MAEs. [Murakami & Shimojo (1996) report further evidence for this type of motion detector in a paper not related to MAE per se]. Murakami and Shimojo's theoretical account is not so different from the distribution-shift interpretation in principle (i.e. both include fatigue as the basis for the MAE); it merely stipulates a higher order motion sensor as opposed to the Reichardt type of motion detectors. Just as Levinson and Sekuler (1976) and as Mather (1980) elaborated the ratio model, Murakami and Shimojo are likewise elaborating the distribution-shift (non-opponent) model.

Recently, Ashida and Susami (1997) using a similar center/surround stimulus as Murakami and Shimojo (1995), extended the investigation of relative motion MAEs. The relative motion signal significantly increased the magnitude of central MAEs while local MAEs in the surrounds were not affected. In addition, Ashida and Susami observed substantial MAEs only when the test stimuli included the surroundings, which is considered to be favorable for relative motion mechanisms. They conclude that their results clearly indicate that the MAE is induced by adaptation to pure relative motion, as well as by local motion, and that the motion aftereffect should be regarded as a composite phenomenon reflecting multiple sites of adaptation including the local and the relative motion levels. Ashida and Susami also argue for the existence of independent detection mechanisms for relative motion processing (i.e. motion contrast detectors).

A paper by Wade, Swanston, and de Weert (1993) offers a brief history of quantitative assessments of interocular transfer of the MAE (see section 1.3.1). They also examined the IOT of MAE to relative motion displays. Their relative motion displays were, however, not entirely equivalent to those used by Murakami and Shimojo (1995).

Interestingly, they measured MAE to illusory rather than real motion. Their setup consisted of three areas; a central square-wave grating with upper and lower gratings of similar dimensions. During adaptation, the upper and lower gratings both drifted in the same direction but the central grating remained stationary. Due to induced motion, however, observers perceived the central grating to be drifting in a direction opposite the surround gratings. Thus, in the test phase, when all three gratings were stationary, observers did report a central MAE which moved opposite to the central grating's illusory direction. This effect was previously reported by Swanston and Wade (1992) and this study tested the IOT of the effect. In general, they did report some IOT of relative MAEs but this transfer was much smaller than that for retinal MAEs. These authors attribute the type of MAE they observed to be due to *relational-motion mechanisms* which would operate in a basically similar way to Murakami and Shimojo's motion contrast detectors with the exception of their proposed anatomical location. Due to the incomplete interocular transfer of their MAEs, Wade et al. suggest that these motion detectors are predominately monocular and thus may not be as "high level" as Murakami and Shimojo imply.

1.4.3.4 MAE Induced in Blind Spot

An intriguing study by Murakami (1995) outlined additional weaknesses of the distribution-shift model. Following adaptation to a moving sinusoidal horizontal grating presented within the blind spot and surrounding area of one eye, MAEs were measured via velocity nulling within the same eye and the unadapted eye (i.e. tested for IOT). Data indicated that subjects filled-in the motion in the blind spot during adaptation, and that prolonged viewing of this filled-in motion induced an MAE for the adapted eye, and finally, that the MAE in the blind spot transferred to the unadapted eye. They interpret their findings as evidence against Mather's distribution-shift model since the blind spot is physiologically unable to encode the adapting stimulus. Such a simple model per se cannot explain the MAE inside the blind spot. In addition, the partial IOT (approximately 50%) of blind spot induced MAE is consistent with IOT size observed with other studies (Wade et al., 1993).

1.4.3.5 Conclusions

Much experimental evidence and many theoretical difficulties strongly suggest that the distribution-shift model is somewhat weak as a working hypothesis for the motion aftereffect. Independent researchers implicate the involvement of numerous motion detectors, each responsible for a different kind of MAE: opponent processors (ratio model by Sutherland, 1961 and Barlow & Hill, 1963), multiple-analyzers (non-opponent or distribution-shift model by Levinson & Sekuler, 1976, and of Mather, 1980, respectively), motion contrast detectors (Murakami & Shimojo, 1995), and relational-motion mechanisms (Swanston & Wade, 1992; Wade et al., 1993). There seems to be a need for a more parsimonious theoretical account for the motion aftereffect.

1.5 RECALIBRATION MODEL

Despite the inherent weaknesses of the traditional models of the motion aftereffect, it remains difficult to think that adaptation is not a direct result of fatigue or satiation of visual neurons, whether this is applied to motion detectors of whichever sort (for MAEs), orientation cells (for tilt aftereffect or other spatial aftereffects), or color sensitive neurons (in the case of the McCollough effect). The (perhaps only) common premise among theories of aftereffects in general, as well as within the traditional theories of MAEs, is the fatigue interpretation. The manner in which we tend to regard the motion aftereffect, and perhaps all aftereffects, is that these phenomena reflect some weakness or flaw in the visual system. It may be possible that the opposite approach would lead to a different theoretical modeling of aftereffects. Aftereffects may instead be viewed as an adaptive function, indicative of the visual system's impressive ability to accurately interpret the external environment.

It is essential to define what fatigue means. With prolonged stimulation, neurons are thought to lose their ability to continue to produce neurotransmitter at high concentrations. To use this as the main (or only) underlying mechanism when explaining aftereffects is perhaps weak considering the following three lines of evidence which demonstrate that the characteristics of MAEs do not match the neural behavior of cells. The first evidence against fatigue stems from the observation that visual aftereffects can be observed even after very brief doses of adaptation such as 200 milliseconds (ms) or less (Wolfe, 1984; Harris & Calvert, 1989; Raymond & Isaak, 1998). It would be disadvantageous that visual neurons could deplete their neurotransmitter stores with such short exposures times. The second physiological evidence, and perhaps the more important one, is that some physiological studies have shown that some visual neurons *do not* fatigue with continued stimulation. Retinal and geniculate cells do not fatigue when continuously activated (van de Grind, Grüsser, & Lunkenheimer, 1973). Similarly, Maffei Fiorentini, and Bisti (1973) recorded from some cells in the cat visual cortex which did not show any signs of reduced sensitivity. Third, and perhaps the strongest evidence against satiation, is the observation that the psychophysical time course for recovery from adaptation does not seem to coincide with recovery from neural fatigue. Indeed recovery from aftereffects can take anywhere from minutes to days and sometimes weeks (as will be discussed in section 1.6). Fatigued cells tend to recover completely anywhere from 5 seconds to 2 minutes post-adaptation (Maffei et al., 1973; Vautin & Berkley, 1977;

Hammond, Mouat, & Smith, 1988; Giaschi, Douglas, Marlin, & Cynader, 1993). These physiological responses do not match the observed psychophysical data. Any explanation which relies predominantly on neural fatigue as the underpinning of the motion aftereffect or any aftereffect may not be a complete explanation.

It seems that adaptation effects might also reflect recalibration that occurs during adaptation. The brain may interpret sensory messages in a different manner following a prolonged and biased perceptual diet such as occurs during adaptation. That is, adaptation offers the visual system a biased stimulation for a period of time. Somehow this information is used by the brain to recalibrate the visual system to reinstate the rules of the external visual environment, and our perception of it is modified accordingly. Exactly how this is accomplished, via which neurophysiological mechanisms, will be explored in the sections to follow. The notion of recalibration has not typically been used in reference to motion phenomena but in fact, it will be postulated that such an interpretation may help explain some aspect of the motion aftereffect, all aftereffects, which neural fatigue alone has difficulties accounting for.

1.5.1 Adaptation Level Theory

The first principle of recalibration is Helson's theory of Adaptation Level (1948). Helson stated that all judgments are made with respect to a frame of reference and this has been observed in psychophysical experiments and studies of attitude-formation and social behavior. The terms, *standard*, *norm*, *value*, *anchor*, *neutral point*, and *frame of reference*, he argued, clearly demonstrate this point. He in fact noted that should a frame of reference not be given to a subject (or if they are not even told to use a frame of reference) people will, by default, make judgments according to their standard or neutral point that they establish themselves. This neutral point is referred to as the *adaptation level* in Helson's theory, and it represents the center of the judgments. Though Helson constructed a quantitative theory to illustrate how adaptation level is computed, suffice it to say that it is basically a weighted average of the set of stimuli so far presented. In Helson's words, "Adaptation-level, defined operationally in terms of the stimulus evoking a neutral or indifferent response, can be quantitatively determined, and since the structure of the behavioral field is fixed by the position of the neutral point, the frame of reference is completely defined once its value is known" (p. 298).

To illustrate, if a subject is given a set of weights with no criterion to determine whether each is light or heavy, subjects will implicitly set up a neutral point based on the weights presented to them. Thus, no matter what the actual distribution of the weights is, some will be judged as light, some as average and still others as heavy, in comparison to the adaptation level adopted by the observer. Subjects will do this even though establishment of a neutral point is not specifically required. This illustration is robust in that it can be demonstrated for most judgments, perceptual or otherwise, experimentally or in the natural environment. In his article (1948) Helson demonstrates adaptation level particularly with weights, as already described, as well as with color. In reference to his color illustration, it is important to note that the adaptation level is perceptually hueless, or white light, independent of the elements. The principle remains that in response to a particular perceptual diet, the visual system responds by continuously and automatically modifying (adapting) the perceived neutral point, whether it be of weight, color, or any other perceptual attribute. Figures 1.2 and 1.3 illustrate Helson's shift in adaptation level following adaptation to color and motion, respectively. Dodwell and Humphrey (1990) discuss Helson's theory in reference to the McCollough effect and interpret the theory to support slow onset of adaptation level modification. Helson may have posited a more rapid

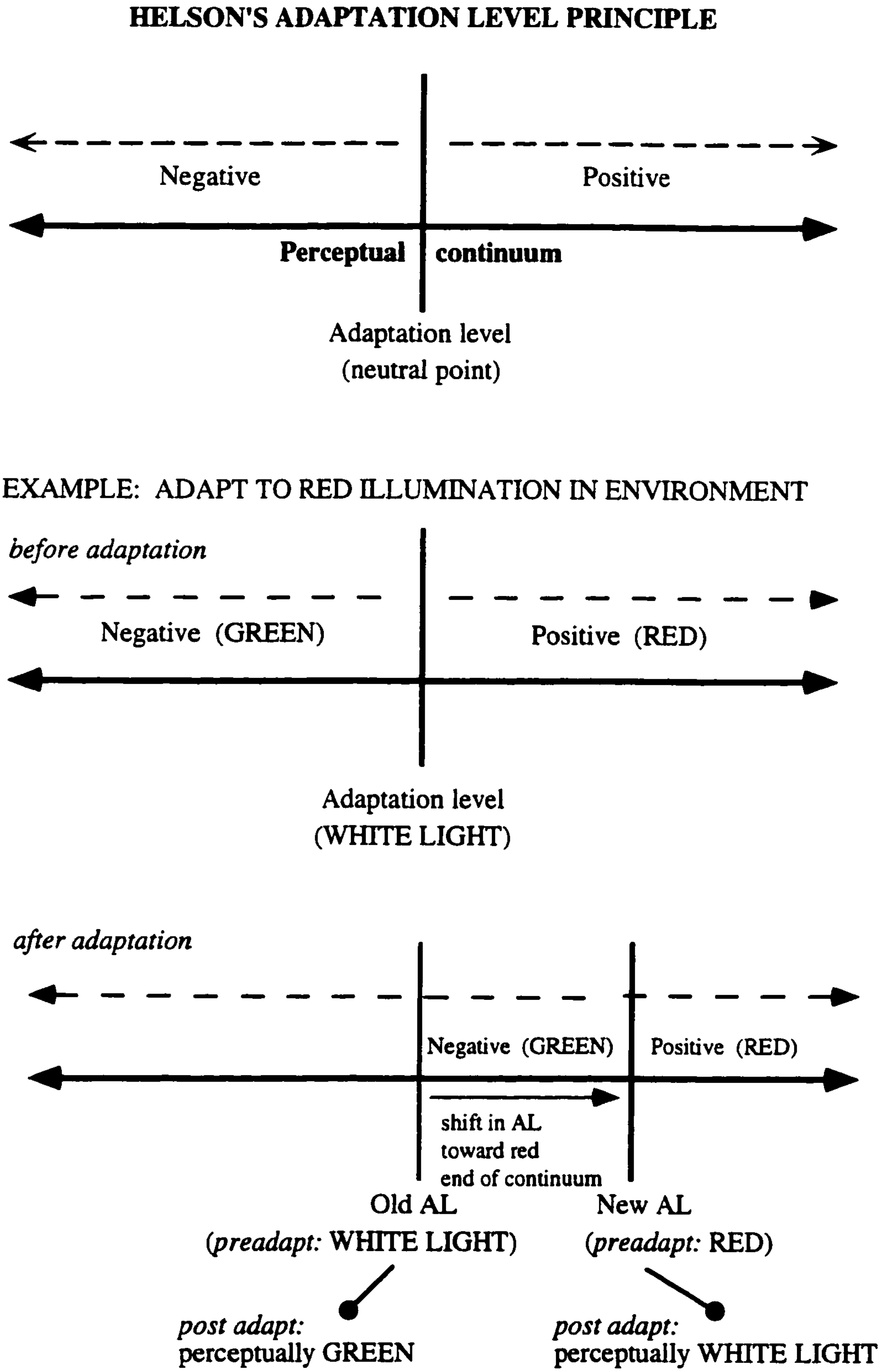

Figure 1.2. A schematic representation of Helson's (1948) adaptation level theory applied to color adaptation.

HELSON'S ADAPTATION LEVEL PRINCIPLE

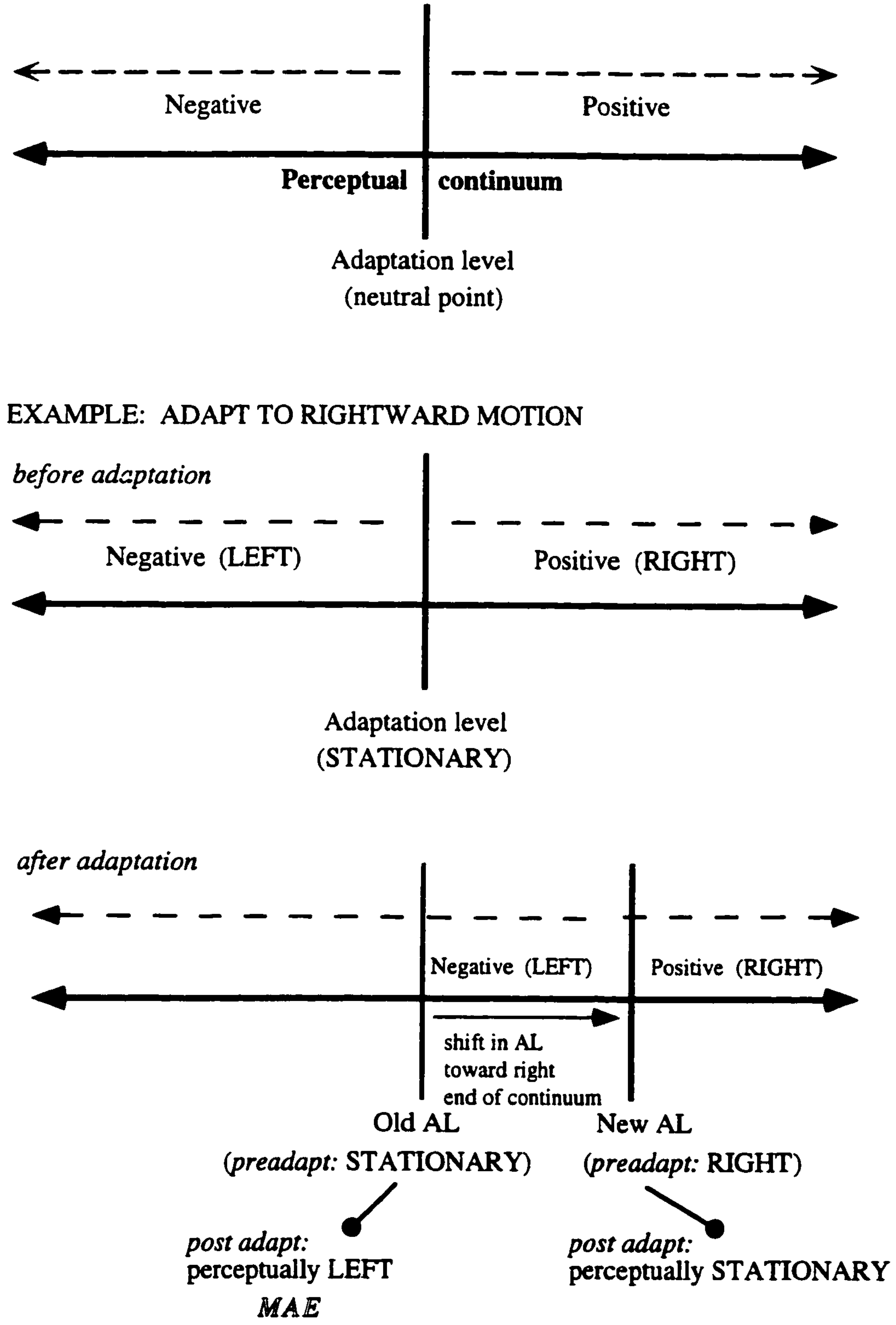

Figure 1.3. A schematic representation of Helson's (1948) adaptation level theory applied to motion adaptation.

flexibility in the visual system following a biased perceptual diet: "we must regard the visual mechanism as a system capable of extremely rapid change, any momentary state of the system representing a quasi-stationary process in dynamic equilibrium" (p.298). It may be that the visual system is continuously working at a rapid pace to maintain the precision in our adaptation levels, but that large deviations in adaptation levels occur more slowly. Just as it would be detrimental for cells to completely deplete their neurotransmitters after a few milliseconds, it would be just as unlikely for the system to completely recalibrate following a very brief episode of adaptation.

It should be noted that to date, Helson's adaptation level principle is not a widely employed theory to explain visual phenomena or processes. Dodwell and Humphrey (1990), in their paper discussing the underlying mechanism for the McCollough effect, are one of the few which have discussed the theory. The application of it to the McCollough effect will be discussed in section 1.5.4, following the description of the second important principle for recalibration. To accept the logic of Helson's adaptation level theory is easy, but the mechanism by which the visual system determines or accomplishes the shift in adaptation level or neutral point remains an issue. Andrews' Error Correcting Mechanism (1964), is a possibility.

1.5.2 Error Correcting Mechanisms

The second principle to help demonstrate how recalibration may take place is the Error Correcting Mechanism of Andrews (1964). His model offers a way in which the visual system may adapt to changes in the environment. The visual system has the complicated task of dissecting the external environment into its visual components and then putting the puzzle together again and finally interpreting this internal representation of the external world. The first step consequently is the initial transformation of information from the environment (E) to the retina (R). Following this, the transfer function (T), from R to internal representation (I) is a mapping that preserves the topology, and perhaps some degree of metric information (Maunsell & Newsome, 1987). This transformation, however, is not as precise as the physical optics and sensory physiology of the transfer from E to R.

The visual system is prone to errors of various kinds, some arising from the optical system of the eye (e.g. lens produces achromatic aberrations in the retinal image; astigmatism produces orientation distortions), others arising from the transformation processes, growth, age, damage, or unexpected changes in the environment. The visual system must overcome these visual obstacles and attempt to fulfill its neuropsychological requirement of maintaining consistency between E and I. Andrews proposed a mechanism for this. The error correcting device (ECD) rapidly and flexibly detects and corrects discrepancies between E and I. How would this function? It is first necessary to define *error* as a discrepancy between E and I or in other words, an inconsistency with respect to some known *rule*. Rules are acquired over time as the visual system determines statistical properties of E which are true in the long run. Examples that Andrews discusses include the average properties of motion and of contour curvature in the visual field. In reference to the former, on the average, movement of elements in the visual field is everywhere and in all directions zero. As argued by Dodwell and Humphrey (1990), there is probably a constant radial bias due to our forward locomotion being more frequent than backward locomotion, yet such a constant bias should not impede the argument. This is a long range statistical property based on characteristics of E which is violated continuously in the short run and as such the ECD should ignore these minor transient violations. In Helson's terms, the adaptation level for motion is, in the long run, zero net movement. Likewise, for contour perception, in the long run all contours in the environment are on average straight. Again this may be temporarily violated in the short term but must be ignored by the ECD. The adaptation level for contours is hence straightness.

1.5.3 Combining the Two Principles

How can Andrew's error correcting mechanism accomplish shifts in adaptation level? Changes in adaptation level are basically changes that attempt to preserve in I certain properties of E that on the average, and in the long run, are always present. The transfer function T, maintains congruence between properties of E and I and works by means of error-correcting codes that detect discrepancies between the known properties of E and the desired properties of I, and modifies T in order to reduce these discrepancies to zero. Although in the mature perceiving organism the congruence between E and I is usually satisfactory, it is possible to feed the system an unusual perceptual diet, e.g. adaptation, in order to bias the input sufficiently to cause changes in T.

Moses, Schechtman and Ullman (1990) describe this process in their words as *proportional multi-gain adjustment* and posit that Andrews error-correcting mechanism may work neurologically like a *self-calibrated collinearity detector.* In their paper they describe the results from computer simulations of the collinearity detector and report that these simulations indeed reflect expected outcomes (normal and adaptation conditions) remarkably well. Their self-calibrated collinearity detector operated by multiple gain controls. Their proposed neural implication of this mechanism is as follows. A main unit is fed by six subunits and each subunit has a gain variable. A subunit, they argue, may correspond to a single cell. These six cells, three excitatory and three inhibitory, converge on a single neuron, the main unit. The gain variables reflect the synaptic strength of these neurons. The response function of the scheme's subunits would be approximately linear.

Collinearity is indicated by a zero output from the main unit induced either by resting activity or equal activity from the excitatory and inhibitory inputs. Activity from the main unit will therefore increase or decrease depending upon the summed activity of the six subunits. The computation implied by their scheme requires only simple updating of the connection strengths based on local signals. In other words, the updating of the gain variables corresponds to a modification of the synaptic strength. This modification, or *gating* as they say, could be accomplished via another neuron such as the *region detector.* The region detector would hence modify synaptic strengths so as to fit the pattern of activity coinciding with the motion criterion of zero net movement in the environment over time. Interestingly, imposing a neuronal pattern of activity in I, which is normally true of E in the long run but does not match the recent activity in E, is what would manifest itself as the perceived aftereffect. To recover from the aftereffect, the neuronal activity would again be modified by the same gating method but in this case to allow the cells to respond according to the actual activity in E. Perceptually, these proposed physiological mechanisms of homeostasis are altering the neutral point of a particular visual parameter. The following illustrations will help demonstrate a possible recalibration process.

1.5.4 Illustrative Examples

In his paper, Andrews (1964) provides two illustrative examples (distorting spectacles and the waterfall illusion) to demonstrate the error correcting device and Dodwell and Humphrey (1990) provide a third, in relation to the McCollough effect. These examples will now be reviewed to illustrate how recalibration occurs via both adaptation level and error correcting mechanisms.

1.5.4.1 Distorting Spectacles

Both Gibson (1933) and Kohler (1964) have shown how the visual system adapts to wearing distorting spectacles (i.e. wedge prisms). When a subject first places the spectacles on, the ordinarily straight-lined world seems curved, but in a systematic way. In time, these distortions gradually dissipate and the curved lines appear straight once again. As previously mentioned, one of the rules of the visual system may be that lines are, in the long run, symmetrical around straight. With the application of the distorting spectacles, however, lines appear systematically curved. As a consequence of the prisms, E has changed significantly. The ECD, which works to maintain agreement between E and I, detects these deviations from the criterion rule and imposes the inverse transformation that will nullify the distortion. To accomplish this, the ECD shifts the adaptation level (AL) from straightness to systematic curvature. That is, prior to wearing the spectacles the observer's neutral point or AL was straightness; straight lines are perceived as straight. Any temporary deviation from this in E (e.g. viewing a ball) would be interpreted as non-straight contours, a perception which is made in comparison to one's reference point or AL. With the distorting glasses, however, the ECD causes a shift in the AL towards the particular curvature which the spectacles induce. The important point made by adaptation level is that whichever perceptual attribute is discussed, the AL is necessarily *neutral.* Thus if the AL is shifted toward curvature (i.e. away from straightness) it does not mean that one perceives curvature. On the contrary, now the observer would perceive a certain curvature as straightness. The distortion, thus, gradually disappears due to a change in the adaptation level (AL) via ECD so as to remove the discrepancy between E and I; to maintain the rule. Note that when the distorting spectacles are removed after some time, the observer experiences the reverse effect. The lines which are straight in E, once again appear curved in the opposite direction. The visual system, via ECD, is again required to shift AL back to its previous state to maintain congruency between E and I.

