A TEST OF THE GAIN CONTROL THEORY OF THE MOTION AFTEREFFECT STORAGE PHENOMENON

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Abstract

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The motion aftereffect (MAE) is a visual illusion that occurs when an individual observes a moving (adapting) pattern for a period of time followed immediately by the viewing of a physically stationary (test) pattern which appears to move in the opposite direction. A variation of the MAE, called storage, temporally separates the adapting pattern and test pattern with an unrelated visual stimulus, leaving a residual MAE. The dominant explanation is gain control theory (van De Grind, Lankheet, & Tao, 2003; van De Grind, van Der Smagt, & Verstraten, 2004; Verstraten, Fredericksen, Grüsser, & van De Grind, 1994), which posits that the residual MAE is the result of gain control mechanisms normalizing the motion sensing cells in the visual system. One method for testing this gain control explanation of the MAE is to employ a diverted-attention manipulation during adaptation, which results in a reduced MAE duration and is generally described as interacting with the gain control mechanisms. This project employed diverted-attention manipulations during MAE storage to test the gain control explanation of MAE storage. The results supported the gain control explanation of the MAE as it pertains to motion adaptation but failed to support the gain control explanation

of MAE storage as it exists in the literature. A modification of the gain control explanation of MAE storage that invokes the concept of interference can explain our results.

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Dedication

I would like to dedicate this project to all of those who supported me through this project. In particular, I would like to thank Dr. Steven Schneider and Dr. Joanne Joseph for giving me the lab space and support that I needed. I would not have been able to have completed this project without your support. Special thanks go to the Air Force Research Laboratory in Rome, New York, particularly Michael Moore. You expressed consistent interest, encouragement, and a warm, dry place to write. Further, I could not have completed this project without the support and input of my committee. Thank you for all that you have given me. Additionally, I would like to include Dr. Malcolm Cohen. You inspired me to pursue this venture. Lastly, I would like to dedicate this to my two boys, Dante and Logan, as well as my wife Deirdre, for putting up with me while I completed this effort. I know that it was not easy for any of you.

INTRODUCTION

One of the more interesting motion perception phenomena is an illusion of motion called the motion aftereffect. The motion aftereffect (MAE) occurs when an individual observes a moving (adapting) pattern for a period of time and then the moving pattern is replaced by a similar, though non-moving (test), pattern. This causes the observer to experience a visual illusion in which the stationary test pattern appears to move in a direction opposite to the original adapting pattern. The MAE has been used for many years as a research paradigm in order to elucidate neuronal processes associated with visual motion perception.

The MAE is a phenomenon that has been recorded as far back as 330 BC by Aristotle who reported that "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. 459). In 1825, Purkinje described observing a cavalry parade for approximately an hour and noted that after watching the parade, neighboring houses appeared to move in the opposite direction (Mather, Verstraten, & Anstis, 1998). The MAE has also been called "the waterfall illusion" owing to Addams (1834) who reported that after observing a flowing waterfall the neighboring rock strata surrounding the waterfall appeared to drift upward.

Over the years, several properties of the MAE have been discovered. Classic observations such as those by Purkinje and Addams demonstrated that the test pattern does not need to be identical to that of the adapting pattern. In general, it is not necessary to use the same spatial frequency content for adapt and test patterns, although laboratory studies have shown that the MAE is most pronounced when the adapt and test patterns have the same spatial frequency content (Bex, Verstraten, & Mareschal, 1996; Cameron, Baker, & Boulton, 1992; Over, Broerse, Crassini, & Lovegrove, 1973). The MAE shows a marked decline as the spatial frequency differences between adapt and test patterns increases (i.e., the MAE is half its normal duration when the spatial frequency between adapt and test patterns differs by one octave) (Anstis, Verstraten, & Mather, 1998).

Another form of motion stimulus, which carries ecological importance, is an optic flow stimulus. An optic flow stimulus refers to a dynamic pattern of motion of images cast onto the retina by stationary objects in the environment during observer locomotion. For forward motion through the environment, this typically creates a characteristic expansive pattern that may contain motion parallax information that can be used in the recovery of heading (Lappe, Bremmer, & van den Berg, 1999). Interestingly, optic flow patterns that simulate forward motion through the environment can produce a robust MAE that simulates self-movement in the opposite (i.e., backward) direction, which is affected by the global optical flow rate (i.e., an egomotion speed measure), as reported by Patterson, Tripp, Rogers, Boydstun and Stefik (2009). These authors factorially varied edge rate and global optical flow rate and found that only the latter significantly affected the duration of the MAE. This result was interesting because studies of egomotion speed perception have suggested that speed perception is more strongly dependent on edge rate than on global optical flow rate (Johnson & Awe, 1994; Larish & Flach, 1990).