1.5.4.2 The McCollough Effect

By pairing a simple pattern with color it is possible to produce a negative aftereffect contingent on the pattern-color combination. For instance, McCollough was first to demonstrate (1965) that if vertical stripes are viewed in combination with some color, red for instance, while horizontal stripes are combined with green for example, when an achromatic test pattern appeared, after a few minutes of pairing, each grating was perceived to have the complementary hue (i.e. the vertical stripes appeared green and the horizontal stripes appeared red). The visual rule, in reference to this effect, is that in the long run, contour orientation and specific colors have zero correlation in E. During induction of the McCollough effect (ME), two contrasting contour orientations, vertical and horizontal for instance, are seen in two contrasting colors, red and green for instance, thus violating the criterion. The AL for red in the presence of verticals is shifted toward the red side of the color continuum and the AL for green in the presence of horizontals is shifted toward the green side of the color continuum. In viewing an achromatic vertical, green is therefore perceived because the neutral point is now red (in terms of physical property, but hueless in terms of percept) for vertical stimuli thus anything to the left of this new neutral (achromatic in terms of physical property) is seen as green. In the same vein, anything to the right of the neutral (a physically stronger red) is thus seen as red. For achromatic horizontals, the opposite occurs. Red is perceived due to the neutral point being shifted toward the green (in terms of physical property but hueless in terms of percept). Anything to the left of this new neutral (a physically stronger green) is thus seen as green while something to the right of the neutral (achromatic in terms of physical property) is seen as red. The shift in AL is necessary to bring the correlation between contour and color in E back to zero. To summarize, the ECD detected a non-zero correlation between contour and color in E which is contrary to the criterion in I and thus to reduce this discrepancy between E and I, changed the ALs in I to fit the criterion rule (zero correlation between contour and color).

This occurs during the induction phase. It is for this reason that the aftereffect is observed later when viewing achromatic stimuli. The ECD then requires time to shift the ALs back to their original neutral point so that the achromatic percept matches the achromatic physical properties in E.

1.5.4.3 The Waterfall Illusion (MAE)

Following prolonged inspection of descending water a stationary surface appears to drift upward (the waterfall illusion). Likewise, after adapting to, for example, rightward motion a stationary pattern perceptually drifts leftward (MAEs in general). These effects can also be explained via recalibration. The motion criterion is that on the average, movement of elements in the visual field is everywhere and in all directions zero. When, for example, linear motion (descending water) is presented in part of the visual field for a substantial period of time this violates this general principle. The ECD thus detects this discrepancy between E and I and shifts the AL for neutral movement toward the adapting direction (towards downward). A certain degree of downward motion in E is thus perceived as neutral (not moving) in I. As a result, a stationary rock appears to drift upward because neutral motion in E is now to the right of the new AL (neutral) which is normally seen as upward motion in I. Again, the ECD detects the discrepancy between E and I and works to move the AL (perceived neutral point) accordingly.

1.6 STORAGE EVIDENCE

As mentioned earlier, the strongest evidence against fatigue models of MAE stems from the recovery time for visual aftereffects. In the previous sections it was demonstrated that the error correcting mechanisms require information from the environment in order to adjust the adaptation levels to their original pre-adaptation positions which are consistent with the rules of the environment true in the long run. In the sections to follow the recovery time course will be reviewed for several types of aftereffects. This type of research is typically referred to as storage evidence due to the observation that the aftereffect fails to dissipate completely (i.e. stores) for some period of time.

1.6.1 The McCollough and related Effects

This effect, named after the researcher first to observe it (McCollough, 1965), was reported by McCollough herself to endure for at least one hour. Since her original observation, the effect has been the subject of much interest and longer storage durations have since been reported. Hepler (1968), for instance, reported that motion-contingent color aftereffects are still observed approximately 24 hours after adaptation. Favreau, Emerson, and Corballis (1972) replicated Hepler's observation and later reported color-contingent motion aftereffects for up to a week following induction (Favreau, 1979). Still others have reported traditional MEs for weeks after adaptation (Stromeyer & Mansfield, 1970; Mackay & Mackay, 1975; Riggs, White, & Eimas, 1974; Shute, 1977). Perhaps the most impressive storage experiment comes from Jones and Holding in their 1975 paper entitled "Extremely long-term persistence of the McCollough effect". In a systematic exploration of the storage of the ME these authors reported ME to be present for up to 3 months following a mere 15 minute induction period.

1.6.2 The Tilt Aftereffect

Wolfe and O'Connell (1986) studied the storage of the tilt aftereffect (TAE) for up to two weeks following variable adaptation times. All adaptation durations produced significant TAEs and the longer the adaptation episode, the longer the observed storage period. Interestingly, the TAE does not dissipate completely (as measured two weeks post adaptation) for adaptation durations of three and four minutes. Wolfe and O'Connell concluded that fatigue of neural mechanisms cannot account for this delayed recovery, although they do not dismiss some role for fatigue. They state that the fast component of adaptation may still be due to a neurotransmitter depletion, while the long-term component may reflect recalibration of the system.

1.6.3 Miscellaneous Aftereffects

Storage of a spatial frequency aftereffect was investigated by Blakemore and Sutton in 1969. They reported that the spatial frequency shift (aftereffect) was longer than that expected from neuronal fatigue and increased with longer adaptation durations. Brief adaptation episodes of 2 to 3 minutes, for example, induced an aftereffect of about the same length. Longer adaptation durations of say 45 minutes, however, produced MAEs still observed more than 4 hours later.

In a study of auditory aftereffects, Ehrenstein (1994) increased or decreased sound signal intensity so that an auditory motion was perceived within the head along a line between the two ears. By using this procedure, subjects could be adapted to specific directions. Ehrenstein found that settings of interaural midline were displaced after auditory adaptation in a direction opposite to the direction of adaptation on average by 1.2

dB. This displacement effect decayed with time after adaptation and was not fully recovered at the time of last testing (e.g. final test was 50 seconds post-adaptation and the aftereffect was still present and remained fairly large).

1.6.4 Motion Aftereffects

In his classic paper on the motion aftereffect, Wohlgemuth (1911 as cited in Wade, 1994) was likely the first to report a type of storage of the effect. He instructed subjects to close their eyes, immediately after adaptation, for a period longer than the normal duration of the aftereffect. When subjects opened their eyes they indeed reported a motion aftereffect which endured half of the length of time of the original effect. Despite long standing interest in the motion aftereffect relatively few investigations have concerned storage capacity. One would think, especially given the proposed MAE models, that many more studies would focus on the delay in recovery and attempt to build a better theoretical interpretation of aftereffects. Spigel (1960) was probably next to study the phenomenon of MAE storage and indeed labeled it as such. In his investigation, he found evidence of storage and in addition noted that darkness in the interval between adaptation and test phases is not necessary for storage to take place. Spiral MAEs produced after long adaptation periods (e.g. 15 minutes) have been observed 24 hours post-adaptation first by Masland (1969) and later replicated by Kalfin and Locke (1972). More than a decade later, Hershenson (1985) found that 30 seconds of adaptation to a rotating spiral induced MAEs which were still present 3 days after cessation of stimulation. Meeker and La Fong (1988) also studied the long term storage of the spiral motion aftereffect. Following five minutes of adaptation, subjects either viewed a stationary stimulus immediately or five minutes post-adaptation and then were retested for MAE at a later date (up to three days post-adaptation). Despite the fact that almost half of their subjects stored the spiral MAEs when tested on the third day, the authors preferred to "view the cup as half empty" and see this as evidence of a lack of storage. In addition, they report that the five minute delay between adaptation and first test (i.e. no visual stimulation) significantly reduces the MAE (once again, the MAE, although reduced, remained present and thus should not be dismissed).

Thompson and Wright (1994) have recently examined the role of intervening patterns in the storage of the motion aftereffect. Their results support the contention that the nature of the pattern shown to subjects post adaptation and pre testing is pertinent in the storage of the MAE. Following 90 seconds of adaptation to a drifting horizontal sinewave grating, one of 11 different intervening patterns was presented for a period of time (not specified in paper) followed by the stationary version of the adaptation pattern. During the intervening pattern presentation MAEs were not formally measured and if any were observed by subjects they were not reported in the paper. Thompson and Wright found that for 10 of the 11 intervening patterns, large and robust storage effects occurred. The only exception was an intervening pattern which was identical to the adapting and testing stimulus. Their data indicate that quick recovery from adaptation seems dependent on inspection of the exact stimulus display.

In an interesting study by Mahmud (1987) the storage of the motion aftereffect was examined in a novel manner. Subjects were adapted to a rotating spiral for 10 minutes (positive adaptation) followed by a 2 second stationary test and their MAEs were recorded (direction: contraction, expansion, or motionless). After a 5 minute interval (the type of interval setting was not mentioned), the spiral rotated in the reverse direction to the first adaptation direction (negative adaptation) for 1 minute. The stationary spiral was then presented once again and MAEs were recorded for 2 seconds. For the next 5 minutes, subjects were repeatedly tested for direction of MAE at 1 minute intervals. Following the positive adaptation, of say contraction, subjects reported movement in the reverse direction (expansion). Following the negative adaptation (expansion) subjects reported the reverse of this (contraction). Finally, during the last five minutes of testing all subject indicated a change back to the original aftereffect direction (expansion). In other words, the original MAE from 5 minutes of adaptation was stored even after the induction of the reverse MAE within the intervening time.

More recently, Verstraten et al. (1996) report a storage related effect with dynamic and static motion aftereffects. They found that the static MAE was almost completely stored (i.e. the same duration as when it is immediately tested) when the static test was preceded by a dynamic test, however, the reverse was not observed. The dynamic MAE was not stored when dynamic testing was preceded by a static test pattern. Thus the random movement of elements seems to retard recovery from the aftereffect. In a recent extension of this study (van der Smagt et al., 1998) the dynamic MAE, in fact, was stored when preceded by the static test pattern, if adapting motion was high speed (11.28 to 14.10 degrees/second, individually adjusted). The reverse was also reported in that, for high speed motion adaptation, static MAEs were stored when preceded by dynamic tests. These storage effects for high speed motion were, however, not as complete as that observed with the static MAE after dynamic tests (i.e. static MAE duration is longer when tested with a static test first than following the dynamic test).

Bowd, Rose, Phinney, and Patterson (1996) measured MAE duration (one episode, thus not storage) following variable adaptation durations (from 1 to 64 minutes). Even though this is not a storage investigation per se, it does offer additional psychophysical evidence against the neural fatigue account of the motion aftereffect. After a certain length of time, adaptation effects should plateau if neuronal fatigue is the cause (once they are depleted, further stimulation should not cause a stronger MAE). Bowd et al. observed that after adaptation to stereoscopic- (adaptation induced by moving binocular disparity information) or luminance-defined moving gratings, aftereffect duration was proportional to the square root of adaptation duration for both types of stimuli. In addition, and most important, is the observation that for both kinds of stimuli there was no sign of adaptation saturation even at the 64 minute adaptation duration.

1.6.5 Conclusions

The reviewed studies illustrate robust storage of the MAE and perhaps aftereffects in general. Hours, days, and months of storage may not be consistent with the neural fatigue interpretations. It is more plausible that neurons would recover from adaptation sooner than this. Although neural fatigue may be a component of adaptation effects, it is possible from these findings that fatigue alone cannot explain aftereffects. The visual system may perform a more long-lasting recalibration when confronted with a peculiar visual diet. Helson's Adaptation Level principle taken together with Andrews' notion of Error Correcting Mechanism may help explain these data and general visual functioning.

1.7 OUTLINE OF THE PRESENT EXPERIMENTS

The purpose of the present thesis was two-fold. First it was an effort to improve our understanding of the motion aftereffect and its characteristics. Second, and more importantly, it was an attempt to determine which theory, fatigue or recalibration, better explains the underlying mechanism responsible for the generation of the motion aftereffect. A psychophysical approach was employed to test these questions.

To investigate the effect, the series of experiments placed emphasis on what is believed to be the most challenging phenomenon for conventional fatigue models. That is, the recovery time or storage of the motion aftereffect. Four different designs were used, each examining some element of MAE storage.

In Experiment 1, MAE duration was recorded for variable adaptation durations and in addition, the decay of the MAE was tracked across extinction trials. Different time courses were expected based on fatigue and recalibration models, with the former expected to be faster to asymptote.

In Experiment 2, MAE duration was measured following uninterrupted versus interrupted-adaptation conditions to test for MAE storage via summation of adaptation episodes. The expectation was that the blank intervals in the interrupted-adaptation conditions would allow for complete MAE storage under the recalibration assumption, but spontaneous recovery and hence no (or less) storage in the case of neural fatigue.

Experiment 3 examined the effect of intervening visual environment on the long-term storage of the MAE. No visual information during the storage interval was expected to allow for complete MAE storage, independent of storage time, for recalibration, whereas, increasing interval time with no visual experience was expected to decrease MAE storage for the fatigue model. More time passed with rich visual information, on the other hand, would either allow for more recalibration (less MAE storage) or would maintain the fatigued state of the cells, thereby increasing MAE storage.

Finally, Experiments 4a and 4b investigated the MAE direction following the successive adaptation of two opposing directions with unequal adaptation time. The recalibration model would likely predict an immediate MAE opposite to the direction which was adapted the longest. The fatigue model, which probably has a more rapid time course of adaptation and recovery, would expect an MAE opposite to the most recent adaptation direction. In addition, the time course of the MAE direction was tracked across a two minute post-adaptation period to test for a reversal of direction, previously reported with the spiral stimulus (Mahmud, 1987), which may imply a role for both fatigue and recalibration.

GENERAL METHOD

2.1 Apparatus and Materials

A Power Macintosh 8100 microcomputer equipped with a high resolution 17" Apple Vision Audio Visual 1710 Color Monitor were employed to generate and present the stimuli, as well as, for data collection. A standard-sized Macintosh keyboard was additionally used to record subjects' responses by keypress. Responses were measured in seconds, with 1/68 seconds precision, and accumulated by the computer. Stimulus luminance was calibrated by a photometer, which expressed the units as candela per meter squared (cd/m^2). The Pixx software program, developed by Peter April for the Vision Lab at Concordia University, was used to construct the stimuli and execute the experiment.

2.2 Stimulus

The display employed for all experiments consisted of a vertically oriented sine-wave grating with a spatial frequency of 0.25 cycles per degree (cpd) and a symmetry of 0.5. The grating drifted perpendicular to its orientation (i.e. in a horizontal direction) with a fixed drift frequency of 1.0 Hz and a contrast of 0.58. The dark bars (i.e. "trough") had a luminance of 14.36 cd/m^2, whereas, the light bars (i.e. "peak") maintained a luminance of 54.15 cd/m^2.

The grating appeared within a square aperture subtending 10 x 10 degrees of visual angle and contained no dark borders. A small black fixation point, of 0.25° diameter and an averaged luminance of 0.94 cd/m^2, was placed in the center of the display. The luminance of the background was held constant at 32.45 cd/m^2, which filled the rest of the screen (96° x 69°). All stimulus parameters for the display were chosen following pilot studies which determined the most sensitive characteristics to induce the motion aftereffect from a dynamic one-dimensional grating. Figure 2.1 illustrates the display.

2.3 Procedure

Subjects were tested individually in a quiet visual perception laboratory. Procedural information was delivered verbally by the experimenter prior to each session. In order to familiarize the subjects with their task, all were first allowed to experience the motion aftereffect with the exact stimulus used in the study. Subjects were seated in front of the screen and viewed the display at a distance of 53.34 centimeters. The observers were made aware of the fixation point positioned in the center of the display and instructed to fixate it and to maintain their fixation continuously while viewing the adaptation and test stimuli. All other procedural information and constraints were dependent on the particular experiment.

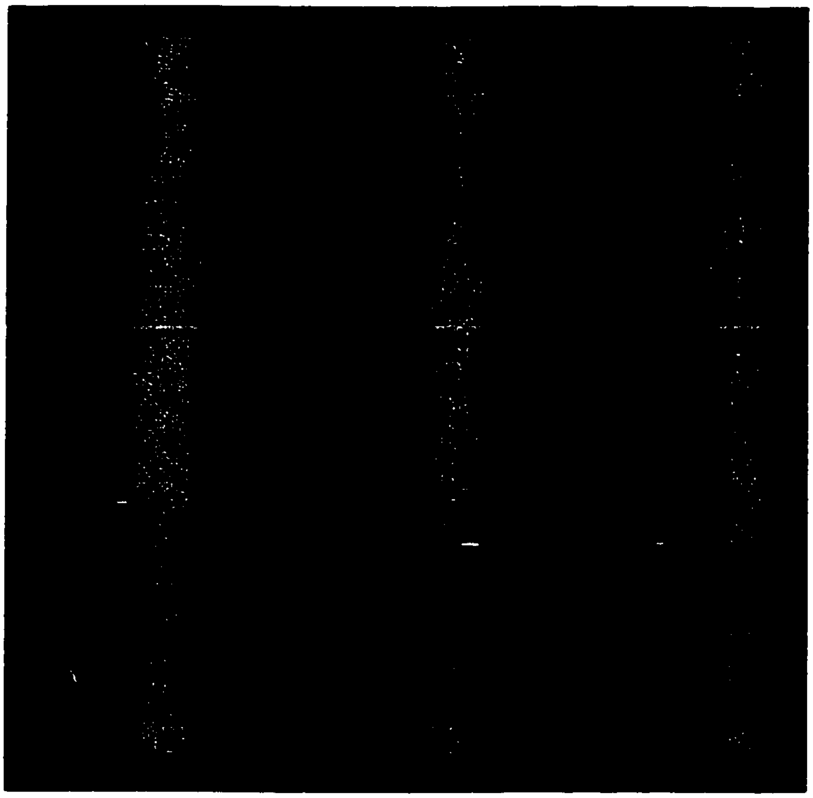

Figure 2.1. The vertical sine-wave grating employed for all five experiments.

EXPERIMENT 1

3.1 Introduction

The first experiment examined the time course for the induction of and recovery from the motion aftereffect. MAE duration was measured following variable adaptation durations. Giaschi et al. (1993) stated that the only consistent finding across single-cell research to date is that prolonged motion stimulation decreases cortical cell sensitivity. The extent of this response decrement, the time course for adaptation and recovery, the direction specificity, and the functional differences between simple and complex cells, is much less consistent and remains controversial in the literature. Yet another problem is that only one study examined the adaptation of MT neurons (Petersen, Baker, & Allman, 1985). These MT findings are somewhat limited given that Wenderoth et al. (1988) discuss many methodological weaknesses of Petersen et al. It is known that direction selectivity is greater in extrastriate areas such as MT and MST than in V1 (Newsome, Britten, & Movshon, 1989; De Yoe & van Essen, 1988). Given this and the recent trends in MAE research examining the role of higher level influences in the production of the MAE, the lack of data in reference to the responses of MT neurons to adaptation, is unfortunate. Testing the fatigue model of the MAE is consequently somewhat limited given the uncertainty of the physiological understanding of cell response. The most current single-unit (cat cortical cells) study is by Giaschi et al. (1993). They examined the physiological time course of adaptation and recovery, by monitoring single cell activity during 120 seconds of adaptation, followed by 120 seconds of recovery. Unlike any other study, they compared the time course of response decrement and recovery in the stimulated versus nonstimulated direction in combination with adaptation in the preferred versus nonpreferred direction of both single and complex cells. They observed an initial fast decrease in neuronal sensitivity (a decrease of about 50%) to asymptote at approximately 20 seconds post-adaptation. This decrement in sensitivity occurred for the stimulated (adapted) and non-stimulated directions, and in addition, this effect was shown for the cell's preferred and nonpreferred directions. The time course for recovery was somewhat similar in function to that of adaptation. There was an initial fast (although less pronounced than that observed in adaptation) recovery of sensitivity within 8 to 24 seconds, with the quicker recovery observed following adaptation in the non-preferred direction. Thereafter, a significantly slower increase in cell response, a plateau in many cases, was shown. By the end of the recovery period, sensitivity had reached just below, at, or above baseline activity. Given that some cells did not reach full recovery two minutes post adaptation, neural fatigue may be consistent with the direction of the MAE. Giaschi et al.'s study is important for the present set of studies because it is the most recent paper that measured single cell activity during adaptation and recovery and in addition, they attempt to control for many of the methodological pitfalls of past single-unit studies (e.g. differences in recording methods, data analysis, and pattern selection). As well, their time course for adaptation and recovery is either consistent with, or more conservative than past studies and hence their findings will be used as the basis for simple neural fatigue predictions of the MAE.

The present study employed adaptation durations of 3, 30, 60, 120, 180, or 240 seconds. Presumably, the length of the MAE would reflect the amount of change in the visual system. Giaschi et al.'s results illustrated a floor effect in cell sensitivity following about 20 seconds of adaptation. In terms of neural fatigue, one would therefore expect that adaptation durations up until 20 seconds would produce increasingly longer MAEs. Adaptation durations longer than 20 seconds, however, should produce MAE durations equivalent to the 20 second adaptation. If cell fatigue is the underlying mechanism of the MAE then it would be difficult to understand why longer adaptation periods would produce longer MAEs even though cell sensitivity remains constant. Consequently, in reference to this study's parameters, the 3-second adaptation should produce the shortest MAE, but all other adapting durations should produce equal MAE durations.

If recalibration plays an important role in the production of the MAE then a different outcome may be postulated. Recalibration stipulates that error-correcting mechanisms would detect this change in environment and compensate by changing the adaptation level accordingly with the consequence of perceiving the adapted direction as neutral. The prediction in this case would be that MAE duration should increase with increasing adaptation duration in that a longer adaptation episode would be seen as "additional evidence" that the motion constraint in the visual environment has indeed changed. As amount of unidirectional motion is increased, the result would be an average motion value which is further away from the true neutral point. At one point, this new neutral point should in theory become the furthest possible away from the true neutral point and thus the MAE length would asymptote thereafter. In the case of rightward motion adaptation, for example, increasing the adaptation period should eventually move the neutral point *completely* rightward. The time course for this is, however, expected to be much longer than fatigue based on physiological and psychophysical research. Bowd et al. (1996) found that the aftereffect duration, following adaptation to stereoscopic or luminance motion, was proportional to the square root of adaptation duration. In addition, there was no sign of adaptation saturation even at the 64 minute adaptation duration. In accordance, the adaptation durations employed in the present study would expect a linear trend to represent the relationship between adaptation duration and MAE length. Specifically, as the adaptation duration increases so should the length of the MAE.

In summary the fatigue account of the MAE predicts a brief MAE following 3 seconds of adaptation. An adaptation duration of 30 seconds will produce a longer MAE than 3 seconds, but equal to those after 60, 120, 180, and 240 seconds of adaptation. In other words, the MAE time course should show an increase in MAE duration from 3 to 30 seconds of adaptation but thereafter plateau. Recalibration, on the other hand, predicts that longer adaptation periods will induce longer MAEs.

3.2 Method

3.2.1 Subjects

Eight subjects, ages between 20 and 52, participated in all conditions. The observers were recruited from diverse educational backgrounds, and reported normal or corrected-to-normal vision. All were right handed and were introduced to the motion aftereffect prior to their participation in the experiment. Two of the observers had no previous experience in psychophysical experiments, and four were naive to the purpose of the experiment. Due to the long hours required for participation in this and the following experiments, the four non laboratory members were paid for their time.

3.2.2 Procedure

Design

The six adaptation durations (3, 30, 60, 120, 180, or 240 seconds) were separated into six experimental sessions, accordingly. This procedure was implemented to avoid possible carryover effects, a potential threat especially following the longer adaptation times. Each stimulus was presented 5 times, thus yielding a total of 5 trials per session.

Experimental sessions were presented in sequential order, from shortest to longest adaptation times with the rational that carryover effects would be minimized in this fashion (i.e. if carryover effects should occur, the residual MAE from a short adaptation session would influence the longer adaptation session to a lesser degree than vice versa). Extinction trials were used to control for carryover between trials (see "subjects' task" for further details). In addition, sufficient time elapsed between testing sessions (e.g. anywhere from minutes to days) to avoid any remnants of the motion aftereffect. As a last precaution, the subject was shown a static version of the display and asked if s/he experienced any aftereffect prior to the commencement of the next experimental session [only if the response was "no" would the subject be allowed to immediately participate in the next session].

Subjects' task

Each trial was initiated by the subject with a key press of the spacebar, according to readiness (e.g., good fixation) and comfort. During the presentation of the moving display, subjects fixated and were instructed to observe the motion, free of other mental activities (since it is known that attention is a key factor in the presence and strength of the motion aftereffect). Immediately following the adaptation period, the stimulus remained on screen in its stationary form and subjects responded by depressing the appropriate key to indicate when their percept of motion in the opposite direction from adaptation (i.e. their motion aftereffect) ceased. Following this response, the stationary display disappeared for three seconds after which is reappeared. The task again was to press the key when their MAE ended. This sequence continued until the subject would indicate, via a different key, that s/he no longer experienced an MAE. The method allowed for (a) tracking of the extinction of the motion aftereffect, and (b) a level of certainty that carryover effects (between trials) would be minimal if present at all. A schematic representation of this procedure is shown in Figure 3.1. Responses were recorded by the computer. Debriefing of subjects occurred following the completion of all experimental sessions.

Length of testing

Subjects completed all trials in all of the sessions. The sessions lasted approximately 5, 8, 10, 15, 20, and 25 minutes (depending on the length of the subject's MAE and on the number of extinction trials the subject required), for 3-, 30-, 60-, 120-, 180-, and 240-second adaptation times, respectively. The overall participation time necessary to complete the experiment was therefore roughly 1 hour and 30 minutes, which was, as previously stated, separated by minutes, hours, and sometimes days between sessions.

3.3 Results

3.3.1 Organization of the Raw Data

For a given adaptation duration, each subject's mean *initial* and *residual* MAEs (in seconds) were calculated from the five repetitions. This procedure was repeated for each experimental session (i.e. for each adaptation duration). From these individual data, the group mean initial and residual MAEs were determined for each adaptation duration. The average number of required extinction trials was also calculated for each subject in each session. Following this, the group average number of extinction trials was determined for each adaptation duration.

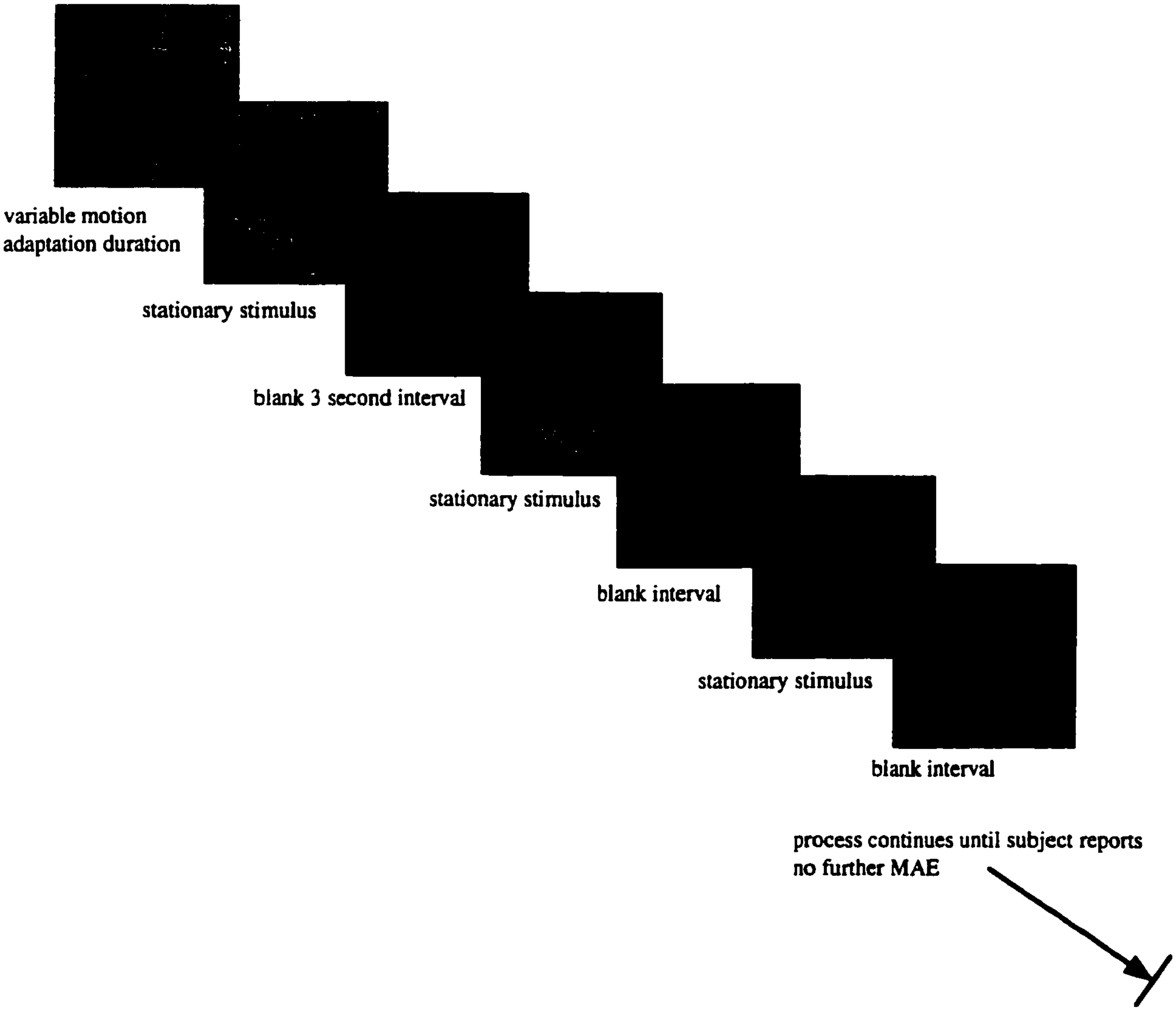

Figure 3.1. The temporal sequence of events on a given trial. Variable adaptation to motion followed by an immediate MAE duration measurement. Thereafter, there was a 3-second blank interval followed by the stationary stimulus and another MAE duration measurement. This process continued until the observer reported no further MAE.

The data were organized along four dimensions: (a) mean length of the initial MAE episode as a function of adaptation duration, (b) mean length of the MAE across extinction trials as a function of adaptation duration, (c) mean number of extinction trials as a function of adaptation duration, and (d) total MAE length (initial plus extinction episodes) as function of adaptation duration. Thereafter, four types of analyses were performed on the data: (a) calculation of slopes via curve-fitting with power functions, (b) calculation of slopes via curve-fitting with exponential functions, (c) one-way analyses of variance with tukey posthoc comparisons, and (d) determination of an MAE index. These analyses will be discussed according to the four aforementioned dimensions into which the data were separated.

3.3.2 Initial MAE Episode as a function of Adaptation Duration

Curve-fitting with Power Functions

First of all, the length of the initial MAE episode was plotted against adaptation duration on double logarithmic axes and was then curve-fitted. It was determined that, in all cases, power functions provided the best fit when compared to other types of functions. The slopes of the best fitting functions were then calculated. This procedure was done for both individual and group data. As shown in Figures 3.2 to 3.9, the slope of the best fitting function was 0.512 for AB, 0.621 for CG, 0.466 for JP, 0.266 for LC, 0.448 for LR, 0.431 for MK, 0.459 for MVG, and 0.426 for SD. The mean of these slopes, 0.468, was quite representative of the individual data (Figure 3.10). In each figure, the results indicate that aftereffect duration increases with increasing adaptation duration according to a power law relation. For example, the duration of the MAE ranged from 3.00 to 6.77 seconds across observers for an adaptation duration of 3 seconds, while the MAE ranged from 12.40 to 57.20 seconds for an adaptation duration of 240 seconds (i.e. 4 minutes).

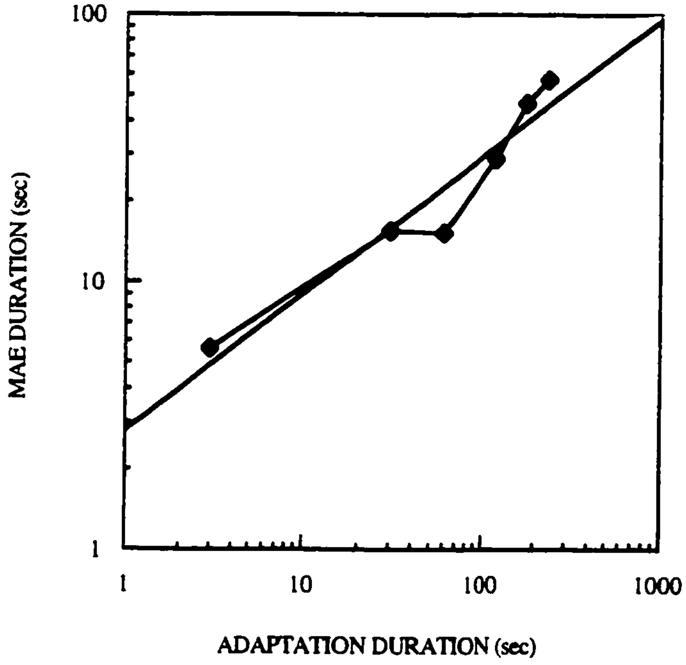

Figure 3.2. Length of the initial MAE as a function of adaptation duration for Observer AB. Error bars not shown are smaller than the symbol used to plot the point. Slope of the best-fitting power function was 0.512.

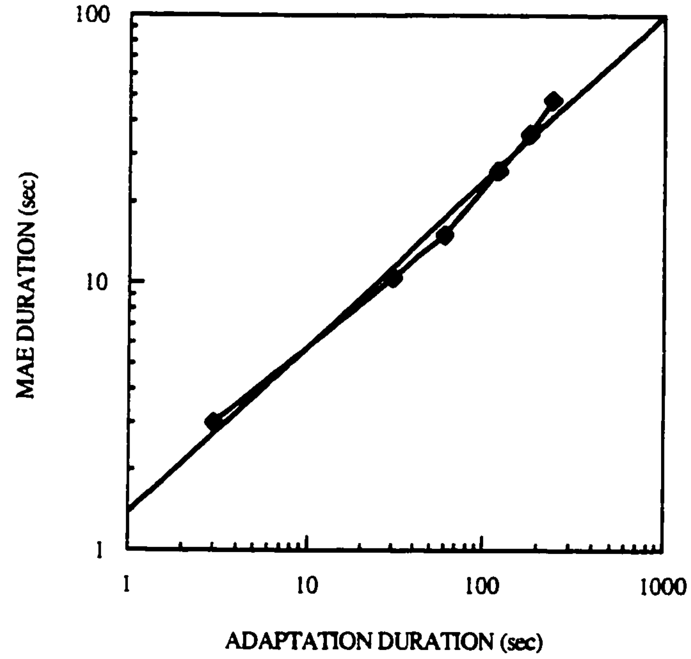

Figure 3.3. Length of the initial MAE as a function of adaptation duration for Observer CG. Error bars not shown are smaller than the symbol used to plot the point. Slope of the best-fitting power function was 0.621.

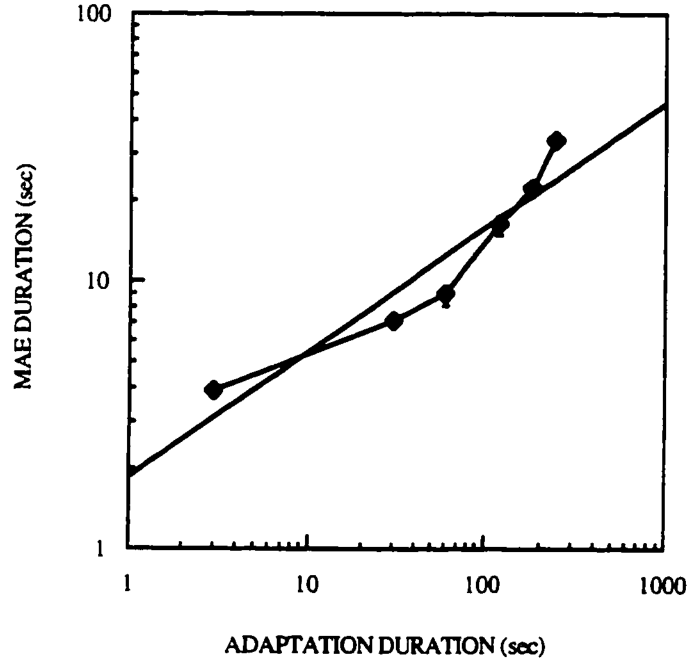

Figure 3.4. Length of the initial MAE as a function of adaptation duration for Observer JP. Error bars not shown are smaller than the symbol used to plot the point. Slope of the best-fitting power function was 0.466.

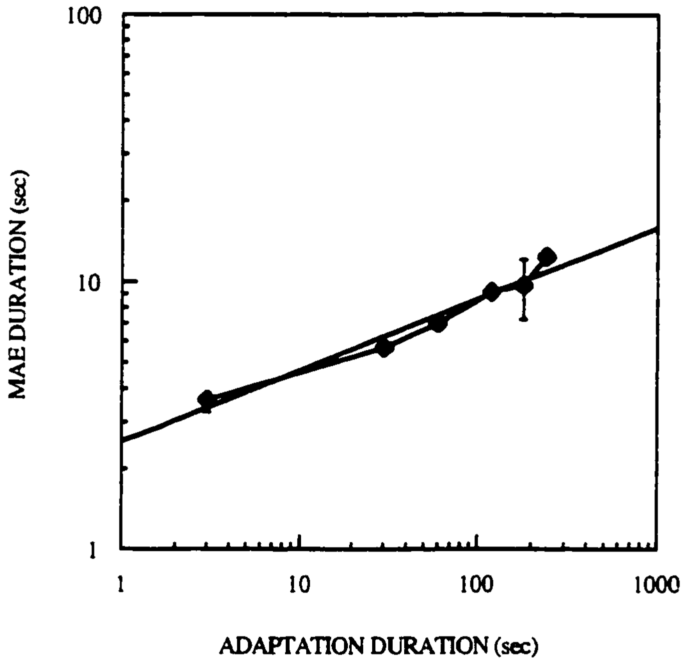

Figure 3.5. Length of the initial MAE as a function of adaptation duration for Observer LC. Error bars not shown are smaller than the symbol used to plot the point. Slope of the best-fitting power function was 0.266.

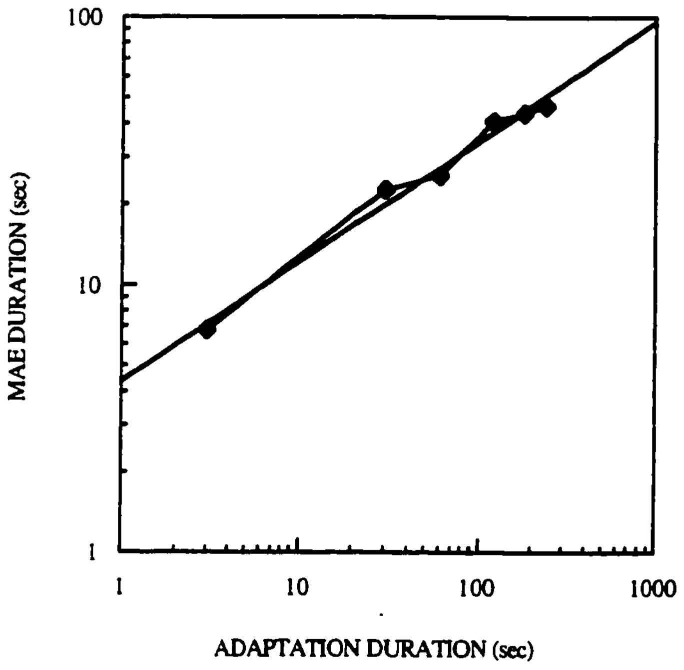

Figure 3.6. Length of the initial MAE as a function of adaptation duration for Observer LR. Error bars not shown are smaller than the symbol used to plot the point. Slope of the best-fitting power function was 0.448.

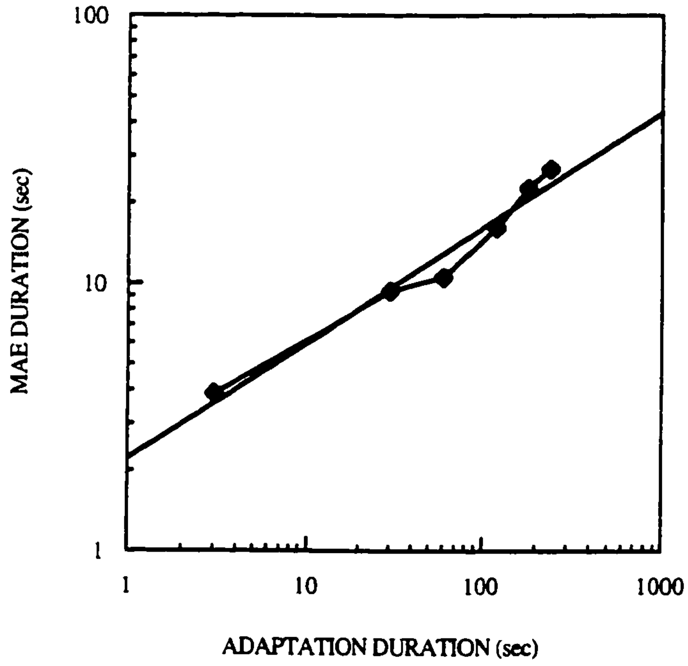

Figure 3.7. Length of the initial MAE as a function of adaptation duration for Observer MK. Error bars not shown are smaller than the symbol used to plot the point. Slope of the best-fitting power function was 0.431.

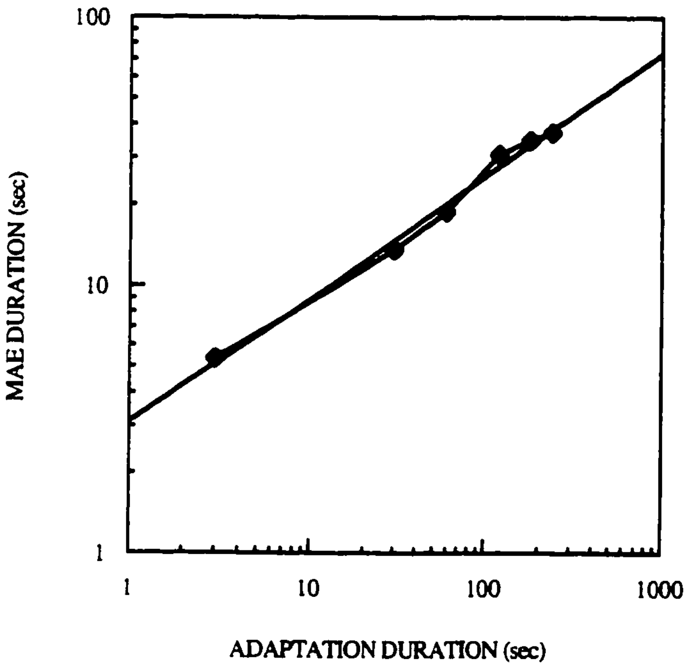

Figure 3.8. Length of the initial MAE as a function of adaptation duration for Observer MVG. Error bars not shown are smaller than the symbol used to plot the point. Slope of the best-fitting power function was 0.459.

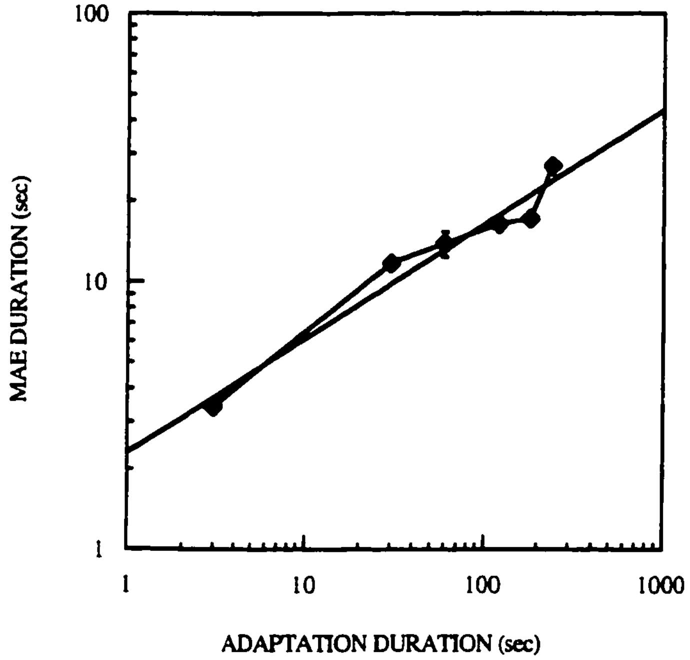

Figure 3.9. Length of the initial MAE as a function of adaptation duration for Observer SD. Error bars not shown are smaller than the symbol used to plot the point. Slope of the best-fitting power function was 0.426.

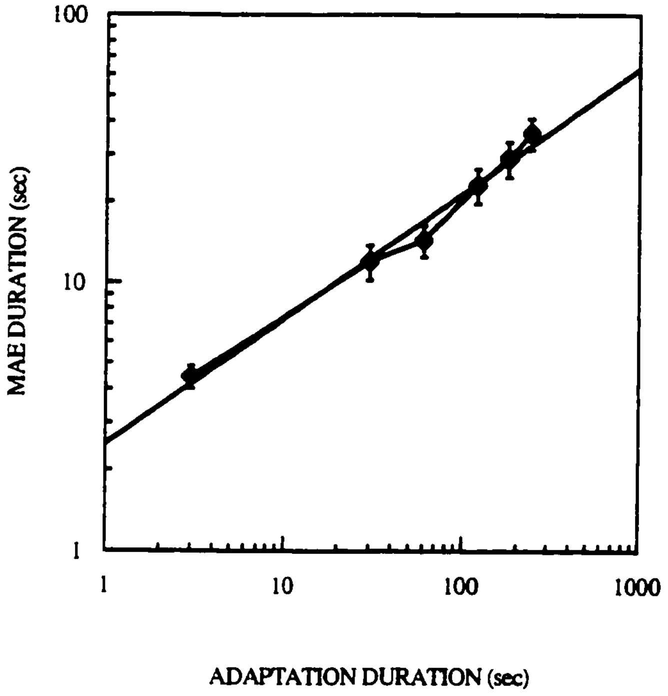

Figure 3.10. Length of the initial MAE as a function of adaptation duration for grouped data. Mean slope of the best-fitting power function was 0.468.

There was no sign that the MAE duration was saturating (i.e. curve did not asymptote). Motion aftereffect duration was related to adaptation duration by a power law with a slope of approximately 0.5, or in other words, aftereffect duration was proportional to the square root of adaptation duration.

Analysis of Variance

As demonstrated above, the data yielded a monotonic curve, whereby subjects' MAE increased as the adaptation duration increased. Average MAEs were 4.44, 12.02, 14.40, 23.09, 29.13, and 36.13, for adaptation durations of 3, 30, 60, 120, 180, and 240 seconds, respectively (Figure 3.11). To test if the obtained MAE durations were significantly different, a one-way analysis of variance (ANOVA) was performed on the length of the initial MAE episode as a function of adaptation duration (6 levels: 3, 30, 60, 120, 180, and 240 seconds). The ANOVA demonstrated that these differences in MAEs, as a function of adaptation duration were indeed significant, $F(5, 35)=30.13$, $p<.05$. Posthoc analysis (Tukey hsd) revealed that MAEs for each adaptation level significantly differed from the MAEs yielded by all other adaptation levels except the level immediately prior to and following it (at the .05 alpha level).

Trend Analysis

The slopes as well as the pattern of significant pairwise comparisons implied a strong linear relationship in the data. Trend analyses were, therefore, computed to examine this possibility. The analysis revealed that the linear trend was a significant descriptor of the relation between aftereffect duration and adaptation duration ($F(1, 7)=37.97$, $p<.05$), with an effect size of .58 (58% of the explained variance). Note that according to Cohen (1977) effect sizes of .01, .06, and .15 correspond to small, medium, and large effects, respectively. The present effect size of .58 is large indeed in reference to these standards. No other trends were significant.

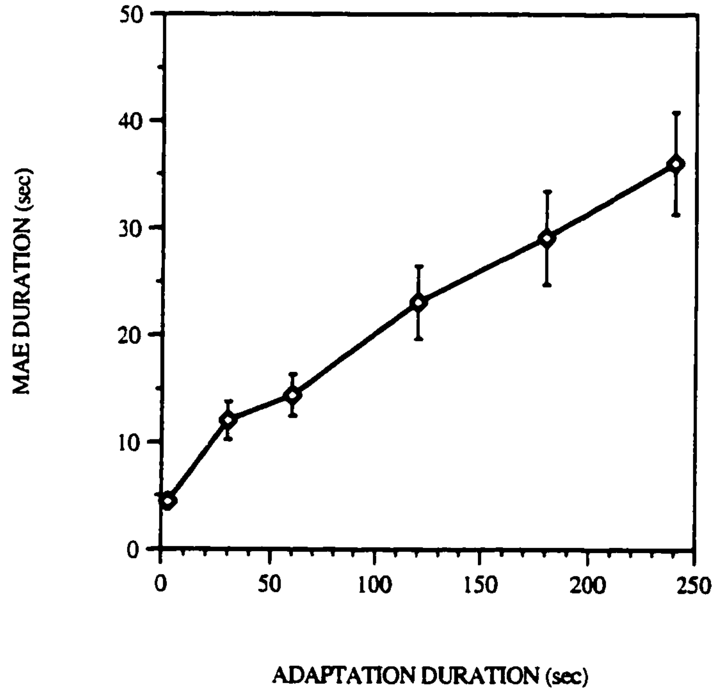

Figure 3.11. Mean length of the initial MAE as a function of adaptation duration. Error bars not shown are smaller than the symbol used to plot the point.