Thus, the perception of illusory motion in one direction can be induced by adaptation to motion in the opposite direction, which can occur for simple laterally moving patterns as well as for more complicated motion stimuli such as optic flow patterns. This suggests that motion adaptation occurs at multiple levels of the visual system, from lower-levels involving the coding of simple translating motion (e.g., level V1) to higher levels involving the perception of egomotion through space (e.g., posterior parietal cortex) (Anstis, Verstraten, & Mather, 1998; Larsson, Landy, & Heeger, 2006; Rees, Frith, & Lavie, 1997; Rezec, Krekelberg, & Dobkins, 2004; Verstraten, Fredericksen, Grüsser, & van De Grind, 1994). Moreover, not only is the MAE interesting for its ubiquitous nature, it also possesses a very interesting property called "storage".

Storage of the MAE was studied by Spigel (1960; 1962a; 1962b), who temporally separated the adapting pattern and test pattern by interposing a contour-free waiting period (referred to as “blackout”). When adaptation was followed by a contour-free period that equaled the duration of the typical MAE, the MAE still occurred (albeit for a relatively shorter duration) once the test pattern was exposed. This suggested that the MAE had been "stored" during the blackout interval.

The storage phenomenon can also be elicited without resorting to a contour-free blackout period. Verstraten, et al. (1994) found that a stimulus that was orthogonal in orientation to the adapting and test patterns could serve as a storage stimulus when the orthogonal pattern was viewed during the interval between the presentation of the adapting and test patterns. This demonstrated that the storage phenomenon depends upon the viewing of a visual pattern, following the adaptation phase but prior to the testing phase, and whose properties significantly deviate from those of the adapting and test patterns. Since storage can take place using an orthogonal pattern rather than just removing stimuli as Spigel had done, it is reasonable to use the term “storage interval” to describe the time period in which an intervening interval (with or without a pattern) temporally separates an adapting pattern and a test pattern.

Verstraten, et al. (1994) have offered an explanation of the MAE, including storage of the MAE. They argued that the motion aftereffect is a recalibration of the visual system to account for changes as we move through the environment at different speeds. This recalibration is achieved through gain control mechanisms that allow the visual system to operate in two major states: moving and stationary. Verstraten, et al. (1994) explained that when a person moves through the environment there are constant motion cues that recalibrate the visual system into a “moving” state. When that same person suddenly stops moving, the motion cues are absent and the visual system recalibrates to a “stationary” state. The observation of an adapting pattern emulates the experience of moving through the environment and recalibrates the visual system into the “moving” state. Once motion stimulation is removed by introducing a static test pattern, the MAE that is experienced is the visual system recalibrating to a “stationary” state. Storage of the MAE is therefore explained as the visual system being recalibrated in the absence of visual information. This is analogous to walking and then closing your eyes while you continue to walk briefly before coming to a halt. The visual system has been recalibrated to a moving state due to egomotion, but once the eyes are closed, there is indeterminacy in the visual system as to whether the individual is continuing to move. Though there is no indication of visual movement, there is also no indication that the individual is standing still. Because the visual system lacks information that the individual is standing still, the change to a stationary state is slow. According to the gain control model, presenting a storage pattern that is orthogonal to the adapting pattern and test pattern is analogous to closing one's eyes because the spatial composition of the storage pattern is different than the adapting pattern and the test pattern (Verstraten, Fredericksen, Grüsser, & van De Grind, 1994). When viewing an orthogonal storage pattern, the visual system lacks the cues that are present in both the adapting pattern and test pattern. Consequently, the visual system is slow to recalibrate, or normalize, to a stationary state when an orthogonal storage pattern is viewed relative to when a test pattern is viewed.