3.3.3 MAE across Extinction Trials as a function of Adaptation Duration

Curve-fitting with Exponential Functions

The length of the MAE was plotted against the extinction trial number again on double logarithmic axes and was curve-fitted to obtain coefficient estimates. In this case, data were best-fitted with an exponential function. This was done for the group data, in addition to calculating specific coefficients for each subject in each of the six adaptation conditions (yielding 48 estimates). The individual coefficients were later used in an analysis of variance. To illustrate, the mean coefficients of the best fitting functions for durations of 3, 30, 60, 120, 180, and 240 seconds were: -0.349, -0.381, -0.261, -0.228, -0.136, and -0.110, respectively (Figures 3.12 to 3.17). In each figure, the results demonstrate that aftereffect duration decays with increasing extinction trials according to an exponential relation. In addition, this decay varies in steepness dependent upon adaptation duration.

Analysis of Variance

A one-way analysis of variance was conducted to determine whether the difference in coefficient as a function of adaptation duration (6 levels: 3, 30, 60, 120, 180, and 240 seconds) was significant. As shown in the previous figures, the steepness of MAE decay decreased as the adaptation duration increased. Average coefficients were -0.349, -0.381, -0.261, -0.228, -0.136, and -0.110 for adaptation durations of 3, 30, 60, 120, 180, and 240 seconds, respectively. These coefficients are graphed in Figure 3.18, which illustrates the relationship between increase in adaptation duration and the subsequent decrease in (negative) coefficient. In other words, the longer the adaptation, the slower the decay. The ANOVA demonstrated that these differences in curves were significant, $F(5, 35)=2.53$, $p<.05$. Posthoc analysis (Tukey hsd) revealed that pairwise comparisons did not reach significance ($p>.05$) despite the significant main effect. In other words, the explained

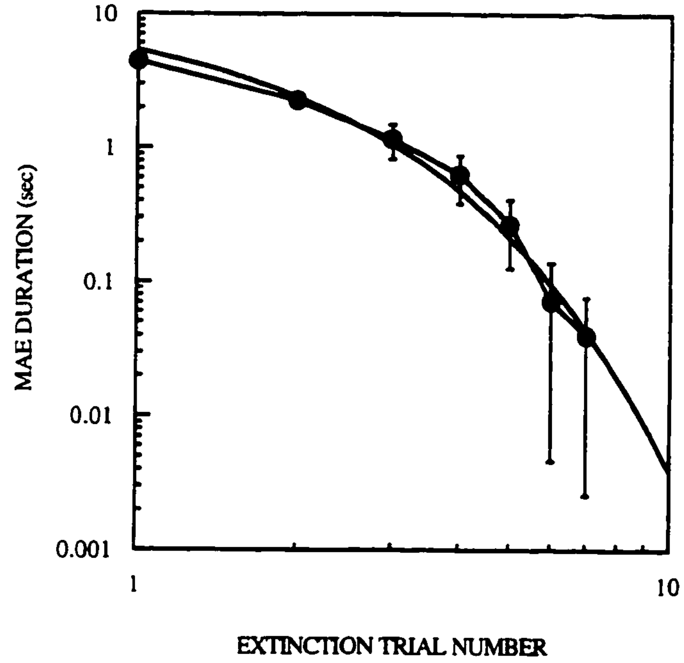

Figure 3.12. MAE duration as a function of number of extinction trials following 3 seconds of adaptation. Error bars not shown are smaller than the symbol used to plot the point. The coefficient of the best-fitting exponential function was -0.349.

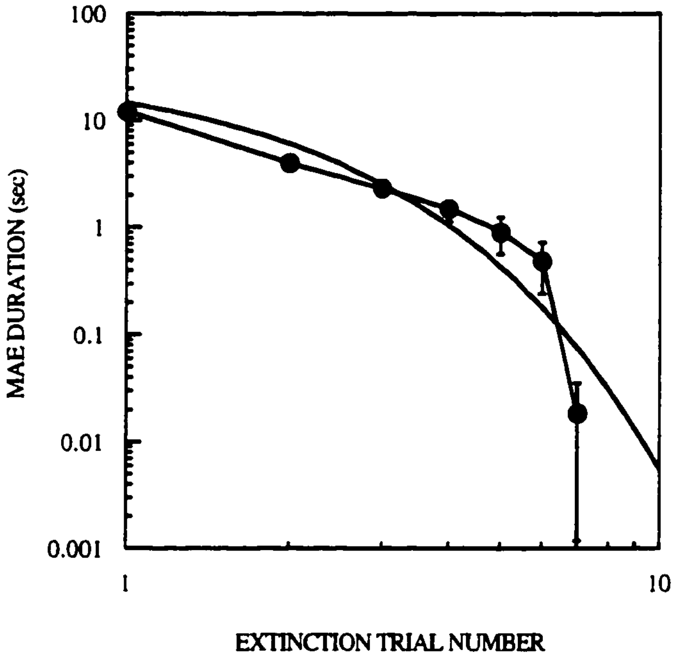

Figure 3.13. MAE duration as a function of number of extinction trials following 30 seconds of adaptation. Error bars not shown are smaller than the symbol used to plot the point. The coefficient of the best-fitting exponential function was -0.381.

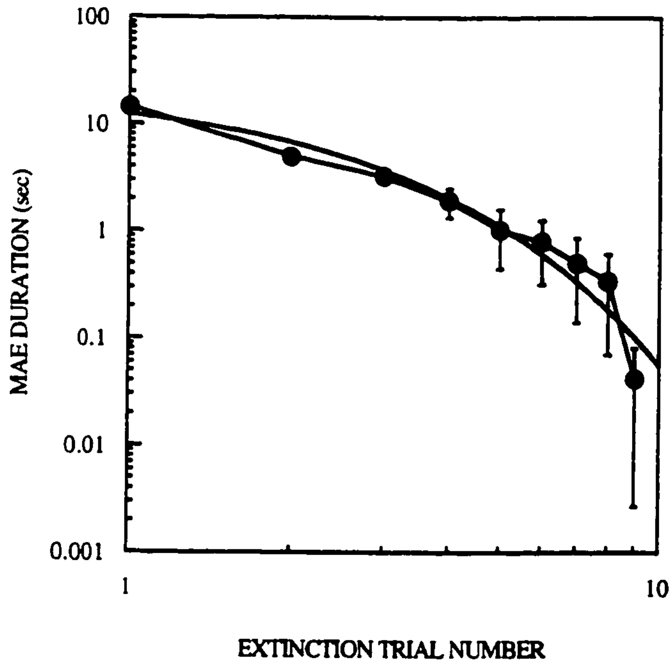

Figure 3.14. MAE duration as a function of number of extinction trials following 60 seconds of adaptation. Error bars not shown are smaller than the symbol used to plot the point. The coefficient of the best-fitting exponential function was -0.261.

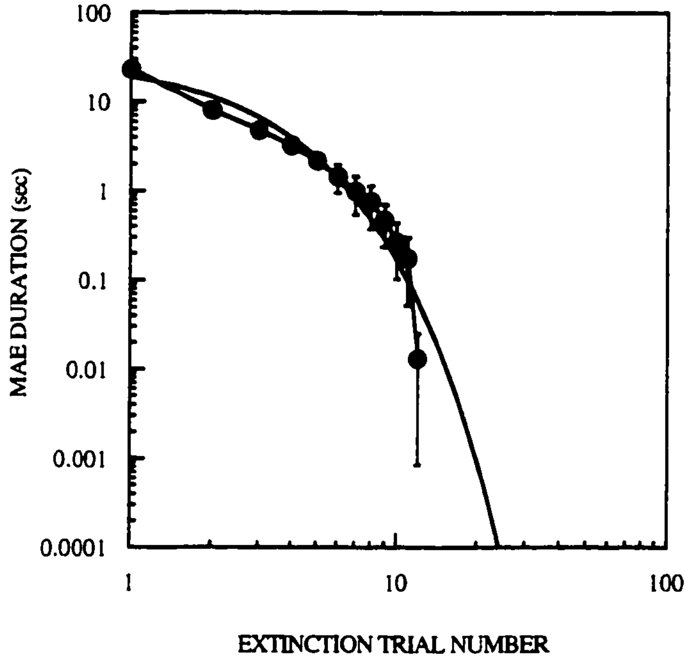

Figure 3.15. MAE duration as a function of number of extinction trials following 120 seconds of adaptation. Error bars not shown are smaller than the symbol used to plot the point. The coefficient of the best-fitting exponential function was -0.228.

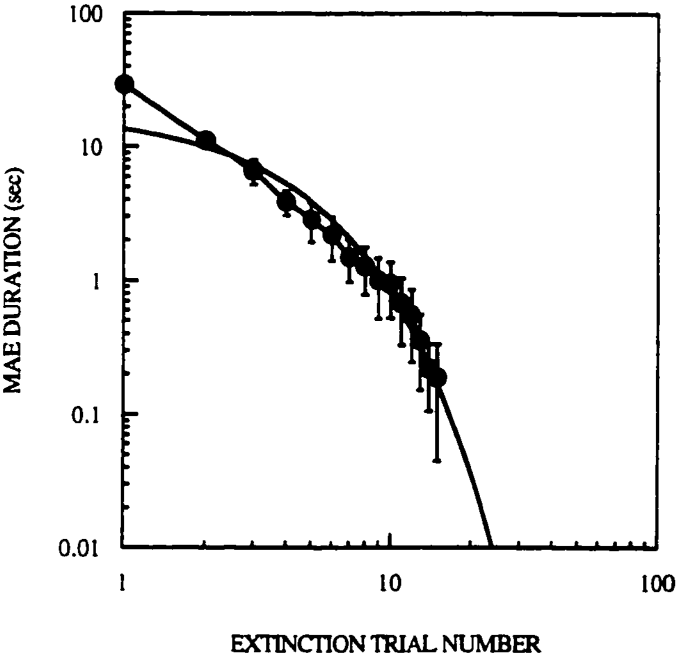

Figure 3.16. MAE duration as a function of number of extinction trials following 180 seconds of adaptation. Error bars not shown are smaller than the symbol used to plot the point. The coefficient of the best-fitting exponential function was -0.136.

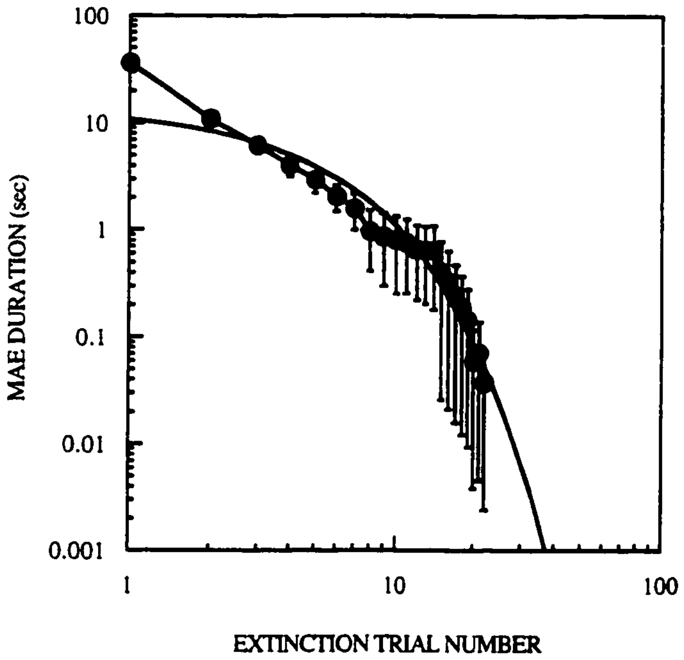

Figure 3.17. MAE duration as a function of number of extinction trials following 240 seconds of adaptation. Error bars not shown are smaller than the symbol used to plot the point. The coefficient of the best-fitting exponential function was -0.110.

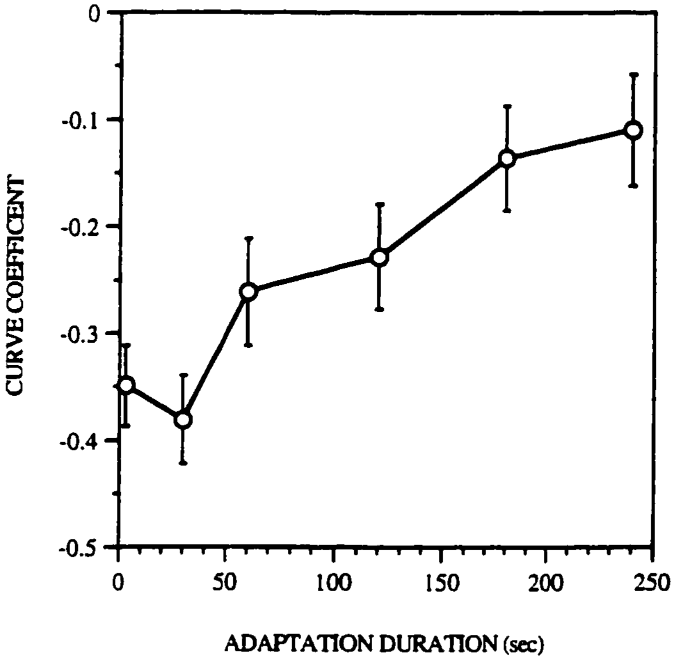

Figure 3.18. Mean MAE decay coefficient as a function of adaptation duration.

variance difference between each curve may not have been large enough to be significant on its own or the unexplained (error) variance may have been too great. The pooled explained variance was, however, statistically significant.

Trend Analysis

Trend analyses revealed that the linear decay in MAE was significant (F(1, 7)=7.68, $p<.05$). The linear trend accounted for a considerable portion of the variance (i.e. effect size was .04). These results are consistent with those from the curve-fitting and ANOVA and thus taken together, emphasize the strong linear decay in MAE as a function of extinction, averaged across adaptation durations. All other trends were not significant.

3.3.4 Number of Extinction Trials as a function of Adaptation Duration

Analysis of Variance

To determine whether the number of extinction trials required to null the MAE differed across adaptation durations (6 levels: 3, 30, 60, 120, 180, and 240 seconds), a one-way analysis of variance (ANOVA) was executed. A monotonic trend was illustrated in the data, as shown in Figure 3.19, whereby subjects' number of trials needed to extinguish the MAE increased as the adaptation duration increased. Average number of extinction trials were 4.13, 5.13, 5.25, 7.25, 9.38, and 9.25, for adaptation durations of 3, 30, 60, 120, 180, and 240 seconds, respectively. The ANOVA demonstrated that these differences in number of extinction trials were significant, F(5, 35)=6.35, $p<.05$. Posthoc analysis (Tukey hsd) revealed that the first three adaptation durations (3, 30, and 60 seconds) had a significantly different ($p<.05$) number of extinction trials from the last two durations (180 and 240 seconds). In spite of their trend, the remaining pairwise comparisons did not differ significantly ($p>.05$). It is relevant to note that the number of

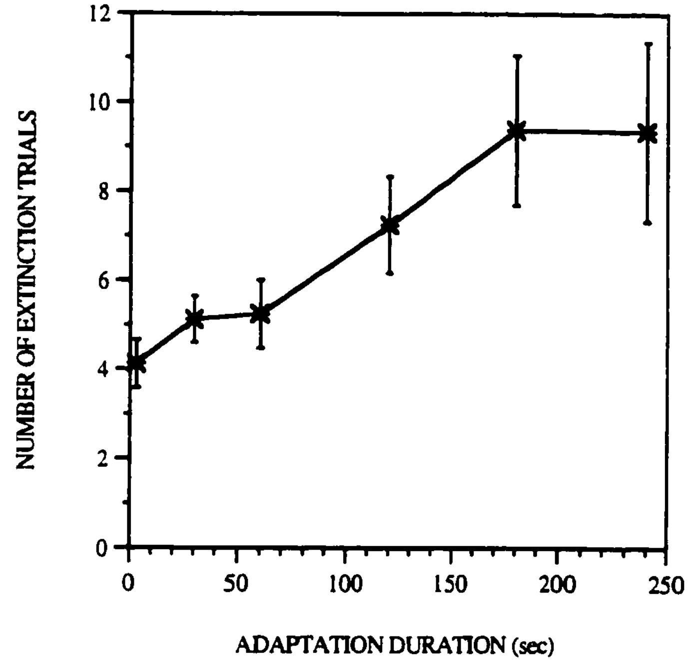

Figure 3.19. Mean number of extinction trials required to null the MAE as a function of adaptation duration.

trials needed following 3 seconds of adaptation ranged from 2 to 7, while the number of trials needed after 240 seconds of adaptation ranged from 2 to 22. Note that one subject, JP, required only 2 episodes to null her MAE regardless of the length of adaptation. All other observers demonstrated the linear increase in the number of extinction trials needed to null their MAE as adaptation time increased. JP's data, thus, led to an underestimation of both the group means and of group differences, which may account for the lack of significant differences for all pairwise comparisons.

3.3.5 MAE Index

The previous sets of analyses allowed for a tracking of the buildup and decay of the motion aftereffect. It was already shown that decay is slower for longer adaptation durations. It is possible that the spread of extinction may combine to yield the same MAE duration as a more rapid extinction as observed with the shorter adapt durations. To test this possibility, a more general index of the total MAE was also calculated. To determine an estimate of the total MAE produced via adaptation length, the initial and extinction MAE episodes were pooled for each subject, and then averaged across subjects, for each adaptation duration. As illustrated by Figure 3.20, total MAEs were determined to be 8.88,

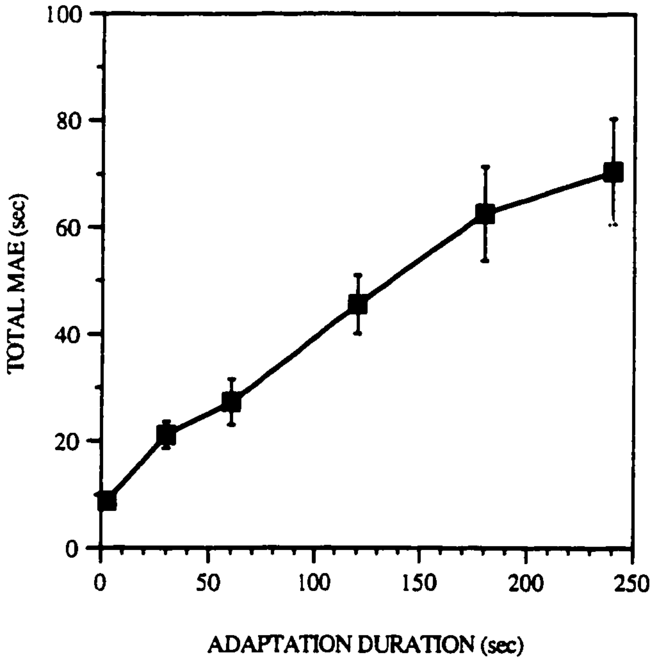

Figure 3.20. Mean total MAE duration as a function of adaptation duration. Error bars not shown are smaller than the symbol used to plot the point.

21.21, 27.29, 45.53, 62.60, and 70.49 seconds for adaptation durations of 3, 30, 60, 120, 180, and 240 seconds, respectively. Following this, an index of MAE was calculated by dividing the total MAE by its number of extinction trials for each adaptation duration. The computed indices were found to be 2.24, 4.25, 5.40, 7.09, 8.53, and 9.96 seconds for 3, 30, 60, 120, 180, and 240 seconds of adaptation, respectively. Interestingly, the MAE index also increases with adaptation duration (Figure 3.21) rather than being some constant, even after the number of extinction trials is factored out.

3.4 Discussion

The preceding analyses revealed four main points, all indicative of how important adaptation duration is to the motion aftereffect. First, the longer the adaptation duration, the longer the initial MAE duration. Second, the MAE decays over time and this decay was slower with longer adapting durations. Third, the number of trials (exposures) needed to extinguish the MAE increased with increasing adaptation duration. Last, that even when the number of extinction trials is factored out, the duration of the total MAE is longer for longer adaptation durations. In the following paragraphs these points will be discussed in more detail.

Only one study to date has examined the duration of the motion aftereffect following variable adaptation durations (Bowd et al., 1996) and reported that the aftereffect duration, following adaptation to stereoscopic or luminance motion, was proportional to the square root of adaptation duration and that there was no sign of adaptation saturation even at the 64 minute adaptation duration. The present study replicates their luminance stimulus observation. MAE duration was found to be dependent on adaptation time in that the longer the adaptation duration the longer the subsequent [initial] MAE duration. Likewise,

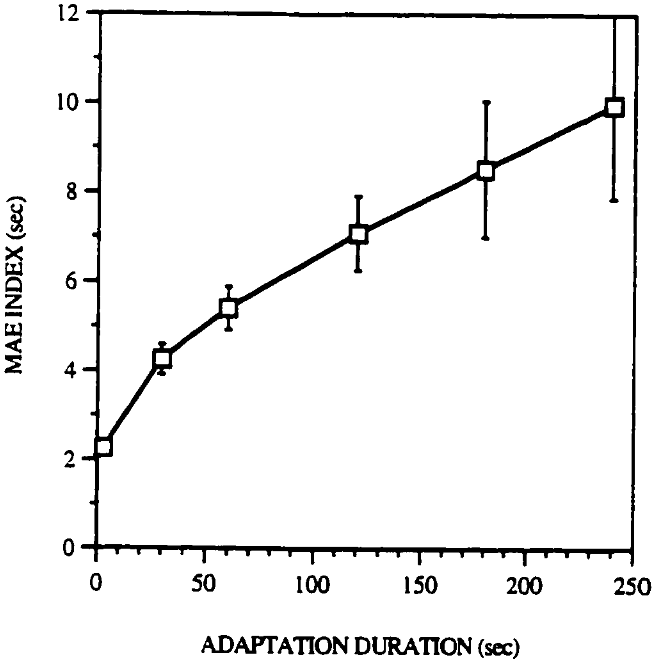

Figure 3.21. MAE index as a function of adaptation duration. Error bars not shown are smaller than the symbol used to plot the point.

this study found that this function did not plateau with increasing adaptation length. Taken together, these findings appear to be evidence against neuronal fatigue models of MAE explanation which would instead predict an asymptotic function between MAE duration and adaptation time after some level of brief adapt duration (approximately 20 seconds according to Giaschi et al., 1993). It seems more likely that the longer adaptation duration stimulates the error-correcting device to detect a discrepancy between the external environment and internal representation, and to recover the rule of zero net motion. The duration of the MAE would be brief for short adaptation durations because presumably the neutral point would only be slightly moved based on the new average motion in the environment. For longer adapting times, however, the ECD would cause a more extreme shift in the adaptation level towards the adapt direction, rightward for example, establishing a new neutral point by which to compare external motion. Rightward motion signals in the environment would appear stationary in theory (or perhaps less rightward) whereas stationary signals in the environment would hence appear to drift leftward (i.e. the MAE). The duration of the MAE would hence be longer following longer adaptation periods because it would take more post-adaptation inspection prior to recovering the original adaptation level.

Generally, it is thought that when one's immediate MAE ceases, the visual system has recovered from adaptation. This initial MAE duration therefore is believed to reflect the recovery time from adaptation. Oddly enough, if subjects are given the opportunity to observe a stationary stimulus again, their MAE returns. This is the now popular storage effect. Knowing that storage is a possibility, the time is takes for the system to *fully* recover from adaptation (i.e. when the MAE no longer returns) was examined. The time course for complete recovery has not been examined for the motion aftereffect prior to the present study. Recovery for the tilt aftereffect was found to take longer for longer adapt periods (Wolfe & O'Connell, 1986). Similarly, the present experiment observed the time course for the recovery from the motion aftereffect. It was also dependent on the adaptation duration. Longer adaptation durations lead to slower recovery from the MAE revealed by two dependent measures. The first was the number of trials needed to cancel the MAE, in other words, how often would the MAE return. Numerous MAE measurements were required to completely extinguish the motion aftereffect. This was dependent on the duration of adaptation. Long adaptation necessitated more extinction trials. The second measure was the length of each of the returning MAEs. Following long adaptation, for instance, the subsequent tests after the initial MAE yielded substantially longer MAE durations. The length of the stored MAE decreased with each return trial. Together, these data indicate that the visual system not only requires more inspection of the stimulus (longer MAE duration within one trial) to completely recover from the aftereffect, but interestingly, many separate experiences are needed (many extinction trials). These data are consistent with the decay of the tilt aftereffect (Wolfe & O'Connell, 1986) which required several trials to recover. There is, however, a significant difference in how Wolfe and O'Connell's tilt aftereffect and the present study's MAE were measured. On each trial, their subjects gave a subjective orientation of the test gratings. They did not observe the stimulus until the lines appeared to be in their pre-adapt state (which would have been analogous to the present study).

Storage of the MAE is not typically studied by providing the opportunity to experience an immediate MAE, but rather having the subjects wait for a certain length of time (the storage period) and then only giving a delayed test. What is interesting with the present study's data is the return of the MAE after the subject's immediate MAE has dissipated. This implies that when one's immediate MAE has terminated, the visual system has not yet fully recovered from adaptation. While this finding is very intriguing, it is challenging to explain with either fatigue or recalibration models. Neither theory can easily account for the return of the MAE observed during the extinction trials. When the MAE stops, either (a) fatigued cells have recovered, or (b) adaptation level is back at the true neutral point. Yet it is as if the system temporarily recovers from adaptation, but then bounces back to the adapted state immediately after the MAE. Perhaps the assumption, that the termination of the (initial) MAE is indicative of a recovered state, is not correct. It is known that if a subject blinks when their MAE appears to have ended, their MAE is reestablished (Wohlgemuth, 1911). The present study provided the "blink" in the methodology, and the results are the same.

One possible explanation might lie in the type of test stimulus. Psychophysical evidence demonstrating greater MAE strength with dynamic test stimuli is rapidly accumulating. In some instances (second-order adaptation), MAEs are only experienced if the test stimulus is moving (Nishida et al., 1994; Bertone & von Grünau, 1998). Interocular transfer of MAEs is more complete when tested with dynamic tests (Raymond, 1993a; Nishida et al., 1994). Unlike static test stimuli, dynamic tests are typically less sensitive to the type of adapting stimulus, in that good cross adaptation effects between first- and second-order stimuli are observed with dynamic tests (Nishida & Sato, 1995; Ledgeway, 1994; Ledgeway & Smith, 1994a; Ledgeway & Smith, 1997). Hiris and Blake (1992) argue this point well by stating that only dynamic test stimuli appropriately activate the *motion system*, whereby static test patterns are engaging the *form system*.

Physiological research on motion adaptation supports this position. Single-cell findings demonstrate that the effects of adaptation are generally negligible when tested with blank screens or stationary test stimuli in comparison to the effects evoked by moving test stimuli (Hammond et al., 1988; Marlin et al., 1988). Two recent functional MRI studies of the MAE storage yield additional support for this notion. Both Culham et al. (1999) and He et al. (1998) illustrate that during the storage period when either pitch black or uniform gray screens were present, respectively, MT activity was at or below baseline in both cases. Following the storage duration, with the presentation of a stationary version of the adapting stimulus, activity sharply increased but did not reach adaptation activity levels. They both interpret the drop and rise in MT activity as a direct correlation between the physiological and perceptual experience of the MAE. It is possible, however, that activity in MT would be as high as adaptation levels (perhaps reflecting a stronger MAE) if the test stimulus was dynamic. Taken together, it seems plausible that dynamic test stimuli may provide a more sensitive technique for measuring post-adaptation changes in sensitivity. Applying this to the present study's results, perhaps the MAE fades away and returns because the static test stimulus is limited in reflecting the true state of the visual system. During each episode of MAE, for instance, there may be some competition between the output of the motion system and the form system. The motion system may initially dominate the percept, hence the MAE, subsequently followed by a stronger response from the form system which would indicate a motionless stimulus. This response competition may occur with each novel stimulus, i.e. with each introduction of the static test until the system has fully recovered. This hypothesis would require further investigation to determine its validity, but it is an interesting possibility with some psychophysical and physiological support.

The motion aftereffect index (MAE-I) was determined to verify whether longer adaptation times induce longer MAE durations or if this relationship was dependent on the number of extinction trials. The data indicate that even with the number of extinction trials factored out longer adaptation durations indeed lead to a longer motion aftereffect percept. As outlined earlier, fatigue models may have difficulty accounting for the fact that the function between adaptation duration and MAE duration does not asymptote earlier. For the same reasons as already highlighted, recalibration would predict and support such an observation.

This experiment provided some evidence contrary to predictions made from a neural fatigue point of view, and some consistent with those postulated from a recalibration interpretation. Findings which are difficult for both theoretical models were also discussed. For this reason, additional evidence is necessary to determine whether recalibration really is a better explanation of the motion aftereffect.

EXPERIMENT 2

4.1 Introduction

Verstraten, Fredericksen, Grüsser et al. (1994) adapted their subjects to uni-directional motion of one random-pixel array for 60 seconds. This stimulus was immediately followed by a second moving pattern of variable display time and its motion direction was orthogonal to that of the first. A stationary pattern was presented immediately after presentation of the second moving pattern. The direction of the resulting MAE was uni-directional, opposite to the vector sum of the two successive motion directions observed in adaptation. These data are indicative of three points. First, there is storage of the first motion signal. Second, the two adaptation directions either interact or cohere prior to the MAE induction *or* two separate MAEs are formed and they interact to yield a coherent MAE percept. Third, and finally, this interaction yields important procedural information for experimentation of the motion aftereffect (i.e. carryover effects).

The following experiment further investigated storage effects across multiple motion signals. This study, contrary to Verstraten et al., did not examine the integration of motion signals via two different motion directions, but rather, it studied whether multiple successive presentations of the same motion direction over time would combine to yield a longer MAE than that from one 3-second presentation, and as well, whether the duration of this combined MAE would equate that from 15 seconds of uninterrupted adaptation. Specifically, there were four conditions which were expected to yield varying degrees of MAE storage according to fatigue versus recalibration hypotheses. Uninterrupted-adaptation consisted of 15 continuous seconds of unidirectional motion adaptation, whereas interrupted-adaptation was defined by 5 successive presentations, each 3 seconds in length, for a total adaptation duration of 15 seconds. One of the interrupted-adaptation conditions was characterized by a 3-second blank interval between each presentation. Another interrupted-adaptation consisted of MAE measurement between each presentation. The last interrupted-adaptation combined the first two, in that, at the end of each 3-second adaptation, the subjects' MAE was measured followed by a 3-second blank interval, and then proceeded with the next 3-second adaptation episode. As an underlying mechanism for the MAE, fatigue and recalibration may yield different expectations as to how much storage will occur under these circumstances.

Uninterrupted versus interrupted with no intervening MAE measurement would presumably lead to the same MAE if recalibration is occurring. The blank screen, or lack of visual information, should not help the visual system recover from adaptation because there is no motion information and because there is no contrast in the visual scene or object to induce an MAE. As such, there should be complete storage of each aftereffect which should yield a final MAE comparable to that observed following uninterrupted-adaptation. Fatigue models predict that there should be some (perhaps not full) recovery during the 3-second blank screen interval. This would result in a longer MAE in the uninterrupted-adaptation condition.

The MAE observed in the interrupted-adaptation with no intervening MAE measurement should be longer compared to the MAE from interrupted-adaptation with intervening MAE measurement, as expected from both recalibration and fatigue models. In terms of calibration, the opportunity to experience an MAE should activate the visual system to begin recovery. The stationary stimulus provided in this intervening interval can be used in the recalibration process because it induces illusory motion information. When no such stimulus is offered to the visual system, recalibration is not likely to occur. Fatigue theory would predict just the same, but for different reasons. Recovery from fatigue should be independent of the presentation of a stationary stimulus. In addition, data from Experiment 1 indicates that the MAE from one 3-second adaptation duration is about 4 seconds, actually longer than the adaptation period. In terms of the mere passage of time, therefore, measurement of the MAE probably provides the visual system with more time to recover sensitivity than the blank interval, and hence a shorter MAE.

Interrupted-adaptation with MAE measurement may or may not produce a different MAE than interrupted-adaptation with MAE measurement followed by a 3-second blank interval, dependent on recalibration or fatigue, respectively. Similarly to the first prediction for this study, a blank interval should not be useful for recalibration processes and since that is the only procedural difference between these two conditions, the recalibration model should predict the same MAE length. Time to recover, according to the fatigue model, is not dependent on visual experience, and therefore, this extra 3 seconds of interval will be additional time to recover function. The resulting MAE should thus be shorter when there is an intervening MAE measurement plus blank screen interval as compared to just intervening MAE measurement.

In general, some degree of storage is predicted for these conditions. The relative amount is dependent on the type of model, recalibration or fatigue. The key factor in this study is the assumption made regarding the blank intervening period and how it relates to both theoretical accounts. In summary, it is expected that this interval would be used as recovery time if the fatigue model is valid, but storage time if recalibration is more characteristic. Measuring the aftereffect between adaptation episodes, however, should slightly reduce the final MAE for both models. It would be used as external information to start the recalibration process, reinstating the original adaptation level consistent with constraints normally observed in the environment. On the other hand, for the fatigue model, time spent perceiving the MAE would be time for the fatigued cells to recover sensory abilities.

The hypotheses for this experiment consequently were (1) multiple successive presentations of the same motion direction over time may combine to yield an MAE as long (recalibration) or shorter (fatigue) than that from one uninterrupted presentation, (2) the MAE duration from multiple presentations with intervening MAE testing would be shorter than multiple adaptation episodes with no intervening MAE testing (both recalibration and fatigue), and (3) the duration of the MAE from multiple presentations with intervening MAE testing plus blank interval would be the same (recalibration) or shorter (fatigue) than the MAE from multiple presentations with intervening MAE testing alone.

4.2 Method

4.2.1 Subjects

Six subjects, ages between 20 and 33, participated in all conditions. The observers were recruited from diverse educational backgrounds, with normal or corrected-to-normal vision. All were right handed and were introduced to the motion aftereffect prior to their participation in the experiment. One of the observers had no previous experience in psychophysical experiments, and three were naive to the purpose of the experiment. Five of the observers were participants in Experiment 1. Once again, non laboratory members were paid for their time.

4.2.2 Procedure

Design

Uninterrupted-adaptation (i.e. 15 seconds of continuous motion) was contrasted with interrupted-adaptation (i.e. a 3-second adaptation duration presented 5 times consecutively to yield a total adaptation duration of 15 seconds). The interrupted-adaptation procedure was manipulated in the following manner to yield three interrupted-adaptation conditions. For two of the interrupted-adaptation conditions, the subject's MAE was measured following each adaptation episode. The stationary display for one of these two conditions would remain on screen and immediately begin the next adaptation episode, while for the other condition it would disappear for three seconds (refer to Figure 4.1). In the third interrupted-adaptation condition, the subject's MAE was not recorded between episodes but only once when the fifth 3-second adaptation duration was finished (i.e. only after the total 15 seconds of adaptation was reached). For this condition, the stimulus was removed between episodes for 3 seconds. There were, thus, four experimental sessions (one uninterrupted-adaptation and three interrupted-adaptation conditions). Each stimulus was presented 5 times, yielding a total of 5 trials per session. Experimental sessions were presented in a randomly permuted order with the rational that carryover and expectation effects would be minimized in this fashion. In addition, sufficient time elapsed between testing sessions and subjects were always tested for residual MAE between sessions.

Subjects' task

Again, following good fixation, the subject initiated each trial by pressing the spacebar. For the uninterrupted-adaptation condition, the subject's task was as follows. Immediately following the 15-second adaptation period, the stimulus remained on screen in its stationary form and subjects responded by depressing the appropriate key to indicate when their percept of motion in the opposite direction from adaptation (i.e. their MAE)

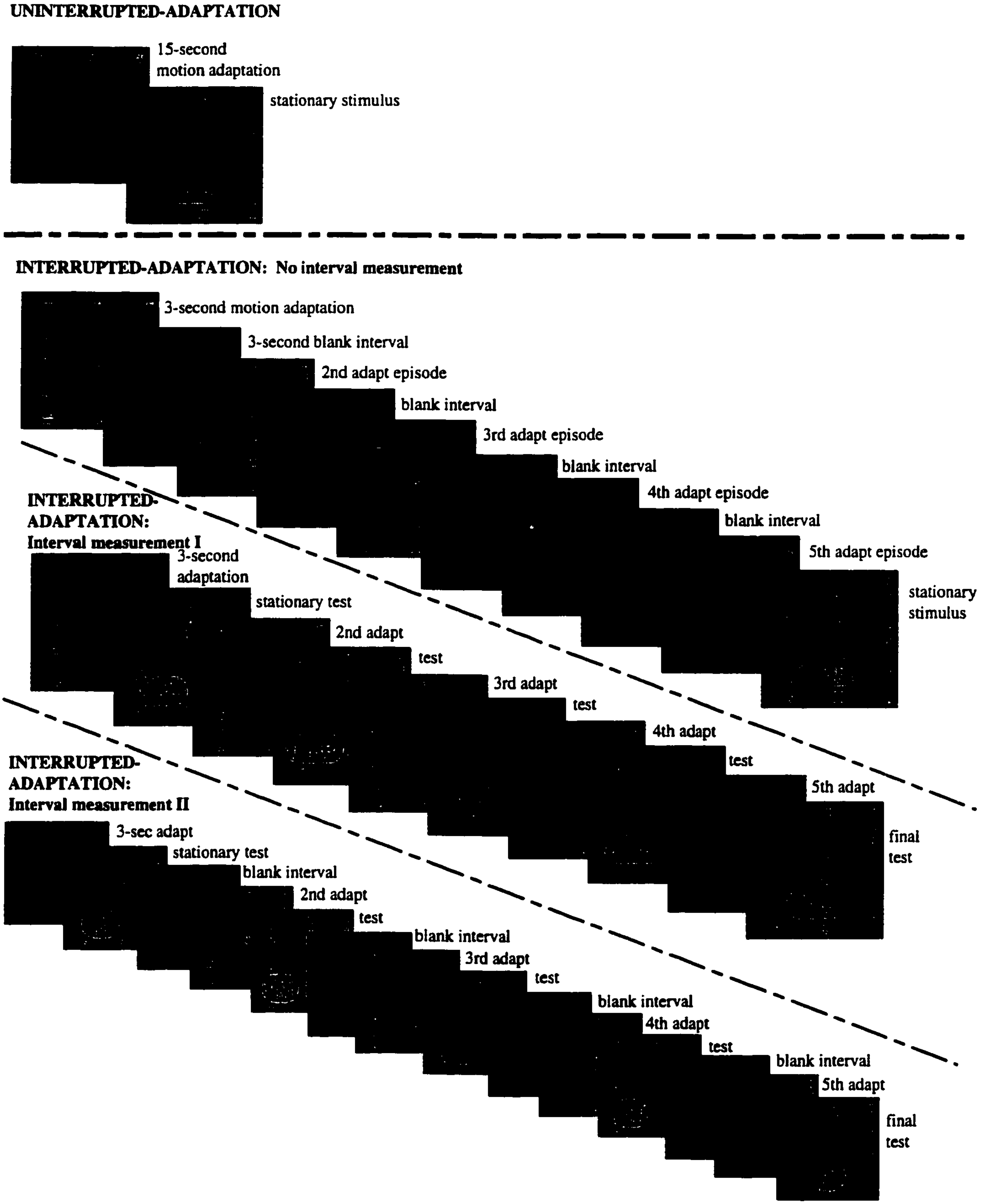

Figure 4.1. The temporal sequence of events on a given trial for the different adaptation conditions, uninterrupted- versus (three) interrupted-adaptation procedures.

ceased. The display then disappeared for 3 seconds after which it would reappear, again stationary. The task again was to press the key when their MAE ended. The stationary display would then disappear for another 3 seconds and then reappear. This sequence continued until the subject would indicate, via depression of a different (adjacent) key, that s/he no longer experienced any motion. For one of the interrupted-adaptation conditions, the display would move for 3 seconds, then disappear for 3 seconds, then reappear and move for 3 more seconds and so on until 15 seconds of adaptation was reached. Following the fifth 3-second adaptation episode, the display remained stationary on the screen and the subjects responded by depressing the key to indicate when their MAE ceased. Extinction trials were then presented. For the remaining two interrupted-adaptation sessions (display on or off between episodes), subjects were instructed to indicate the duration of their MAE, in the same manner as before, following each 3-second adaptation episode. The extinction trials were presented in this case only after the MAE was measured following the final 3-second episode in a trial. See Figure 4.1 for a schematic representation of this procedure.

Length of testing

Subjects completed all trials in all of the sessions. Each session lasted approximately 10 to 15 minutes (dependent upon the length of the subject's MAE and on the number of extinction trials an individual subject required. The overall participation time necessary to complete the experiment was therefore roughly one hour. As with the previous methods, the sessions were separated in time.

4.3 Results

4.3.1 Organization of the Raw Data

For a given condition, each subject's mean MAE (in seconds), following each episode of adaptation (i.e. in the case of interrupted-adaptation) or each uninterrupted adaptation, was calculated from the five replications. The MAEs from the extinction trials were not analyzed in this experiment as they were already examined in the previous experiment (they were employed simply as a control measure against carryover between trials). This procedure was repeated for each of the four experimental sessions. From these individual data, the group means were determined for each condition.

The data were organized along three dimensions: (a) mean length of the MAE as a function of the number of adaptation episodes (for the interrupted-adaptation conditions), (b) mean length of the MAE as a function of type of adaptation, and (c) carryover MAE. Thereafter, three types of analyses were performed on the data: (a) one- and two-way analyses of variance with tukey posthoc comparisons and planned comparisons, (b) trend analyses, and the (c) calculation of a MAE storage index. These analyses will be discussed according to the aforementioned manner in which the data were separated.

4.3.2 MAE as a function of the Number of Adaptation Episodes

Analysis of Variance

There were two types of interrupted-adaptation conditions in which the observer's MAE was measured following each episode of adaptation [note: the third type of interrupted-adaptation measured the MAE following the last adaptation episode only and will be analyzed in the next section]. The obtained MAE following each episode of adaptation was the first variable in a two-way analysis of variance (ANOVA). These two types of interrupted-adaptation differed in one aspect: the display would either disappear for three seconds between adaptation episodes or remain on screen and immediately start the next adaptation episode following the subject's response. This methodological difference was the second variable in the two-way ANOVA. The data yielded a monotonic trend, whereby subjects' MAE increased with each adaptation episode. Interestingly, the same pattern was found for both interrupted-adaptation conditions. To illustrate, average MAEs were 2.71, 3.38, 3.92, 4.25, and 5.14, for the five consecutive adaptation episodes, respectively, for the interrupted-adaptation condition in which the display remained on screen between adaptation episodes. The comparable average MAEs for the interrupted-adaptation condition in which the display was removed between adaptation episodes were 2.94, 3.52, 4.08, 4.38, and 4.91, for the five consecutive adaptation episodes, respectively (Figure 4.2). To test the significance of this pattern of results, a two-way ANOVA was performed on the MAE durations with the Number of adaptation episodes (5 levels: 1, 2, 3, 4, and 5) and the Type of interrupted-adaptation (2 levels: display off vs. display on between adaptation episodes) as factors. The two-way ANOVA supported this pattern of results with a significant main effects of Number of adaptation episodes ($F(4, 20)=30.19$, $p<.05$), a nonsignificant main effect of Type of interrupted-adaptation ($F(1, 5)=0.10$, $p>.05$), and a nonsignificant interaction of Number of adaptation episodes by Type of interrupted-adaptation ($F(4, 20)=2.18$, $p>.05$). Posthoc analysis (Tukey hsd) of the main effect revealed that MAEs for each adaptation episode significantly differed from the MAEs yielded by all other adaptation episodes except the level immediately prior to and following it (with one exception: the fourth and fifth episodes significantly differed, $p<.05$).

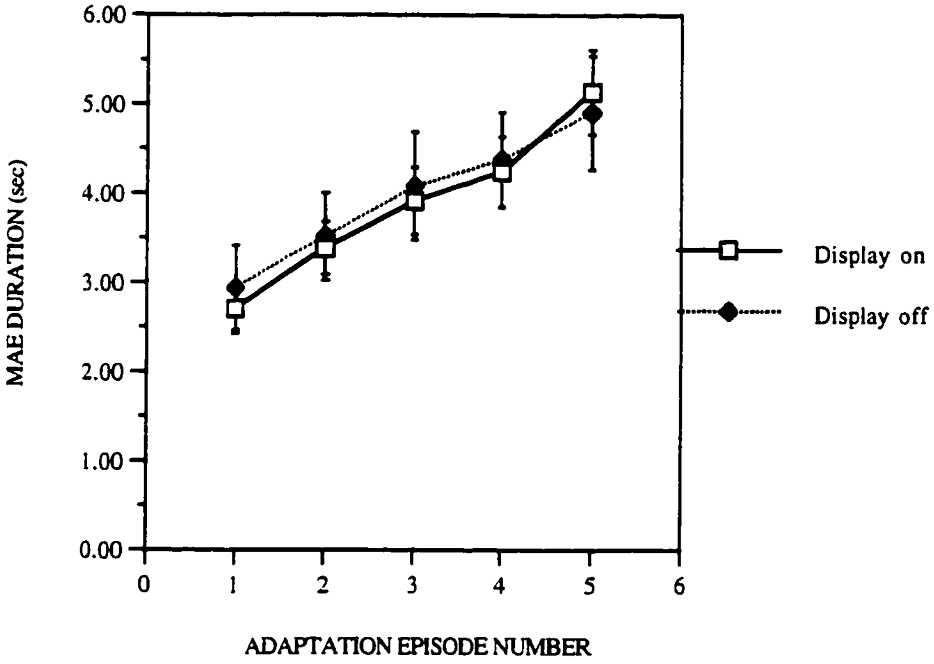

Figure 4.2. Mean MAE duration as a function of the number of adaptation episodes in the interrupted-adaptation condition either with or without display between episodes.

Trend Analysis

The pattern of significant pairwise comparisons suggested a strong linear relationship in the data. A trend analysis was, therefore, computed to examine this possibility. The analysis revealed that the linear trend was indeed the only significant descriptor of the relation between aftereffect duration and number of adaptation episodes (F(1, 5)=36.49, p<.05), with a large effect size of .29.

4.3.3 MAE as a function of Type of Adaptation

Analysis of Variance

A one-way analysis of variance was conducted to determine whether the MAE varied as a function of Type of adaptation [3 levels: (1) uninterrupted-adaptation, (2) interrupted-adaptation with no measurement between adaptation episodes, and (3) interrupted-adaptation with measurement between adaptation episodes, but only the last MAE was used in this analysis]. Because the previous analysis determined that there was no difference between the display removed versus display remaining on screen between adaptation episodes, the data from these two conditions were collapsed and their means were used for the third condition in this analysis. As demonstrated in Figure 4.3, the data from the three adaptation conditions yielded a slight monotonic trend. Uninterrupted adaptation produced a mean MAE of 8.70 seconds, slightly greater than but comparable to, the 6.78 seconds yielded by interrupted-adaptation with no measurement. The MAE computed for the interrupted-adaptation with multiple measurement condition was slightly less (5.03 seconds), but approximated the mean MAE of the interrupted-adaptation with no measurement between episodes condition. It is important, however, to note that this value is significantly larger than the 2.82 seconds of MAE produced via one 3-second episode of

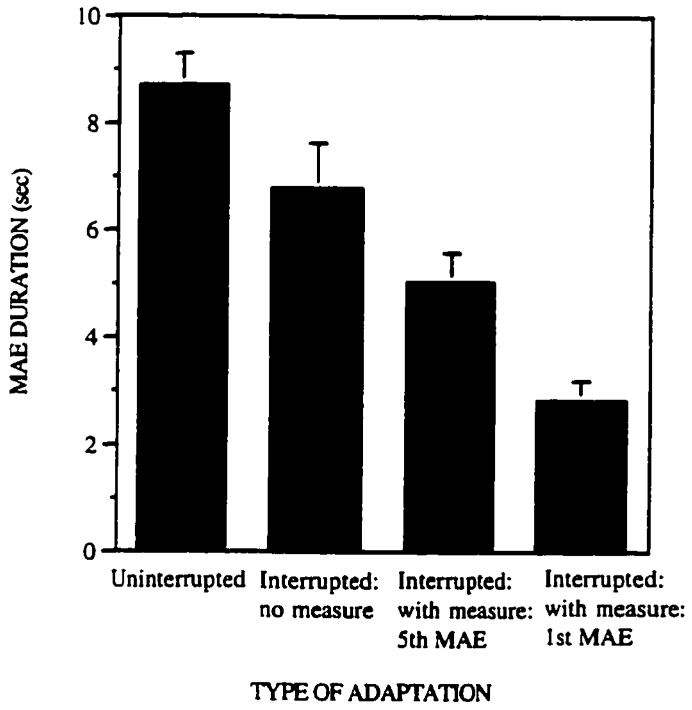

Figure 4.3. Mean MAE duration as a function of the type of adaptation.

adaptation. The MAE following the fifth 3-second adaptation episode, therefore, is a better estimate of the MAE from a 15-second episode of adaptation, uninterrupted or interrupted (so long as there is no measure of MAE between interruptions) than a one 3-second adaptation episode. The ANOVA supported this graphical interpretation with a significant main effect (F(2, 10)=8.07, p<.05) due largely to a significant difference between uninterrupted-adaptation and interrupted-adaptation with multiple MAE measurements (planned comparison F(1, 5)=68.37, p<.05). Statistically, uninterrupted-adaptation was not different from interrupted-adaptation with no measurement (planned comparison F(1, 5)=2.31,p>.05), and interrupted-adaptation with no measurement was not different from interrupted-adaptation with multiple measurement (planned comparison F(1, 5)=4.28, p>.05).