A recent model of the storage phenomenon by van De Grind and colleagues (van De Grind, Lankheet, & Tao, 2003; van De Grind, van Der Smagt, & Verstraten, 2004) expands the recalibration concept expressed by Verstraten, et al. (1994). This model is based on an approach involving automatic gain control processes in neural networks that code for the direction of motion. Here, adaptation produces a lowering of the gain (sensitivity) in the adapted directional pathway (i.e., recalibration) from which it takes some amount of time to recover. Because the outputs from multiple directional pathways are combined to produce the perception of movement in a given direction, the combination of signals from adapted plus non-adapted pathways induces an illusory perception of motion in a direction opposite to the direction of adaptation when a stationary test pattern is viewed. This occurs because the signals coding the opposite direction of motion are now relatively stronger. The aftereffect ceases when the adapted pathway is recalibrated by viewing the stationary test pattern and the gain returns to baseline level (i.e., the normalization process terminates).

Important for the phenomenon of storage, this model by van De Grind and colleagues (2003; 2004) also assumes that, during a storage interval, the lowered gain from adaptation takes more time to return back to the normal set-point. This is because a test stimulus with properties similar to that of the adapting stimulus is needed for the adapted pathway to quickly become normalized and recover from adaptation. Without the presence of such a test stimulus, the adapted pathway takes longer to recover from adaptation. Thus, according to this model, "storage" results from a retarded normalization process that occurs in automatic gain control mechanisms in the neural networks that encode the direction of stimulus movement.

The present study tested the explanation by van De Grind, et al. (2003, 2004) that MAE storage is the result of delayed recovery of automatic gain control processes. To test this idea, another manipulation known to involve gain control was needed so that its effects on storage could be assessed. If the phenomenon of storage is due to a gain control process, then it should be possible to either cancel or facilitate that process with another manipulation known to involve gain control. Cancellation and facilitation would be evidence that the two phenomena are likely produced by a common (i.e., gain control) mechanism. Visual attention is an ideal choice for such a manipulation because it is thought to influence the gain of the visual system and can be incorporated in a MAE paradigm.

Visual attention is known to exert a modulatory effect on sensory processing. For instance, Moran and Desimone (1985) recorded the activity of cells in the visual cortex of monkeys that had been trained to attend to some visual stimuli and ignore other stimuli. They found that when both attended and unattended stimuli were in the same receptive field of a cell, the response of the cell was significantly reduced, which demonstrated a suppressing effect. In a study using fMRI, O'Connor, Fukui, Pinsk, and Kastner (2002) found that the neural activity of the lateral geniculate nucleus (LGN) in humans was modulated based on the placement of visual attention. When visual stimuli were ignored, activity of the LGN was reduced. This demonstrated a suppression, or gain reduction, effect of the visual signals. When visual stimuli were attended to, there was increased activity of the LGN, which demonstrated an enhancement, or an increased gain, of the visual signals. Carrasco and McElree (2001) found that covert attention enhanced the accuracy as well as accelerated the speed of perceptual processing. These authors refer to attention as having an enhancement effect on visual processing. Treue and Martinez-Trujillo (1999) found similar results when they used moving stimuli. These authors recorded the activity of motion sensitive cells in area MT of the monkey brain and found that "attention enhances the sensory gain of the neuron" (p. 575). The evidence in the literature clearly indicates that attention interacts with gain control mechanisms in the visual system and thereby alters signal strength of attended stimuli (Carrasco, Ling, & Read, 2004; Hawkins, Hillyard, Luck, Mouloua, Downing, & Woodward, 1990; Hillyard, Vogel, & Luck, 1998; Ling, Liu, & Carrasco, 2009; Ress, Backus, & Heeger, 2000).

With respect to visual attention and the MAE, it is known that the duration of the MAE is reduced when attention is selectively diverted during adaptation. This is commonly achieved through the use of a secondary task that observers perform during adaptation. For instance, Chaudhuri (1990) found that when observers engaged in a secondary character recognition task while they adapted to motion, the duration of the MAE was reduced relative to when they did not engage in a secondary character recognition task. Likewise, Georgaides and Harris (2000) required observers to either verbally repeat digits (diverted-attention condition) or fixate on a non-moving “0” (normal condition) while they observed a moving pattern. They found that the MAE duration was reduced in the diverted-attention task relative to the normal condition.

Rees, Frith and Lavie (1997) used an expanding field of dots as an optic flow adapting motion stimulus. They asked observers to participate in two different word discrimination tasks, during which time observers ignored the pattern of moving dots. These authors found that diverted-attention decreased the duration of the MAE. In the same study, cortical activation of motion processing areas was measured through the use of fMRI. The fMRI results show that when attention was diverted, activity along the V1 and V2 border as well as in area V5 was reduced relative to when attention was not diverted. Similar MAE duration results were reported by Patterson, Fournier, Vavrek, Becker-Dippman, and Bickler (2005) using the same word discrimination task as Rees, et al. (1997) when the observers adapted to bars presented in depth.

Because the van De Grind, et al. (2003, 2004) model posits that storage represents a lowered gain mechanism returning back to baseline at a slower rate, and diverted visual attention lowers the gain of unattended visual stimuli, then introducing a diverted-attention manipulation during storage should produce a longer MAE duration relative to when attention is not diverted during storage. In other words, by diverting attention during storage, the normalization process should be especially retarded due to the lowered gain. Accordingly, the MAE should be longer (i.e., slower recovery from adaptation) with diverted-attention during MAE storage relative to MAE storage without diverted-attention.

DESIGN AND RATIONALE

In the present study visual attention was diverted using a Rapid Serial Visual Presentation (RSVP) task. There were three conditions in each experiment that were based upon the implementation of the RSVP tasks which varied attentional load. The three conditions were No load, Low load, High load. All observers experienced four trials of each of the three conditions. The order of the conditions was randomized for each participant. While observers participated in the RSVP task they were asked to ignore the presence of any background visual stimuli. Two different RSVP tasks were used in this study that required observers to identify target words among a sequence of rapidly presented five-letter single words. In the first task the sequence of words contained one-syllable and two-syllable words. When each word was presented, the observer was required to indicate as quickly and as accurately as possible if the word contained two syllables. In the second task the sequence of words contained words that were in uppercase letters and in lowercase letters. When each word was presented, the observer was required to indicate as quickly and as accurately as possible if the word was presented in uppercase letters. Research by Rees, et al. (1997) has shown that the first task is more difficult that the second task, both in terms of behavioral performance, but also in terms of neural activation. For this reason the first task is called "High load" and the second task is called "Low load." An additional control condition called the "No load" was used. During the No load condition, there was no attentional load imposed upon the observer. Instead, in the No load condition the observers viewed a stationary fixation cross and they were to attend to the visual stimuli that were presented (i.e., the motion or the storage pattern). The visual stimuli that were presented in the No load condition were the same ignored stimuli that were in the background during the High load and Low load conditions. It should be noted that these are the same attentional manipulations that were used by Rees, et al. (1997) and Patterson, et al. (2005). In both of those studies the RSVP tasks were performed during motion adaptation and the resultant MAE duration was measured. This study utilized these accepted methods of attentional manipulation during adaptation, but also implemented those same attentional manipulations during the storage interval. To date, there is no known work that has combined a diverted-attention manipulation with the MAE storage paradigm. Therefore the introduction of a diverted-attention manipulation during the storage interval is a novel approach to testing the gain control explanation of MAE storage.

According to van De Grind, et al. (2003, 2004), when an individual continuously adapts to motion for a period of time, disequilibrium of the motion-processing pathway is produced. This disequilibrium results from automatic gain control mechanisms lowering the sensitivity (gain) of cells that process visual motion information. Observation of a non-moving test pattern following motion adaptation evokes a normalization process of the adapted motion processing units. During the normalization process, the gain of the previously affected motion pathways returns to the normal set-point, thereby recovering the motion pathway from the previously incurred disequilibrium. Viewing a pattern that has been temporally interposed between the adaptation and test patterns produces storage of the MAE. During the interval in which the storage pattern is viewed, the automatic gain mechanisms will recover, but at a reduced rate.

One would expect that diverting attention during storage should lengthen the MAE duration relative to just the presentation of the storage interval without diverting attention. Recall that when there is a storage interval, the normalization process takes place at a slower rate. This means that automatic gain control mechanisms creep toward their normal set-point, producing a residual MAE duration following the storage interval. Also recall that diverted visual attention lowers the gain of the visual system. When storage and a diverted-attention task are combined, the result should be an increase in the MAE duration relative to when attention is not diverted. This is because when attention is diverted during storage, the storage pattern is the unattended visual stimulus. By diverting attention during storage, the gain, or sensitivity, of motion processing units is lowered during a time when those same units should be normalizing. Diverting attention during storage should retard the normalization process, thereby producing a longer MAE duration relative to when attention is not diverted during storage. Accordingly, the van De Grind, et al. (2003, 2004) gain control model of MAE storage was tested by manipulating visual attention during the storage interval using the RSVP tasks, based on the logic described above.