4.3.4 MAE Storage Index

The previous sets of analyses established that the motion aftereffect does not extinguish with one test trial, but rather, leftover MAE is stored and added to the effect of the following adaptation period. It was then determined precisely how much of the MAE is stored and thus carried over between trials. To have an estimate of the amount of MAE stored, each MAE episode was subtracted from the following MAE episode. This was done for each subject, and then means were computed. Again, to avoid redundancy, this was only done for the pooled data between the two interrupted-adaptation with multiple measurement conditions, since the previous ANOVA determined that the two were not different. As illustrated by Figure 4.4, the mean MAE leftovers were determined to be 0.68, 0.53, 0.53, and 0.89 seconds between adaptation episodes 1 & 2, 2 & 3, 3 & 4, and 4 & 5. Following this, the index of MAE storage, calculated via the average carryover time was determined to be 0.61 seconds. Interestingly, the MAE storage index, while

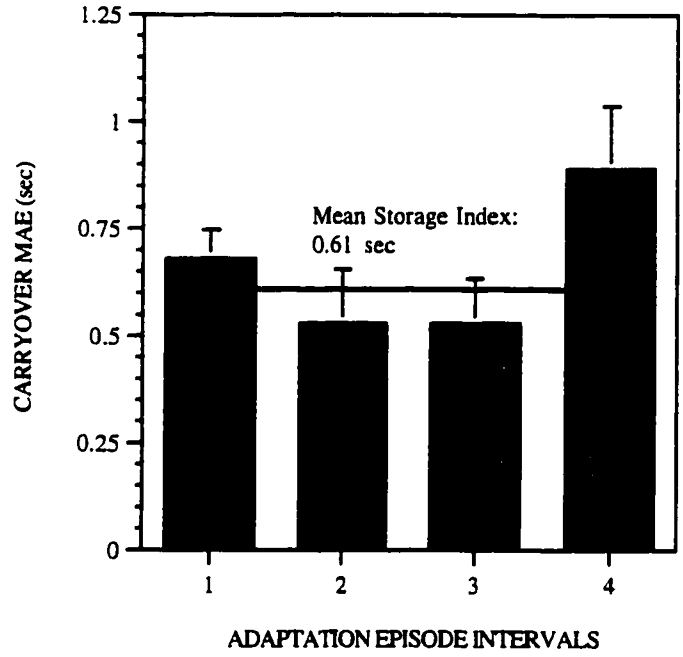

Figure 4.4. The MAE storage index for each interval between the five adaptation episodes. The mean MAE storage index was calculated to be 0.61 seconds.

seemingly small, does add with each adaptation episode and thus does accumulate over time, as illustrated in this experiment.

4.4 Discussion

This experiment further investigated storage effects across multiple motion signals. Specifically, it studied whether any residual MAE would store between multiple successive motion adaptations with intervening MAE measurement or whether the MAE duration would be about equal following each adapt episode. In addition, this study examined whether five successive 3-second presentations of the same motion direction over time would combine to yield a stored MAE longer than that from one 3-second presentation, and as well, whether the duration of this stored MAE would equate that from 15 seconds of uninterrupted adaptation.

As illustrated in the first section of the results, MAE duration was dependent on the number of adaptation episodes. With each additional 3-second episode of adaptation, the MAE lengthened in duration. This finding is indicative of significant carryover or storage of the motion aftereffect. Simply having a subject report the duration of his/her MAE following a brief 3-second adaptation is not sufficient to cancel the aftereffect. This is apparent because after another 3-second period of adaptation the observed MAE was found to be longer than following the first 3-second adaptation, thus revealing a residual MAE (i.e. storage) from the previous adaptation. This effect was observed with each additional adaptation episode. If this degree of storage occurs following brief adaptation periods like those employed here, the amount of residual MAE following longer adaptation durations is likely to be even more striking. That maintaining or temporarily removing the stimulus display between adaptation periods does not change this pattern of results illustrates the robustness of MAE storage over time and tends to support the prediction made based on the recalibration model. Removal of the display following the MAE measurement should have provided the fatigued cells with more time to recover and a shorter MAE would have been expected. This extra 3 seconds of blank screen, on the other hand, would not be useful for the system's recalibration process.

In addition, this study found that MAE duration was somewhat dependent on the type of adaptation, uninterrupted versus interrupted. When MAE measurement did not occur in the intervening period between the adapt and the test, the final and resulting MAE duration did not differ significantly from the MAE duration following 15 seconds of uninterrupted adaptation. The nonsignificant difference between these two conditions does coincide with the recalibration prediction in that the blank screen does not provide useful motion information, nor a contextual opportunity to experience the MAE, and thus the system remains in a changed state as reflected by a completely stored MAE. Although nonsignificant, uninterrupted adaptation does elicit a longer MAE. For this reason, one cannot be over confident in this as strong evidence for recalibration. There is a slight degree of recovery occurring, which is consistent with the fatigue model.

Measuring the MAE in the intervening period did not induce a significantly different final MAE duration from multiple adaptation with no intervening measurement. Statistically, this result does not offer support for either theory. Again, statistically there is no difference but there is a slightly longer final MAE when the MAE is not continuously measured. The trend, thus, is consistent with the expectation from both recalibration and fatigue. The multiple measures would either help the system reset itself to the true neutral point, or would offer additional passage of time for fatigued cells to increase their sensitivity.

Uninterrupted adaptation did, however, stimulate a significantly longer MAE duration compared to the interrupted-adaptation with measurement. This finding does not help differentiate the relative role of fatigue or calibration, because it is consistent with both theoretical frameworks. Importantly, the observed MAE duration from this interrupted-adaptation with measurement as just noted in the previous paragraph was significantly longer than that following one adapt episode. These results do strongly suggest that adaptation, however it occurs across time and even if the subject has opportunity to experience the aftereffect, has "lasting" effects on our perceptual experience. Indeed the motion aftereffect storage index (MAE-SI) was calculated to be 0.61 seconds for every brief 3-second adaptation episode. Results from the first and present experiment would predict that this MAE-SI would likely increase with longer adaptation periods. This study adds to the accumulating evidence supporting the combining of motion signals and hence the storage of the motion aftereffect over brief periods of measurement (Verstraten, Fredericksen, Grüsser et al., 1994; Verstraten et al. , 1996).

EXPERIMENT 3

5.1 Introduction

Wohlgemuth (1911 as cited in Wade, 1994) instructed his subjects to close their eyes immediately after adaptation for a period longer than the normal duration of the aftereffect. When subjects opened their eyes they reported a motion aftereffect which endured only slightly shorter than the original effect. Two separate fMRI studies exploring the MT brain activity during adaptation, storage period, and MAE both reported that brain activity was well correlated with percept (He et al., 1998; Culham et al., 1999). Culham et al. found that following a storage interval lasting the duration of each subject's immediate MAE, subjects experienced an aftereffect lasting approximately 74% of the immediate MAE duration. He et al. report a similar stored MAE following 10 seconds of blank interval, although they do not state the actual MAE duration. Despite long-standing interest in the motion aftereffect relatively few investigations have centered on the storage capacity. Spigel (1960) noted that darkness in the interval between adaptation and test phases is not necessary for storage to take place. Spiral MAEs produced after 15 minutes of adaptation have been observed 24 hours later by Masland (1969) and Kalfin and Locke (1972). More than a decade later, Hershenson (1985) found that 30 seconds of adaptation to a rotating spiral induced MAEs which were still present 3 days after cessation of stimulation. Almost half of Meeker and La Fong's (1988) subjects stored the spiral MAEs when tested on the third day. They also report, however, that the five minute delay between adaptation and first test (i.e. no visual stimulation) reduced the MAE. Thompson and Wright (1994) have recently observed that the nature of the pattern shown to subjects post adaptation and pre testing is rather important in the storage of the MAE. When the intervening stimulus was sufficiently different from the adapt/test stimulus, there was robust MAE storage (the length of the intervening period was not mentioned in their paper). Because the investigations of long-term storage of the MAE have been so scarce, the purpose of this experiment was to determine whether the MAE following adaptation to a drifting sinusoidal grating would store following 5, 10, or 15 minutes. To examine the influence of the intervening visual experience on the storage of the MAE, subjects were either blindfolded in a darkened laboratory or permitted to walk freely in the environment during the storage period. In this case, fatigue and recalibration models offer different predictions.

The blindfolded condition, in general, should yield little storage according to the neural fatigue model because recovery would occur during the post-adapt pre-test interval. Cells tend to recover completely in two minutes with the majority doing so in much less time (Barlow & Hill, 1963; Maffei et al., 1973; Vautin & Berkley, 1977; Hammond et al., 1988). Giaschi et al. (1993), however, did find that some cortical cells had not completely recovered their baseline sensitivity two minutes post adaptation. Exactly how much more time would have been necessary for full recovery is not known because they did not test past the two minute duration. Recalibration would, of course, predict storage in that no visual information about the external environment would be readily available for the person to shift the adaptation level to its normal criterion. Fatigue accounts predict that increasing the storage duration would reduce the MAE duration due to increasing time to recover. Recalibration, on the other hand, predicts no difference in the MAE duration as a function of storage duration due to the lack of visual information necessary to modify the criterion.

In the free-time condition, the fatigue account would predict more storage than the blindfolded condition. Adapted cells would have little chance to recover during free-time because they would be continuously stimulated in the motion rich environment as opposed to the opportunity to spontaneously recover in the dark nonstimulated condition. Increasing the intervening period may lead to further stimulation and adaptation, and therefore produce more MAE storage. Because there may be some spontaneous recovery during the intervening period, however, increasing the storage duration may not lead to more MAE storage but maintain it at a more constant level. Recalibration, on the contrary, would expect less storage in this condition than in the blindfolded one due to the rich visual information which would stimulate a change in the motion criterion. In addition, it is expected that increasing the intervening period would increase the amount of visual information and hence allow less MAE storage.

It was thus hypothesized that if the fatigue model account for the MAE is true, (1) the overall MAE would store less in the blindfolded condition than in the free-time condition, (2) in the blindfolded condition the MAE would decrease with increasing length of the intervening period, and that (3) in the free-time condition, the stored MAE will either be highest following the longest intervening period or remain constant across intervening periods. If recalibration explains the MAE then (1) in general, the MAE should store less in the free-time condition, (2) the MAE duration in the blindfolded condition should not vary as a function of intervening period length, and that (3) the MAE duration in the free-time condition will decrease as storage duration increases.

5.2 Method

5.2.1 Subjects

Four of the 8 observers were participants in Experiments 1 and 2, one was a participant in Experiment 2, and three were new to this set of studies. The age ranged between 20 and 33 years old. All other information and requirements were the same as in the previous experiments.

5.2.2 Procedure

Design

The three storage durations (5, 10, and 15 minutes) were separated into different sessions for both types of visual input conditions, yielding 6 experimental sessions. This procedure was implemented to avoid possible carryover effects, a potential threat especially following the shorter storage durations. Due to time constraints, each stimulus was presented only once. Experimental sessions were presented in a random order, separated in time, and the residual MAE was tested to minimize expectation and carryover effects.

Subjects' task

Upon good fixation, subjects initiated each trial. Immediately following the 240-second (4 minutes) adaptation period, the display disappeared for either 5, 10, or 15 minutes (dependent on the condition) leaving a uniform gray screen. For the no visual input condition, subjects were instructed to pull down their blindfold (already on their head) at this time and relax seated in the chair until the computer beeped, signaling that the test stimulus would appear in 3 seconds time and to lift the blindfold. In the rich visual input condition, subjects were instructed to walk freely in the environment for the storage duration. Following the storage duration, the stationary test display then reappeared on screen and subjects responded by depressing the appropriate key to indicate when their MAE ceased. The subject would indicate, via depression of a different (adjacent) key, on the other hand, if s/he had not experienced a motion aftereffect. Refer to Figures 5.1 and 5.2 for an illustration of the blindfolded and free-time procedure, respectively.

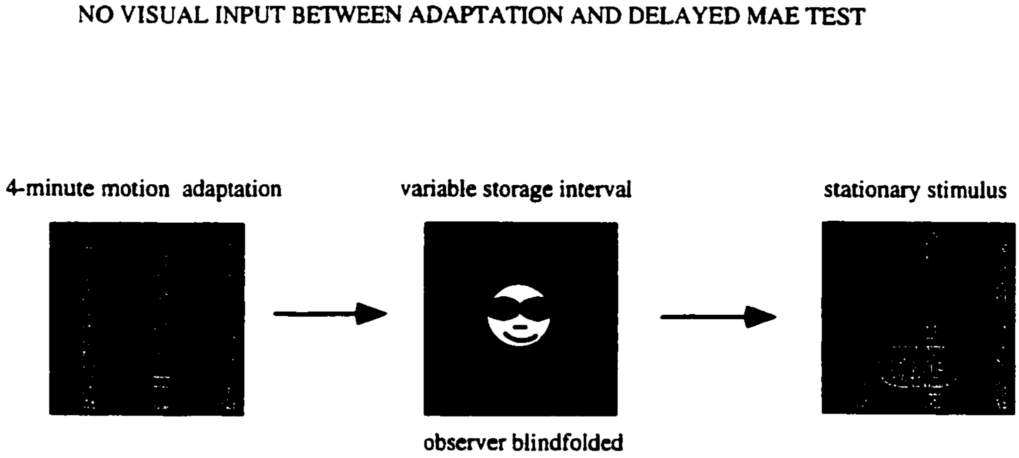

Figure 5.1. The temporal sequence of events on a given trial. Following four minutes of motion adaptation the subject was blindfolded for 5, 10, or 15 minutes. After the storage period was finished a stationary stimulus was presented and the subject's MAE duration was recorded.

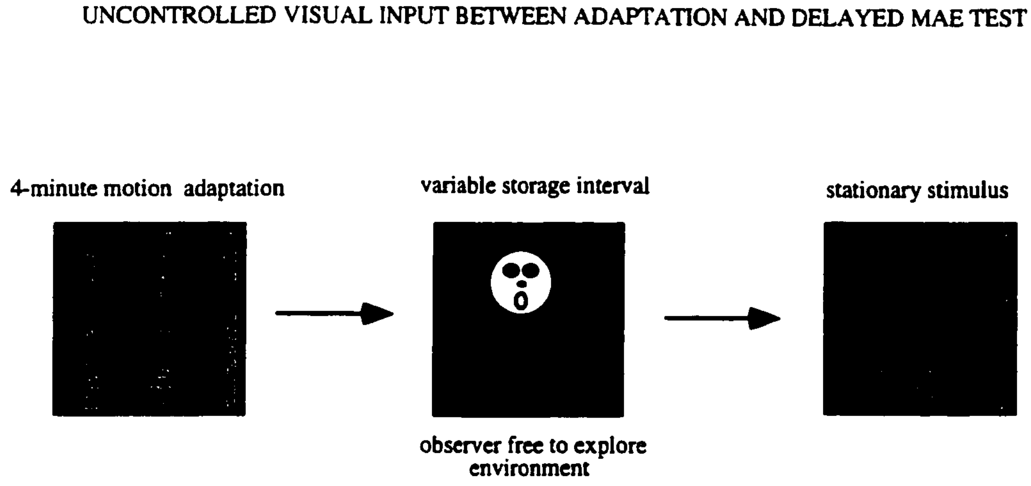

Figure 5.2. The temporal sequence of events on a given trial. Following four minutes of motion adaptation the subject was free to explore the environment for 5, 10, or 15 minutes. After the storage period was finished a stationary stimulus was presented and the subject's MAE duration was recorded.

Length of testing

Subjects completed all six experimental sessions. The sessions lasted approximately 10, 15, and 20 minutes (dependent upon the length of the subject's MAE) for storage durations of 5, 10, and 15 minutes, respectively. The overall participation time necessary to complete the experiment was therefore roughly 90 minutes.

5.3 Results

Analysis of Variance

For each condition, subjects' MAEs (in seconds) were examined. From these individual data, the group mean MAEs were determined as a function of the length of the storage duration (5, 10 and 15 minutes) and type of intervening period (blindfolded and free-time). Thereafter, a two-way analysis of variance (ANOVA) and planned comparisons were performed on the data. For both types of intervening experience, the data yielded monotonic trends, whereby subjects' MAE decreased with longer storage durations. Interestingly, MAEs were observed for all conditions for the majority of subjects. In the blindfolded condition, decreasing MAE durations were 24.43, 17.53, and 9.11 seconds for the three increasing storage times (5, 10, and 15 minutes), respectively. In the free-time condition, decreasing MAE durations were 16.51, 8.01, and 6.84 seconds for the three increasing storage times (5, 10, and 15 minutes), respectively (Figure 5.3). A two-way analysis of variance was conducted on the MAE duration with the Storage duration (3 levels: 5, 10, and 15 minutes) and the Type of visual input (2 levels: controlled and uncontrolled) as factors. The ANOVA illustrated significant main effects for both Storage duration and Type of visual input, $F(2, 14)=8.30$, $p<.05$ and $F(1, 7)=11.67$, $p<.05$, respectively, and no interaction, $F(2, 14)=1.47$, $p>.05$ (see Figure 5.3). The mean MAE duration for a controlled visual input during the storage period was 17.02 seconds, which

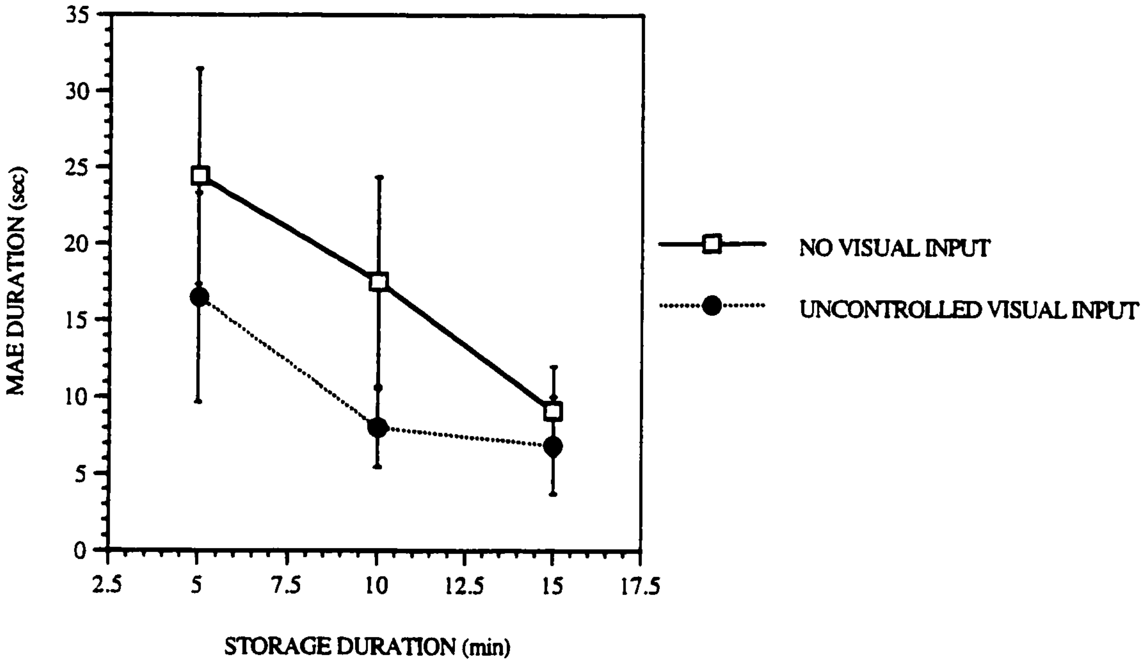

Figure 5.3. Mean duration of the stored MAE following 5, 10, and 15 minutes of either no visual input or uncontrolled visual input.

was significantly larger than the 10.45 seconds observed for the uncontrolled visual input storage period. The MAE, therefore, had a tendency to be greater (i.e. more MAE was stored) if there was no visual input between adaptation and testing periods. Planned comparisons were then computed to better understand the effect of storage duration in the blindfolded condition. All three comparisons were significant. The MAE following a storage duration of 5 minutes was significantly longer than the MAE yielded by the storage duration of 10 minutes ($F(1, 7)=15.33$, $p<.05$). Likewise, the 5-minute stored MAE was significantly longer than the 15-minute stored MAE ($F(1, 7)=10.48$, $p<.05$). In addition, the 10-minute stored MAE was significantly longer than the 15-minute stored MAE ($F(1, 7)=4.67$, $p<.05$). A similar pattern was observed in the effect of storage duration in the uncontrolled visual input condition. Two of the three planned comparisons were significant. The MAE was significantly longer following 5 minutes of storage compared to 10 and 15 minutes ($F(1, 7)=5.22$, $p<.05$, and $F(1, 7)=6.74$, $p<.05$, respectively). The MAE following 10 minutes of storage was not different from the MAE after 15 minutes ($F(1, 7)=0.81$, $p>.05$).

Trend Analysis

The pattern of significant pairwise comparisons suggested a strong linear relationship in the data for both type of visual input conditions. Trend analyses were, therefore, computed to examine this possibility. The analysis revealed that the linear trend was indeed a significant descriptor of the relation between aftereffect duration and storage duration for the blindfolded condition ($F(1, 7)=10.48$, $p<.05$), with a moderately large effect size of .12. The free-time condition also yielded a significant linear trend ($F(1, 7)=6.74$, $p<.05$), with a medium effect size of .08. Higher level trends were not significant.

5.4 Discussion

There have been relatively few studies conducted on the interesting phenomenon of MAE storage and the majority of them employ the spiral stimulus. In addition, few studies have systematically investigated the effect of the type of visual experience during the intervening period between adaptation and test on MAE storage. The present study has demonstrated robust storage effects following adaptation to one-dimensional motion. That aftereffects can be observed even following time spent in the visual environment confirms previous work which reported motion aftereffects after one day (Masland, 1969; Kalfin & Locke, 1972) and three days (Hershenson, 1985; Meeker and La Fong, 1988) post-adaptation. The aforementioned studies, however, differ from the present one in that the former employed spiral motion stimuli.

MAEs were observed following all three storage durations for both types of visual input in the intervening period. Predictions were made based on both the fatigue and recalibration interpretations and the observed data do not exclusively correspond to either of these theoretical models. To test the different theoretical models, the data need to be discussed in three ways: (1) the effect of type of visual input, (2) the effect of storage duration during the controlled visual input condition, and (3) the effect of storage duration in the uncontrolled visual input condition.

The influence of the type of visual experience in the intervening period yielded support for the recalibration theory. There was greater MAE storage in the "controlled visual input" condition. It seems that the visual information in the "uncontrolled visual input" condition allowed a faster recovery from adaptation. The effect of storage duration on the MAE during the controlled visual input condition, however, supported the influence of neural fatigue. When blindfolded, longer intervening periods reduced the stored MAE.

Longer periods of no visual input should not provide any assistance in adaptation recovery from a recalibration point of view. Longer periods of no visual input do on the other hand allow for more spontaneous cell recovery which would lead to less stored MAE according to the fatigue interpretation. While these data seem to be more consistent with fatigue, one still needs to consider that MAE storage after five minutes is still a little surprising from a fatigue perspective given that most of the literature seems to indicate a more rapid recovery. Though some research may support a longer recovery for some cells (Giaschi et al., 1993), still others find some cells which show no depressed activity from adaptation (Maffei et al., 1973). The effect of storage duration on the MAE during the uncontrolled visual input condition, on the contrary, supported the recalibration model. Less MAE was stored following longer storage periods in the free-time condition. When free to explore the environment, longer intervening periods should allow the visual system to recalibrate to "normal" and hence less MAE storage should occur.

Findings from He et al. (1998) demonstrated a close correlation between sensation and percept in that activity in MT was high throughout adaptation, absent during the dark gray storage interval, and somewhat high during the delayed MAE. They expected this close relationship and stated that if an MAE is not experienced during the blank storage interval then it follows that brain activity should be absent (nothing = nothing). Data from single-unit recording studies do suggest that imbalance in neural circuitry is illustrated best if the visual scene is present and in motion (see Experiment 1 Discussion). This does not mean that the changed responsiveness is not present or is necessarily in a fixed state. MAEs do not store completely even in a pitch black environment, which necessarily implicates some degree of spontaneous recovery from adaptation. Likewise, present data show that the stored MAE decays with the passage of time in that the delayed MAE following 15 minutes is significantly shorter than that of 5 minutes, for instance. A lack of

MT activity during the storage interval, thus, cannot imply a complete lack of recovery from adaptation.

The combined data, therefore, suggest a role for both neural fatigue and visual recalibration in the storage of the MAE. Fatigue accounts seem to be able to explain the spontaneous recovery observed in the blindfolded condition. This suggests that even with no visual stimulation our visual system can recover from adaptation. Recovery is faster following the rich visual experience that provides information to the contrary of the "conditions" observed in adaptation. This implies that our visual experience can speed up the otherwise normal spontaneous cell recovery. Alone, neither the fatigue nor the recalibration theory can explain the storage of the MAE. It seems more likely that each process contributes to the observed storage effects.

EXPERIMENT 4a

6.1 Introduction

Mahmud (1987) examined the storage of the motion aftereffect in a novel manner. Subjects were adapted to a rotating spiral for 10 minutes (positive adaptation) followed by a 2 second stationary test and their MAEs were recorded (direction: contraction, expansion, or motionless). After a 5 minute interval (setting not specified in paper), the spiral rotated in the direction opposite to the first adaptation direction (negative adaptation) for 1 minute. The stationary spiral was then presented once again and MAEs were recorded for 2 seconds. For the next 5 minutes, subjects were repeatedly tested for direction of MAE at 1 minute intervals. Following the positive adaptation, of say contraction, subjects reported movement in the reverse direction (expansion). Following the negative adaptation (expansion) subjects reported the reverse of this (contraction). Finally, during the last five minutes of testing all subjects indicated a change back to the original aftereffect direction (expansion). In other words, the original MAE from 5 minutes of adaptation was stored even after the induction of the reverse MAE within the intervening time.