The current study involved four experiments that were designed to test the gain control theory of the storage phenomenon. Experiment 1 replicated the existing body of literature on diverted-attention and the MAE by asking observers to participate in the RSVP tasks while undergoing motion adaptation. Experiment 2 was identical to Experiment 1 except that a storage interval followed motion adaptation and served as an intermediate step between Experiment 1 and Experiment 3. Experiment 3 implemented the RSVP task during the storage interval instead of during adaptation in order to test the gain control explanation of MAE storage. Experiment 4 was identical in design to Experiment 3 except that a counting task was used to divert attention non-visually.

Experiment 1

The purpose of Experiment 1 was to replicate the general findings that already exist regarding diverted-attention and the MAE. This was done by asking observers to participate in the RSVP tasks while undergoing motion adaptation. For each trial of Experiment 1, the MAE was measured after the observers underwent either the No load condition or one of the two RSVP diverted-attention conditions (Low load or High load) during adaptation as described above. There was no storage interval used during this experiment. Based on the literature reviewed above, the MAE duration should be reduced when attention is diverted relative to when attention was not diverted. Specifically as attentional load increases, the MAE duration should decrease. Therefore we should expect that the shortest MAE duration will be found in the High load condition, a longer MAE duration in the Low load condition than in the High load condition, and the longest MAE duration should be found in the No load condition.

Method

Observers.

Thirteen observers from the State University of New York Institute of Technology agreed to participate in this experiment. Two of the observers did not see the MAE and were excluded from the study, leaving eleven observers in this experiment. The observers were recruited from undergraduate psychology and criminal justice studies courses and were offered extra credit as compensation. None of the observers had any prior experience with motion aftereffect research. All observers were 18 years of age or older and gave their consent to participate. Each observer had normal or corrected to normal vision. Visual acuity was tested using a Snellen chart.

Stimuli and apparatus.

All stimuli were controlled by custom software written in Visual Basic 2008. The software was run on a non-networked Dell Dimension 4500 computer running Windows XP Professional Operating System. The computer was equipped with a 2.4 GHz Pentium 4 CPU, 768 MB RAM, and a 64 MB GeForce2 MX graphics card. Visual stimuli were displayed on a Gateway DL-36 (Gateway, Inc.) 36 in. monitor and viewed from a distance of 114 cm. At this viewing distance, the dimensions of the monitor were 27.5 arcdeg (height) x 35.2 arcdeg (width).

The adapting pattern was an optic flow stimulus that simulated observer self-motion in the forward direction over terrain imagery seen in perspective view (Figure 1). The terrain imagery was composed of a homogenous gray ground plane upon which poles were placed evenly. The poles were 7 m tall and 1 m wide and were arranged in a grid pattern on the ground plane with a density of 576 poles/ km^2. The visual angle of the poles when they were in the nearest position to the observer was 7.5 arcdeg (height) x 0.5 arcdeg (width), and their visual angle in the farthest position was 0.5 arcdeg (height) x 0.05 arcdeg (width). The test pattern used for measuring the duration of the MAE was a non-moving image of the terrain seen in perspective view (i.e., a static version of the adapting pattern).

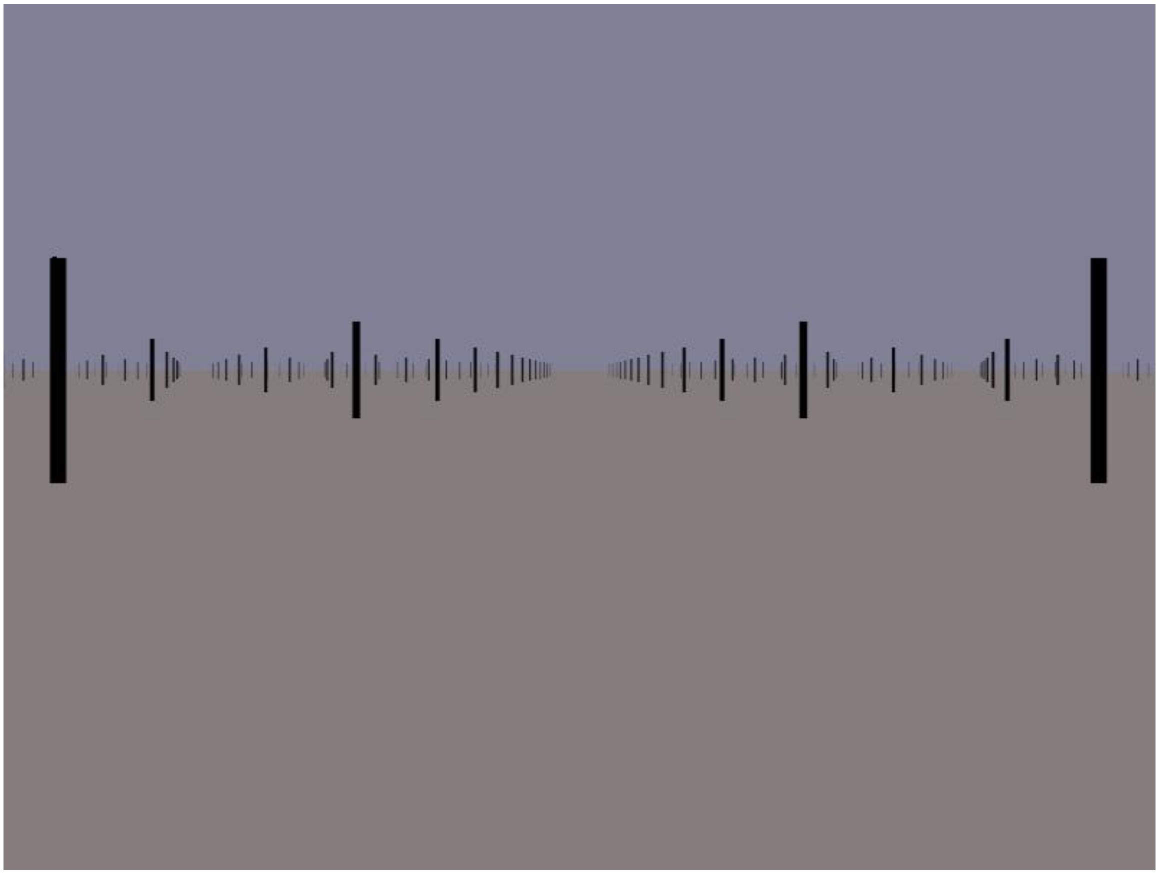

Figure 1. Picture of the visual display showing the non-moving test pattern.

Procedure.

Attentional load was manipulated during motion adaptation through the implementation of Rapid Serial Visual Presentation (RSVP) tasks. There were three conditions (No load, Low load, High load) based upon the degree of attentional load that was imposed during motion adaptation. In the No load condition there was no attentional load imposed upon the observer. Instead the observer was presented with a fixation cross and asked to attend to the motion. This served as a control condition that is very similar to what others in the literature have used (Patterson, et al., 2005; Rees, et al., 1997). In the Low load and High load conditions, the RSVP tasks were performed for the duration of motion adaptation. While participating in the RSVP tasks, the observers were asked to identify as quickly and as accurately as possible when a target word was presented while ignoring the background motion. The order of presentation of target words and non-target words was random. In the Low load condition, each word was presented in either all lowercase letters or all uppercase letters. The target words were words that were presented in all uppercase letters. In the High load condition, each word that was presented had either one syllable or two syllables. The target words were two-syllable words. All observers experienced four trials of each of the three conditions. The order of the conditions was randomized for each participant.

At the beginning of the experiment the observer was seated and viewed the CRT monitor from a distance of 114 cm. Trials were initiated by the observer pressing the spacebar on the computer keyboard. Once the trial was initiated, the adapting pattern was presented for 120 seconds. In the center of the display, during adaptation, there was a small rectangular light-gray area whose dimensions measured 0.95 arc degrees x 2.16 arc degrees. This was used for the presentation of either a fixation cross or words. In the No load condition, a fixation cross was presented. In the Low load condition and High load condition 5-letter words were presented using a monospaced font. The words appeared at a rate of one word every second and each word was displayed for 750 ms with an ISI of 250 ms. The words were matched for their frequency of occurrence in the English language and were taken from the Coltheart MRC Psycholinguistic Database (Coltheart, 1981).

Immediately following the adapting pattern, the RSVP task (if any) was halted and the test pattern was presented continuously until the observer indicated that the MAE was no longer visible by pressing the spacebar on the computer keyboard. The computer then wrote the duration of the MAE in milliseconds to a data file. After each trial, a rest period of no less than two minutes was given.

Results and Discussion

Motion aftereffect duration.