The fourth, and final experiment reported in the present set of studies employed a method similar to the one reported above. Different from Mahmud, this procedure employed a drifting sinusoidal grating and slightly different adaptation and test durations. The question was whether subjects would store their first MAE (induced by a longer adaptation duration) after a subsequent induction of the opposite MAE (induced by a shorter adaptation duration). Given that the adaptation level (AL) is proposed to be a mathematical average based on one's visual experience, recalibration theory would predict an MAE opposite to the direction which was adapted for the longest time and not necessarily the most recently adapted direction. Fatigue model predictions rely heavily on the recovery time course and consequently two scenarios may be possible. If time for cells to recover a significant amount of sensitivity is very long for the longer adapt duration, then the imbalance of neural responses possibly may favor an immediate MAE opposite to the first direction. If, on the other hand, the time during the second adaptation is sufficient for full (or almost full) recovery for the cells affected by the first adaptation, then the imbalance of activity would predict an MAE opposite to the most recent adapt direction. From the single-cell recordings to date, the latter of these hypotheses is more plausible for the fatigue model. The majority of recovery of cell sensitivity occurs rapidly during the first 8 to 24 seconds post-adaptation (Giaschi et al., 1993).

It was hypothesized that with long adaptation in one direction subsequently followed by a shorter adaptation in the opposite direction, the fatigue model would predict an immediate MAE to the second adaptation, whereas the recalibration model would expect an immediate MAE to the first adaptation.

6.2 Method

6.2.1 Subjects

Seven of the eight subjects had participated in the previous experiments. They ranged in age from 20 to 33. All other details and requirements were identical to the previous experiments.

6.2.2 Procedure

Design

The five storage durations (3, 10, 30, 60, and 120 seconds) were presented in the same session in a randomly permuted order with the rational that expectation effects would be minimized in this fashion. Each stimulus was presented 6 times, thus yielding a total of 30 experimental trials.

Subjects' task

Each trial was initiated by the subject with a press of the spacebar. During the presentation of the moving display, subjects fixated and were instructed to observe the motion, free of other mental activities. On each trial, the display would first drift in one direction (e.g. left) for 60 seconds, and then drift in the opposite direction (e.g. right) for 15 seconds. Note that the first direction was sometimes left and other times right, in a counterbalanced fashion, so as to control for expectancy effects. Immediately following the 15-second adaptation period, the display remained on screen and stationary and the subject's task at this time was to indicate their perceived direction of motion via a 2-alternative-forced choice response (i.e. left or right) by pressing one of two adjacent keys on the keyboard. Following the subject's response, the display would disappear for either 3, 10, 30, 60, or 120 seconds leaving a uniform gray screen. The computer would beep to announce the reappearance of the stimulus display in three seconds, and subjects were again instructed to fixate the display and indicate if the stimulus appeared to move either left or right. Figure 6.1 illustrates this procedure. Responses were recorded and accumulated by the computer. Debriefing of subjects only occurred following the completion of all experimental sessions.

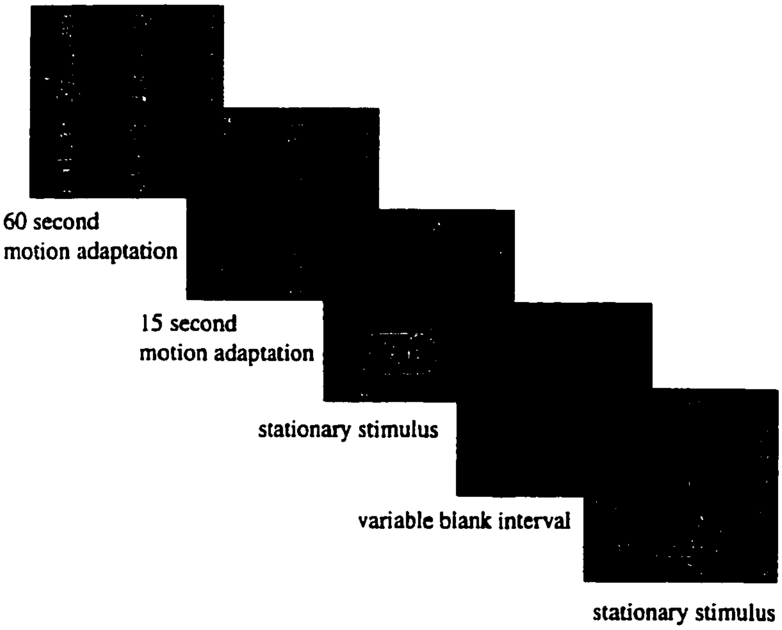

Figure 6.1. The temporal sequence of events on a given trial. Sixty seconds of adaptation to one motion direction was immediately followed by 15 seconds of adaptation to the opposite direction. Immediately after the second adaptation period a stationary stimulus was shown and the observer indicated their MAE direction. Subsequently, a variable storage period was followed by another stationary stimulus and the observer's MAE direction was again recorded.

Length of testing

The experiment lasted approximately 60 continuous minutes. Observers were, thus, obliged to complete all experimental trials in one sitting, with only brief breaks between trials.

6.3 Results

For each storage duration, a subject's mean immediate and delayed MAE *direction* was calculated. From these individual data, the group mean MAE directions were determined as a function of time of subject's response (immediate vs. delayed) and of storage duration. Thereafter, a two-way analysis of variance (ANOVA) with tukey posthoc comparisons was performed on the data. For the first MAE response, subjects typically reported perceived motion opposite to the more recent motion direction (i.e. opposite to the 15-second adaptation direction). Since the first response was recorded prior to the storage period, this specific finding was unrelated to the storage duration. Nonetheless, the five mean MAE directions were 95.83, 93.75, 97.92, 100.00, and 95.83 percent opposite to the most recent, 15-second adaptation direction. These values can be interpreted as a baseline for which to compare the mean MAE directions from the variable storage durations. The second MAE direction, on the other hand, changed perceived direction as a function of storage duration. To illustrate, for shorter storage durations, the perceived direction of MAE tended to be opposite to the most recent motion adaptation direction (i.e. opposite to the 15-second adaptation direction), whereas, for longer storage durations, the tendency was for perceived motion to be opposite to the longest adaptation direction (i.e. away from the 60-second adaptation direction). The relationship appeared to be decreasing monotonically, with mean percentages of 62.50, 43.75, 27.08, 22.92, and 18.75 percent opposite to the most recent adaptation direction (15-second) following storage durations of

3, 10, 30, 60, and 120 seconds, respectively (Figure 6.2). A two-way ANOVA was conducted on MAE direction as a function of Time of response (2 levels: immediate MAE and delayed MAE) and Storage duration (5 levels: 3, 10, 30, 60, and 120 seconds) as factors. This analysis found significant main effects for both Time of response (F(1, 7)=16.61, p<.05) and Storage duration (F(4, 28)=4.73, p<.05). The main effects were not meaningful, however, due to the significant interaction (F(4, 28)=17.14, p<.05). The simple effect analysis of this significant interaction supports the aforementioned graphical tendencies. Immediate MAE direction was not dependent on storage time (due to procedure), whereas, the delayed MAE direction was heavily dependent on storage duration, perceived as decreasingly opposite to the shorter adaptation duration with increasingly longer storage times. A tukey (hsd) analysis demonstrated that this significant simple effect was due to (a) MAE direction following 3 seconds of storage time was significantly different from the MAE direction following 30, 60 and 120 seconds of storage time, and (b) MAE direction following 10 seconds of storage time was significantly different from the MAE direction following 120 seconds of storage time. The remaining pairwise comparisons did not reach significance. Perhaps the increments in storage duration were not spread enough.

6.4 Discussion

It was hypothesized that long adaptation to one direction followed by a shorter adaptation to the opposite direction would immediately yield an MAE corresponding to either the second adaptation for the fatigue model, or to the first adaptation for the recalibration model, respectively. The immediate MAE was perceived to be opposite to the most recent (and shortest) adaptation direction. This finding does not seem consistent with the recalibration account of MAEs. The neutral point, or rather, a change in neutral point is

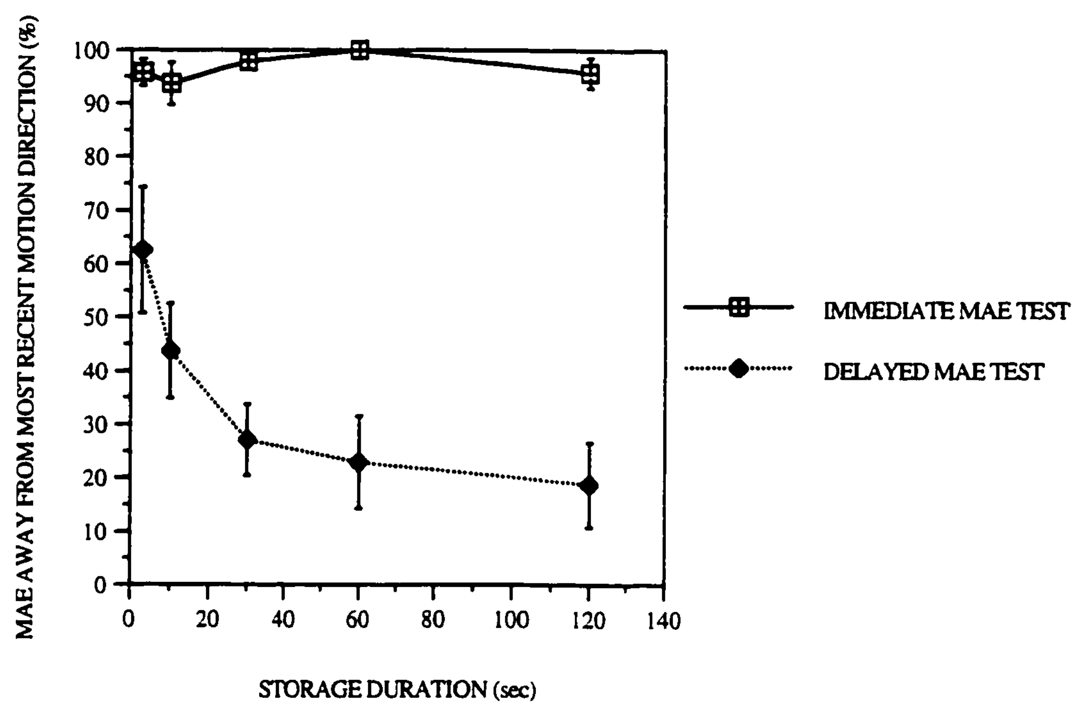

Figure 6.2. Mean percentage of MAE direction opposite to the most recent and shorter adaptation episode (15 sec) as a function of storage duration (ranging from an immediate test up to 120 seconds post-adaptation). Note that the "immediate MAE test" was always measured prior to the storage duration and thus acts as a baseline value. Decreasing percentage on the scale indicates MAE direction increasingly opposite to the first and longer adaptation episode (stored MAE).

determined by our most recent perceptual diet. An important factor in this study's prediction related to recalibration theory is the definition of "a more recent perceptual diet". It was assumed that a given trial would comprise the subject's recent visual experience and thus the mathematical average of motion directions would yield more motion in the first adaptation's direction, inducing an MAE to it. In retrospect, it is possible that one's most recent experience could be limited to the second motion adaptation with a corresponding MAE to it. This explanation, however, seems less consistent with the content of recalibration theory. The very element which makes this model more attractive than neural fatigue is that it can account for long term changes in perception (e.g. long term aftereffects). It thus seems contradictory that the same theory would define such a brief time period (to consider the second adaptation alone) as *recent* experience. The neural fatigue explanation may be able to account for this immediate MAE as discussed in the introduction of this study. If the imbalance of activity in the cells responding to the second adaptation is greater than the imbalance induced by the first adaptation the immediate MAE would reflect this. What is even more interesting is that the direction of the MAE switches with time to reflect adaptation to the first direction.

With re-testing the MAE direction became opposite to the first adaptation direction (i.e. storage of the first MAE). As the time between immediate and delayed testing increased, the percentage of responses in accord with the stored MAE increased. Following the longest storage period, the direction was, however, not 100% opposite to the stored direction (approximately 81%). It may be that longer storage periods would have continued this trend and complete MAE storage would have been observed. Though, given the data of other related storage research (Verstraten et al., 1996; Culham et al., 1999), this is not likely. Complete storage has not yet been observed. An MAE opposite to the first and longest adaptation direction is consistent for recalibration, but the time frame is somewhat puzzling. As mentioned earlier, recalibration would seem to predict an MAE to the first direction, regardless of time of testing. Alternatively, simple fatigue interpretation may be able to account for the data with assumptions about the time courses for recovery. It is not known if the time course for recovery is dependent on adaptation duration. If recovery is slower following longer adaptation then this could explain the return of the first MAE. By the time the MAE to the second motion direction has dissipated, presumably reflecting a recovered state for those cells implicated by the second adaptation, the cells which were affected by the first and longer adaptation may remain imbalanced. This would be expressed as an MAE to the first direction. The acceptance of this explanation is premature as the physiological nature is not yet fully understood.

Another possibility may be that fatigued cells may cause the immediate MAE and the stored MAE reflects a change in neutral point. This would imply that the satiated cells, rather than a recalibration of neural circuitry, yield a temporarily dominant percept, at least until they recover their sensitivity. In this manner, the short term fluctuations in the environment (i.e. the second adapt direction) would be accounted for by the temporary imbalances of cell activity due to neural fatigue (i.e. the immediate MAE). Substantially longer adaptation would induce long term modification to the system (i.e. from the first adapt direction) and just as brief adaptation can temporarily override normal perception, it may override the newly established system, as reflected by the stored MAE. The only problem with this explanation is whether or not one considers the first adaptation duration of 60 seconds to be substantially long. The present data, are in correspondence with the immediate and delayed spiral MAEs observed by Mahmud (1987). In his study, all subjects indicated a change back to the original aftereffect direction. The adaptation durations he used were, however, much longer and the procedure was slightly different. He favors the theoretical interpretation just mentioned, in that the immediate MAE and stored MAE reflect short- and long-term modifications of the visual system, respectively.

The present study used adaptation durations which were relatively different. It is important to examine what type of MAEs would be produced if these durations became increasingly comparable in length. This may aide in the understanding of whether fatigue, recalibration, or a composite of the two is best to account for motion aftereffects. The next study investigates this question.

EXPERIMENT 4b

7.1 Introduction

The data from the previous experiment suggested storage of the MAE which could be explained by some aspects of the neural fatigue and recalibration interpretations. A comprehensive understanding of the possible theoretical accounts was limited by the single combination of adaptation durations. The purpose of this study is to extend the conditions of Experiment 4a in search of a better theoretical account of the MAE. For this reason, the procedure was repeated with additional second-adaptation durations (30 and 60 seconds) to determine the amount of negative adaptation time necessary to prevent MAE storage of the first adaptation.

7.2 Method

7.2.1 Subjects

Only four of the eight subjects from Experiment 4a participated.

7.2.2 Procedure

Design

The same five storage durations (3, 10, 30, 60, and 120 seconds) were presented in this session, with two second-adaptation lengths, and each stimulus presented 6 times, for a total of 60 experimental trials.

Subjects' task

On each trial, the display would first drift in one direction (e.g. left) for 60 seconds, and then drift in the opposite direction (e.g. right) for either 30 or 60 seconds. All other aspects of the methodology were identical to Experiment 4a (refer to Figure 7.1 for a schematic representation of this procedure).

Length of testing

This experimental session lasted approximately 120 continuous minutes.

7.3 Results

The organization and analysis of these results were about the same as in Experiment 4a with some minor modifications. For each storage duration, a subject's mean immediate and delayed MAE direction was calculated. From these individual data, the group mean MAE directions were determined as a function of the time of subject's response (immediate vs. delayed), storage duration, and also of the length of the second adaptation. All subjects always reported an immediate MAE opposite to the most recent adaptation direction (similar to Experiment 4a) and thus these data were not entered in the analysis. A two-way analysis of variance (ANOVA) with tukey posthoc comparisons was performed on the data. Like

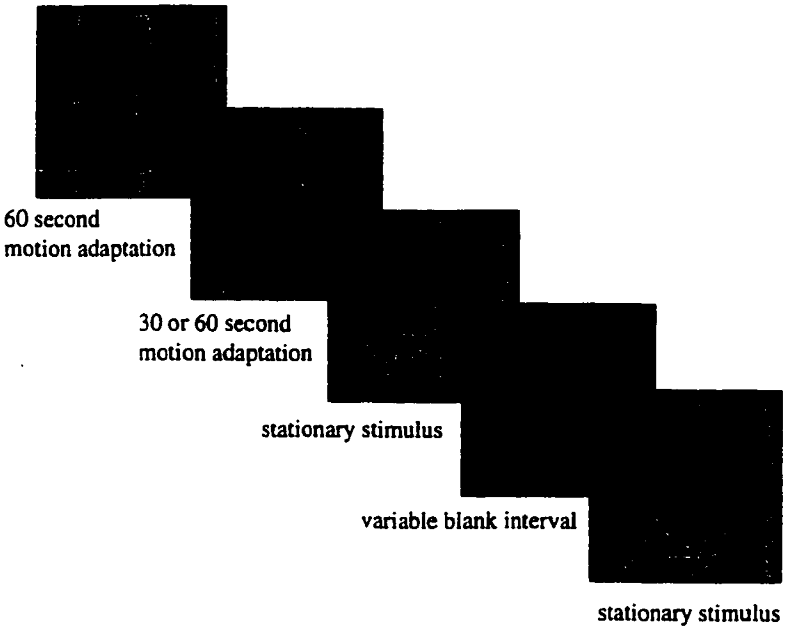

Figure 7.1. The temporal sequence of events on a given trial. Sixty seconds of adaptation to one motion direction was immediately followed by 30 or 60 seconds of adaptation to the opposite direction. Immediately after the second adaptation period a stationary stimulus was shown and the observer indicated their MAE direction. Subsequently, a variable storage period was followed by another stationary stimulus and the observer's MAE direction was again recorded.

the previous study's data, the second MAE direction changed perceived direction as a function of storage duration. For the 60/30-second adaptation conditions the perceived direction of MAE tended to be opposite to the most recent motion adaptation direction (i.e. opposite to the 30-second adaptation direction) for brief storage durations, whereas for the longer storage durations, the MAE was opposite to the longest adaptation direction (i.e. away from the 60-second adaptation direction). Again, the relationship appeared to be decreasing monotonically, with mean percentages of 95.83, 83.33, 41.67, 20.83, and 33.33 percent opposite to the shorter adaptation direction (30-second) following storage durations of 3, 10, 30, 60, and 120 seconds, respectively (Figure 7.2).

The 60/60-second adaptation sequences, however, lead to a slightly different pattern of results. For brief storage durations, the MAE was opposite to the most recent adapting direction (identical to the other test conditions). Interestingly, as the storage duration increased, there was no sign of an MAE to either adaptation direction. The subjects' responses were random. For storage durations of 3, 10, 30, 60, and 120 seconds, the mean percentages of MAE perceived opposite to the most recent adapt direction were 100.00, 100.00, 87.50, 70.83, 45.83, respectively (Figure 7.3). A two-way ANOVA was conducted on MAE direction as a function of Length of second adaptation (2 levels: 30 and 60 seconds) and Storage duration (5 levels: 3, 10, 30, 60, and 120 seconds) as factors. This analysis indicated a nonsignificant main effect for Length of second adaptation ($F(1, 3)=5.35, p>.05$) but a significant main effect for Storage duration ($F(4, 12)=18.74, p<.05$). The interaction approached but did not reach significance ($F(4, 12)=3.18, p>.05$). Tukey (hsd) analysis demonstrated that all pairwise comparisons were significant except the conditions immediately following one another. Finally, the data from Experiment 4a and 4b were graphed together to illustrate how storage of the first MAE is dependent on the relative adaptation time of the two directions. Figure 7.4 depicts how an MAE reversal was possible when the first adaptation was longer than the second (60/15-

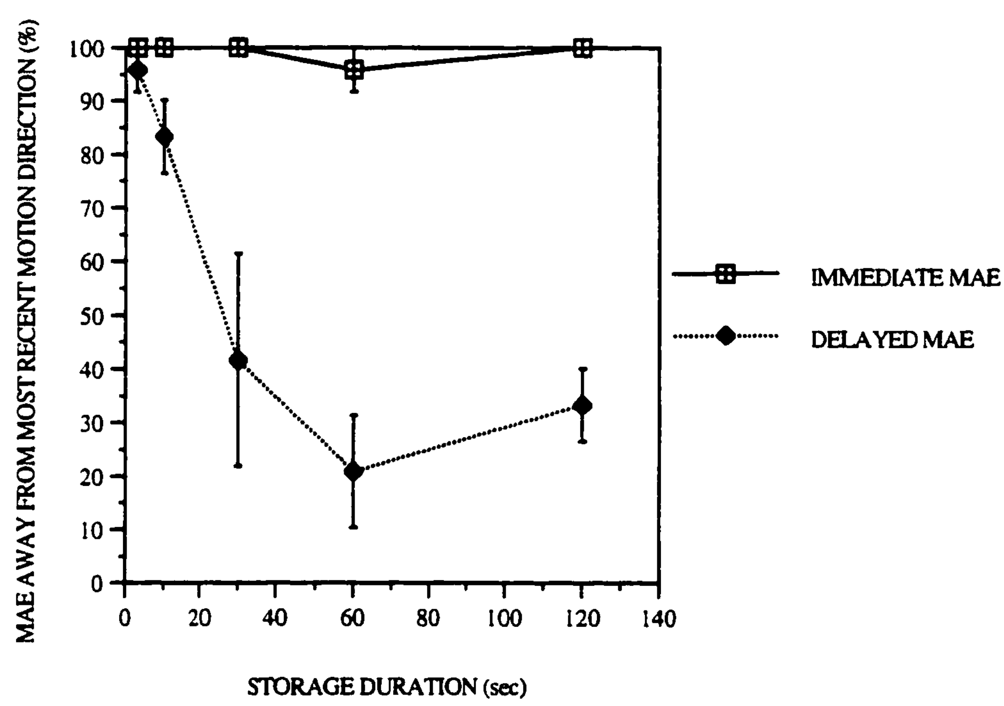

Figure 7.2. Mean percentage of MAE direction opposite to the most recent and shorter adaptation episode (30 sec) as a function of storage duration (ranging from an immediate test up to 120 seconds post-adaptation). Note that the "immediate MAE test" was always measured prior to the storage duration and thus acts as a baseline value. Decreasing percentage on the scale indicates MAE direction increasingly opposite to the first and longer adaptation episode (stored MAE).

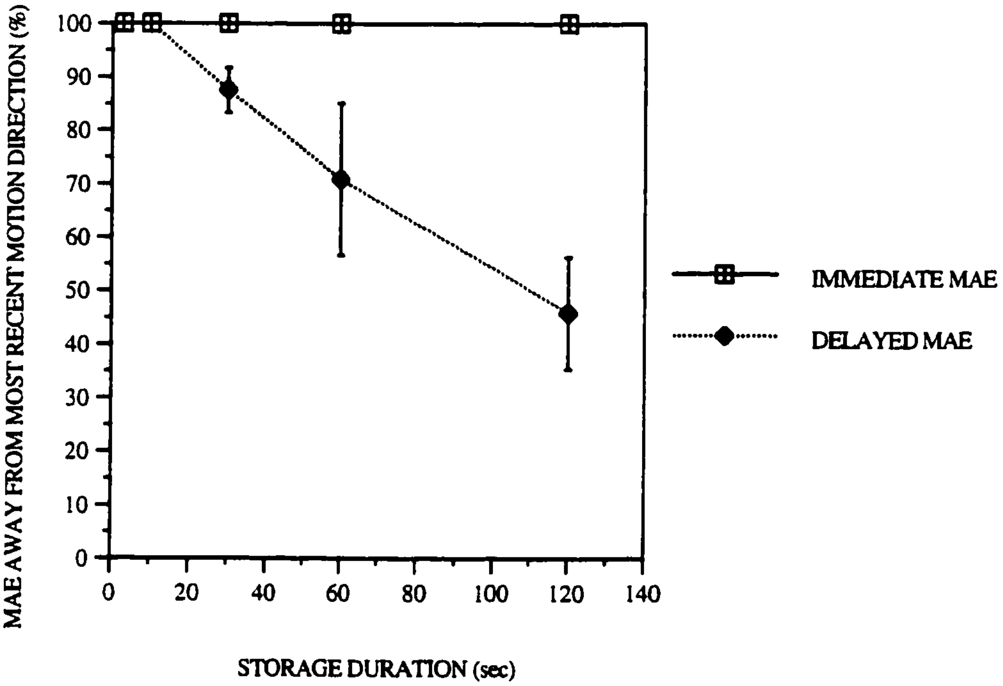

Figure 7.3. Mean percentage of MAE direction opposite to the most recent adaptation episode (the same length as the first adaptation episode: 60 sec) as a function of storage duration (ranging from an immediate test up to 120 seconds post-adaptation). Note that the "immediate MAE test" was always measured prior to the storage duration and thus acts as a baseline value. Decreasing percentage on the scale indicates MAE direction increasingly opposite to the first adaptation episode (stored MAE).

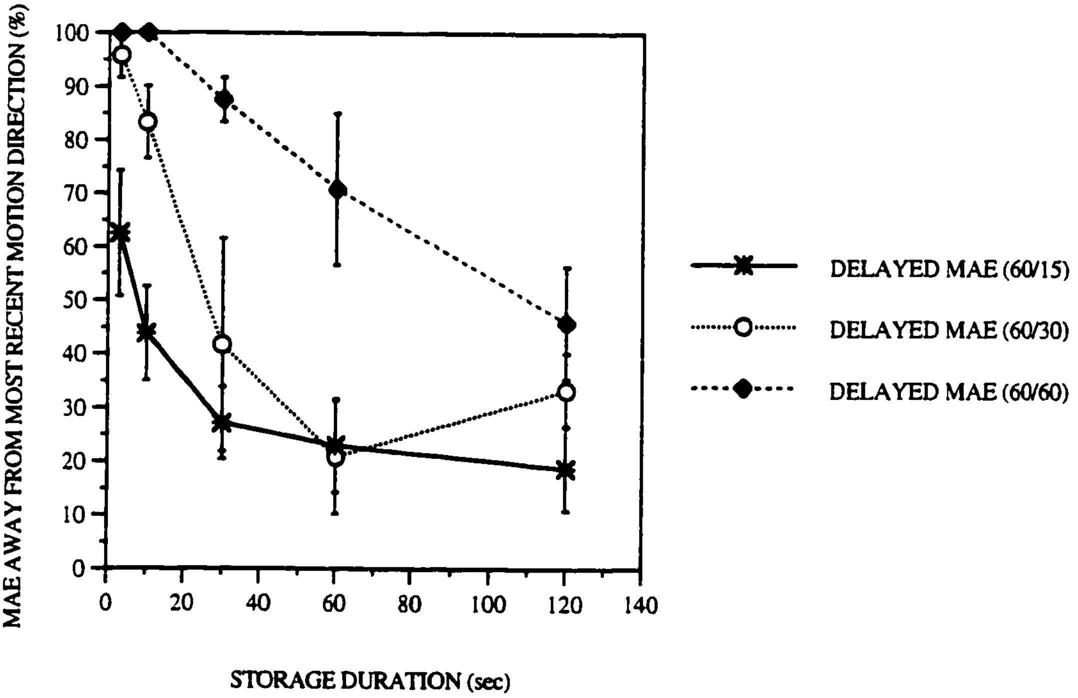

Figure 7.4. Mean percentage of MAE direction opposite to the most recent adaptation episode (15, 30, or 60 seconds) as a function of storage duration. Decreasing percentage on the scale indicates MAE direction increasingly opposite to the first adaptation episode (stored MAE).

and 60/30-second conditions). When the opposing directions were presented for the same time, the MAE to the second direction decayed slower than if it were proceeded by a longer duration of opposite motion. In addition, there was no reversal of MAE, in other words, there was no storage of the first MAE. After 60 seconds post adaptation (second direction) subjects' responses were at random (50%). These data were converted to a difference score above or below baseline (50%: no MAE), and re-graphed to clearly illustrate this pattern. Fifty percent was subtracted from values originally over 50%, which indicated MAE opposite to the most recent adaptation, yielding positive scores. Values originally under 50%, which illustrated MAE opposite to the first adaptation, were subtracted from 50 yielding negative scores. All of the resulting values were then divided by 100 and graphed (Figure 7.5).

7.4 Discussion

A similar pattern of results was observed for the condition of 60 seconds of adaptation to one direction followed by 30 seconds of adaptation to the opposite direction, as compared to those found in Experiment 4a. That is, there was an immediate MAE to the most recent direction followed by an eventual reversal of MAE to become opposite to the first direction. It is noteworthy that the stored MAE seemed to decay faster than in the 60/15-second condition, as evidenced by the 33% away from the most recent motion direction 120 seconds post-adaptation (the subjects' responses seem to begin to re-approach baseline, or lack of MAE). The probability of seeing an MAE opposite to the most recent direction for the longest storage interval for the 60/15-second condition was less than 20%. Storage of the first MAE was therefore less complete in the 60/30-second combination. When the two adaptation directions were equated in length, subjects reported an MAE to the second direction only. In addition, this MAE dissipated at approximately

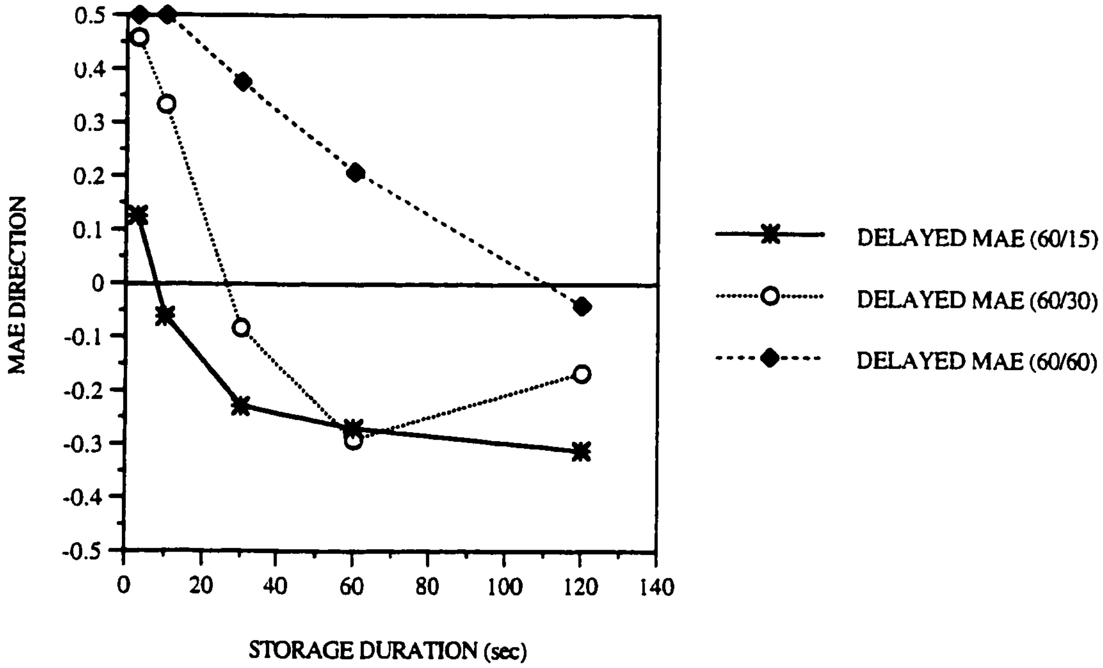

Figure 7.5. MAE direction opposite to either the second adaptation (15, 30, or 60 sec) or the first adaptation (60 sec) as a function of storage duration. Positive scores indicate MAE opposite the most recent motion adaptation, whereas negative values indicate MAE opposite the first motion adaptation (stored MAE). As positive scores increase or negative scores decrease, the MAE is increasingly opposite to the second or first adaptation direction, respectively. The horizontal line at 0 represents ambiguous MAE or lack of MAE. This was the 50% point from Figure 7.4.

120 seconds post adaptation. Under these conditions there was no sign of storage of the first MAE.

As was the case in Experiment 4a, the immediate MAE to the second adaptation direction is difficult to explain in terms of recalibration. This model would have expected an immediate MAE to the first direction in the 60/30-second condition in which there is still an overall greater amount of time observing motion in the first adapting direction. In addition, no MAE should be seen in the 60/60-second condition where there is overall equal net motion. Again, these expectations were made under the assumption that the system would consider all information during a given trial in calculating the amount of motion. The same criticisms already discussed in the previous study apply to this discussion as well. The stored MAE is, of course, consistent with the expectations from recalibration. This delayed aftereffect reflects a change in the neutral point due to the overall average of motion energy within a trial during the first adaptation period. Exactly why this effect is not apparent immediately is the reason why this theory, like fatigue, cannot by itself explain the MAE.

In distinction, under the same assumption as Experiment 4a's discussion, the fatigue model may be able to explain the present data in terms of differential recovery rates from variable adaptation duration. The 30 or 60 seconds during the second adaptation period would provide the previously adapted cells with time to recover and hence the difference in the imbalance due to cell fatigue should be greater for cells fatigued by the second adaptation. The result is a dominant and immediate MAE to the second adaptation. The delayed or stored MAE in the 60/30-second condition is understood in the same manner as the 60/15-second one. Perhaps the cells recover more quickly from 30 seconds of adaptation than from 60 seconds. With longer storage intervals it may be that the cells from the 30-second adaptation are more recovered than those from the 60-second adaptation, yielding a delayed MAE to the first adaptation period. In the 60/60-second condition no storage was experienced and in addition, the immediate MAE to the second direction lasted for 120 seconds post (second) adaptation. This seems to indicate that recovery from 60 seconds of adaptation is complete in about 2 minutes. If so, then perhaps a reversal would have occurred with longer storage periods (2 minutes was the longest in this study).

Following the discussion of the previous experiment, it may be possible that two mechanisms can jointly account for the MAE. Shorter adaptation durations indicate short-term fluctuations in the environment and are experienced as temporary aftereffects. Longer adaptation durations induce more long-term changes in the visual system but can be temporarily overridden by the small fluctuations. It is not exactly clear how this would apply to the 60/60-second condition. The two adaptation periods are the same length so there are no short- or long-term changes in the environment. Perhaps in this case, the system does not make any long-term modification to the visual system due to an overall zero net motion, and the observed MAE is only reflective of the neural fatigue component to the most recent motion. These theoretical implications will be explored further in conjunction with the integration of all data from this set of studies in the General Discussion to follow.

GENERAL DISCUSSION

8.1 Summary of Experiments

In all five experiments a type of storage related phenomenon of the motion aftereffect was predicted and observed. To summarize briefly, the MAE duration increased and decay was slower with increasing adaptation time (Experiment 1). MAE duration was, to varying degrees, comparable following uninterrupted versus interrupted-adaptation conditions (Experiment 2). There was long-term storage of the MAE both with and without rich visual information in the adapt-test interval, although more so in the latter (Experiment 3). Finally, it was shown that an MAE can be stored even following a subsequent and opposite induced MAE (Experiments 4a and 4b). These data were interpreted as evidence against the exclusive capacity for either the conventional neural fatigue model or the proposed recalibration theory to account for MAE storage phenomena. It seems more plausible that each play a contributory role in the induction and storage of the motion aftereffect.

8.2 Discussion of the Recalibration Model

The visual system can make remarkably accurate judgments of sensory activity and yet it seems unlikely that they are simply a consequence of very precise prewiring of the visual system. Specified genetics has difficulty to explain the observed plasticity of the visual system when confronted with the irregularities of growth, brain insult, or compensation to bizarre environments (i.e. aftereffects). It seems to indicate that the visual system is a dynamic modifiable unit which can calibrate and recalibrate when confronted with the need. This recalibration may be achieved via the principles of an error correcting device (Andrews, 1964) and adaptation level (Helson, 1948). The calibration may not always be representative of the external environment. Following motion adaptation, for example, the visual system indicates movement in a motionless test stimulus. While in principle the theory of recalibration seems veridical, the set of predictions derived from it were only partially supported.

One weakness of recalibration theory is related to the shift in adaptation level or neutral point during adaptation. Following adaptation to rightward motion the neutral point would be shifted towards right motion, which explains the perceived leftward motion in a stationary stimulus. The problem is that even for very long adaptation durations, subjects do not report that rightward motion becomes stationary as this theory would seem to imply. It is possible that this has not been properly measured and perhaps there is a reduction in motion perception in the adapted direction. Raymond (1993a) has observed that subjects become less sensitive to the adapted direction, in that the threshold for coherent motion in the adapted direction is increased following adaptation. However, she also reports a lack of increased sensitivity in the non-adapted directions, including the direction of the MAE. This result is difficult for not only fatigue models, but also for recalibration.

The amount of adaptation and of recovery time required to warrant a shift in the neutral point is not really understood. It would seem that short term fluctuations should be ignored and only long term changes in the environment should warrant long term modification of the visual system (Dodwell & Humphrey, 1990). One potential weakness of this theory, therefore, would be explaining very rapid aftereffect onset following brief adaptation periods such as 200 ms (Wolfe, 1984; Harris & Calvert, 1989; Raymond & Isaak, 1998). As well, very long-term storage of an aftereffect following rich visual experience, which provides evidence to the contrary of the newly adjusted AL, is just as challenging for recalibration theory. The distinction between natural environment and laboratory induced settings may be important to consider. The constraints of the visual system are imposed by experience in the natural environment. Short-term fluctuations in the environment, such as a car driving rightward may not be sufficient to shift the neutral point. This is a short-term violation which is imbedded in an array of other simultaneous motion signals. A computer generated stimulus moving for the same brief duration in a laboratory setting, free from any other motion stimuli, may be more powerful to recalibrate. In addition, the observer is instructed to attend to the peculiar stimulus in the laboratory. Attention has been found to be important in the susceptibility of MAE generation (Chaudhuri, 1990; Takeuchi & Kita, 1994; Lankheet & Verstraten, 1995). The characteristics in the laboratory may consequently induce AL shifts after significantly shorter exposures of perceptual diet. Mather and Harris (1998) suggest that methodology in laboratory studies is important to consider when determining how brief the adaptation exposure is. They argue that many brief exposures may accumulate to yield an adaptation duration significantly longer than one particular trial. Support for their hypothesis was observed in the present set of studies (Experiment 2).

Very long term storage, even after an abundance of visual information indicative of the original neutral point, is more puzzling. It seems that actually experiencing the aftereffect is sometimes necessary to eliminate the aftereffect completely and hence shift the AL back to its original position (i.e. true in the long run). In some cases an aftereffect is only experienced with the same stimulus characteristics as in the adapt conditions and hence if these are not observed in the natural environment (and likely they are not) then the aftereffect is stored to some extent. This implies that there is a degree of stimulus specificity in adaptation and recovery from it. Stimulus-dependency for expression of MAE, for example, is evident from studies which show that no (or little) MAE is observed when adapt and test conditions do not match (Thompson & Wright, 1994). Maybe it is possible that in some cases the visual system recalibrates properties in reference to a particular stimulus. Determining a separate neutral point for each stimulus seems to contradict the underlying principle that the criterion for motion is calibrated based on *all* stimuli presented thus far. Why would all information in the external environment be used to set the true criterion but then adaptation effects be specific? On the other hand, perhaps the system has been more generally modified but these changes are only apparent with the use of most effective test stimuli (i.e. when they match the adapting stimuli). Another possibility is that perhaps the opposite motion direction needs to be matched with the same stimulus parameters in the environment to speed up recalibration. In situations where the stimuli observed in the laboratory are not likely to be experienced in the natural environment, recalibration may be long indeed. This may explain some of the very long term aftereffects experienced following adaptation to complex or unnatural stimuli such as spirals or contingent stimuli (e.g. McCollough effect). The chance of undoing some of these contingencies by opposite pairings would be quite improbable in our typical experience.

Yet some studies have demonstrated cross-adaptation effects. Adaptation of one type of motion stimulus, e.g. second order, can induce an MAE when viewing a different stimulus, e.g. first order, although these cross-adaptation effects are typically weaker (Ledgeway, 1994; Ledgeway & Smith, 1994b; Nishida et al., 1994; Nishida, Ledgeway, et al., 1997). Further still, adaptation to spiral motion can yield a subsequent aftereffect with almost any surface (e.g. face). The original waterfall illusion was observed on a stationary rock. Perhaps most impressive are studies which demonstrate cross-modal adaptation effects, such as auditory displacement following adaptation to visual motion (Ehrenstein & Reinhardt-Rutland, 1996). These data are better evidence for a role of visual recalibration, where integration of many stimulus attributes takes place, even across modalities.

The typical lack of complete storage of the aftereffect is also problematic for the recalibration theory (present studies; Verstraten et al., 1996; Culham et al., 1999). The strict interpretation of this theory rests on the notion that visual evidence from the environment is necessary to calibrate the system. When no visual evidence is available there still is, however, some degree of spontaneous recovery. It is a possibility that even complete darkness could be considered as zero net motion and hence used to shift the neutral point. As stated by Mather and Harris (1998), "The walls of an experimental laboratory or the surfaces of experimental apparatus have a microtexture, as well as the dark field produced by closing the eyes. Thus the visual system is being presented during the storage interval with information about stationary patterns, as would be required by accounts such as recalibration." (p. 182). If a lack of test stimulus (or more extreme, total darkness) is helping the system to recalibrate, it is not as efficient as a visually rich experience as indicated by the difference in recovery rates for these two experiences (Experiment 3). Wohlgemuth (1911) reported the possibility of a subjective MAE. When subjects closed their eyes, they perceived a weak MAE. This finding does support Mather and Harris's argument. Given that the MAE is weaker would help to explain why objective experience with the visual environment is more useful in the calibration process. It may also be a possibility that the visual recalibration has a slower but automatic recovery of the true constraints, somewhat independent of the visual scene. To permanently erase or ignore all past visual experience seems inconsistent with the notion of calibration.

The strongest support for recalibration theory from the present set of studies, and from the literature in general, is that storage of the MAE does occur and that given what is known about single-cell recording studies, neuronal fatigue is a less likely explanation. Also consistent with this theory is that general visual experience (Experiment 3), and specific MAE experience (Experiment 1 & 2), significantly speed up the rate of recovery (or reduce storage). As aforementioned in the discussions following each experiment, some of the findings could also be accounted for by the traditional fatigue explanation.

8.3 Discussion of the Fatigue Model

One of the positive elements of the fatigue model is its simplistic nature. It offers a direct link between physiology and perception. The analogy of a scale which can be off balance or at equilibrium is a straight forward explanation. Unfortunately, there is accumulating evidence against the simplistic nature of the visual system as it adapts. Consequently, the fatigue interpretation is inadequate by itself to account for the motion aftereffect. The best strength of the recalibration model is the most significant pitfall of the fatigue model: MAE storage. There is a degree of spontaneous recovery, independent of visual stimulus, which is what fatigue models would predict. Ironically that the MAE stores at all supports long term modification of the system, but the lack of complete storage coincides with the time course for recovery of fatigued cells. Limitations of recalibration do not justify the removal of the fatigue model as a possible mechanism.

It is difficult to know the extent of the weaknesses and strengths of the fatigue explanation because of our limited data and understanding of the cell response characteristics. As discussed by Giaschi et al. (1993), there is no general consensus even within the physiological studies concerning the response modification of cells during and following adaptation. This is compounded by the inconsistent methodology employed by the single-cell recording studies. Giaschi et al. do offer preliminary data which demonstrate that two minutes post adaptation some cells have not fully recovered baseline sensitivity. Cell responses need to be recorded over the long term (coinciding with psychophysical studies of long term MAE storage) to examine if fatigue explanations are possible. Until this is accomplished, and furthermore, until physiology data cohere, it is too early to eliminate fatigue models as an influence in motion adaptation effects.

Functional MRI studies offer an exciting new way to investigate MAEs. This technique does not yet offer precise support for a physiological mechanism for adaptation. The fMRI data illustrate a strong correlation between perception and physiology (in terms of brain activity), in that activity is high during the experience of the MAE and low during a blank interval (He et al, 1998; Culham et al., 1999). A lack of (or lower) activity during a blank interval may imply the system is not actively recovering and hence does seem to support recalibration. It may also be consistent with fatigue. An imbalanced state of neural activity and spontaneous recovery of sensitivity perhaps do not activate the system if the system is not required to provide a visual response (i.e. during a darkened interval). Appreciable fMRI activity is maybe only detected when the visual system is stimulated (a test stimulus). This idea is supported by the finding that cells demonstrate maximum decrement when stimulated with moving stimuli as opposed to stationary ones (Marlin et al., 1988). Perhaps further studies will combine this technique with other psychophysical or physiological methods to yield further insight into the underlying mechanism(s) of the MAE.

The last reason that we cannot confidently critique the fatigue model is that the majority of single-cell recording studies have examined the properties of the neurons in the primary visual cortex or lower visual areas. Only one study has investigated the responsiveness of direction-specific extrastriate cells during motion adaptation (Petersen et al., 1985). Given the abundance of psychophysical support for a high level site of motion adaptation, these extrastriate areas (e.g. MT, MST and 7a) need to be further examined during and following motion adaptation.

8.4 The Short and Long of it

One difficulty in deciding which theoretical account is the best is that they appear to make very similar predictions. The purpose of the present set of studies was to make differential predictions for recalibration and fatigue models. The overall conclusion is that there is not enough strong and coherent evidence to fully support recalibration or to fully eliminate fatigue. In some circumstances there was more support for recalibration, while in other situations, fatigue seemed more plausible. Perhaps both play a role in motion adaptation. This may appear to be a convenient explanation, but the data simply do not warrant preferential support for just one theory.

The time course for recovery is the first issue which may support a dual-process. The fatigue model can account for short-term adaptation effects. It posits a fast decrement in cell response and a similarly fast recovery of sensitivity. As such, fatigue may be used to explain MAEs to very brief motion adaptation, as well as short-lived MAEs. Recalibration, on the other hand, easily explains long-term adaptation effects such as MAE storage. Exactly how much adaptation initiates recalibration has not been postulated in the literature. When physiological research determines, with confidence, the time course of cell fatigue and recovery, we may be able to indirectly hypothesize when recalibrating processes would begin. Even if the visual system is recalibrating, cell fatigue may be interacting or contributing to the effect. In Experiment 3, for example, there was less storage when subjects were in the visually rich environment. This supports recalibration processes. The passage of time, however, also reduced storage which seems more consistent with fatigue. It may be, therefore, that both processes operate simultaneously. If there is short-term fluctuation in the environment, perhaps only fatigue plays a role. If there are long-term changes in the environment, however, recalibration and fatigue may both be having an effect on perception. Data from Experiment 4a and 4b may also support this interpretation. Presumably the adaptation sequence initiated conflicting short- and long-term modification. The long-term change was stored and overridden by the more recent short-term change. If so, this would imply that response patterns from direction-selective units may be temporarily dominant in perception (in cases like those designed in Experiment 4).

The element of stimulus-specificity in the experience and storage of the MAE is another issue to discuss in regard to a dual process. Cross-adaptation effects, especially cross-modal adaptation, implicate a high level site for the underlying mechanism of MAEs, in that the specific attributes of the adapting stimulus are not important for the induction of an MAE. Integration of all visual information and other modalities perhaps occurs only in the case of recalibration. Noteworthy, cross-adaptation effects are typically less strong than MAEs from matching adapt and test stimuli. When the stimulus attributes match there is a longer MAE, which yields a more precise measure of the adapted state. When those cells which were directly fatigued during adaptation are stimulated again in the test condition their imbalanced state might compound the recalibrated system. This argument is similar to the reason why dynamic test stimuli may be more sensitive tools to observe MAEs than static tests. The movement in the dynamic test activates the motion system specifically and adaptation effects are more direct and thus stronger.

8.5 Conclusion and Future Directions

The psychophysical literature on the motion aftereffect as highlighted in the General Introduction implies both low- and high-level sites involved in the generation of the MAE. The scarcity and lack of consensus within the physiological research on the MAE compound the problem. The present study offers data which support both neural fatigue and recalibration predictions. The lack of a coherent theory explaining the physiological substrate for the motion aftereffect may imply that just one mechanism (of the ones currently discussed, that is) cannot account for adaptation effects. Conversely, it remains possible that either (1) the time course for fatigue and recovery is much longer than traditionally assumed, or that (2) recalibration processes include a spontaneous recovery component, independent of visual experience. It is premature to determine the validity of these hypotheses. Certainly, more single-cell recording studies are necessary, especially in extrastriate motion sensitive areas like MT, MST, and 7a. Functional MRI offers an exciting new manner to examine this question, and combining it with the psychophysical approach may lead to great insights concerning the MAE. For example, is there a difference in the amount of activity to different types of test stimuli (static or dynamic; match the adapt stimulus or not). Some of the same studies here should be repeated with dynamic tests and compared with the static ones to determine if dynamic tests are more sensitive in storage experiments. The weaknesses of the recalibration model discussed earlier (e.g. incomplete storage; failure to perceive stationarity during a long adaptation period) should be explored further to determine the validity and extent of its role in motion adaptation specifically and the visual system in general. The return of the MAE after it has dissipated (Experiment 1 and 2) should be explored further to understand why it returns and what mechanism accounts for this. Last of all, the degree of stimulus-specificity in the experience and storage of the aftereffect needs to be further investigated. These are many important avenues to pursue which may lead to a better understanding of whether the MAE reflects the maladaptive or functional capacity of the visual system.

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