The MAE durations for each of the diverted-attention conditions are presented in Figure 2. The graph shows that the No load condition had the longest MAE duration. The Low load and High load conditions were roughly equivalent and reduced relative to the No load condition.

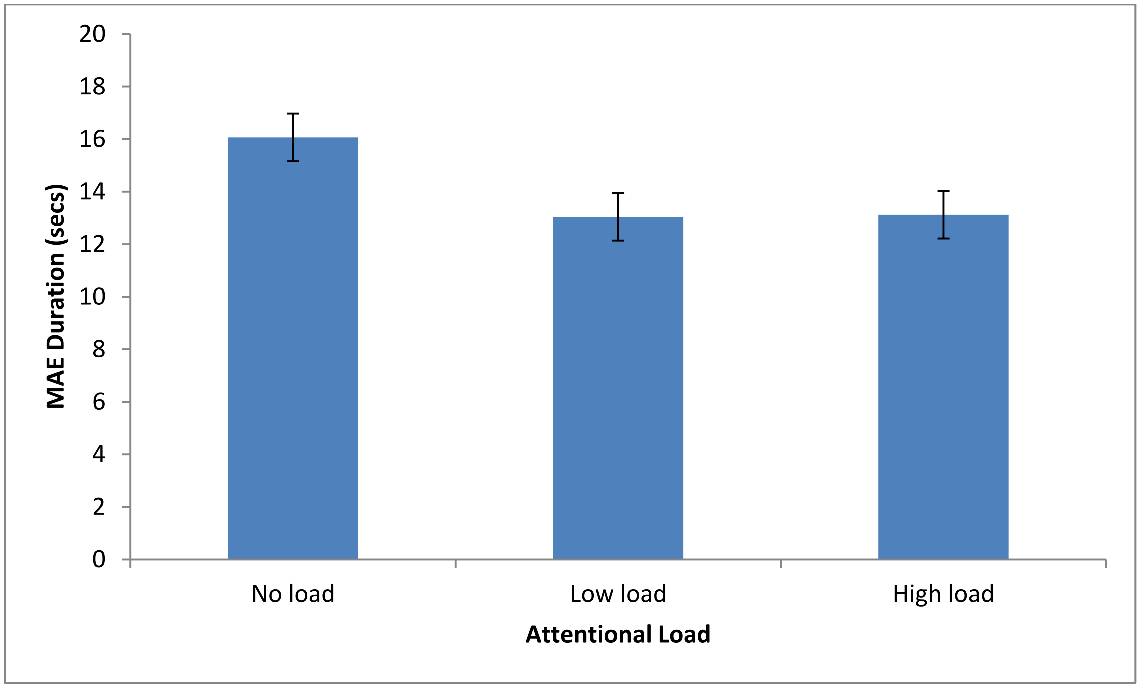

Figure 2. Results of Experiment 1. The motion aftereffect duration obtained under the three diverted-attention conditions (No load; Low load; High load). Attention was diverted during adaptation with the RSVP tasks in the Low load and High load conditions. Each bar represents the mean of eleven observers. Error bars represent +/- one within-subjects standard error of the mean.

An analysis of variance (ANOVA) for within-subjects designs was conducted to analyze the effect of diverted-attention on MAE duration. There was a single factor (attentional load) with three-levels (No load, Low load, High load). Mauchly's Test of Sphericity was not significant so no adjustment to the degrees of freedom in the ANOVA was necessary. The ANOVA revealed a significant effect of diverted-attention on MAE duration, $F(2, 20) = 4.07$, $p < 0.03$, $MSe = 8011310.48$. The within-subject standard error of the mean (Loftus & Masson, 1994; Masson & Loftus, 2003) was 908.25. Pairwise comparisons were conducted using the Least Significant Difference (LSD) test. The LSD test was used for pairwise comparisons because the comparisons were planned a priori and in the case of three comparisons it does control for familywise error (Cohen, 2001; Sheshkin, 2007). There was a significant reduction of the MAE duration in the High load condition relative to the No load condition, $p < 0.04$. The pairwise comparisons between the No load condition and the Low load condition was not significant, $p < 0.07$, nor was the comparison between the Low load and High load, $p < 0.91$.

These results generally correspond to existing literature regarding diverted-attention and the MAE. When attention is diverted through a secondary visual task, the resultant motion aftereffect duration is lowered. It was expected that the MAE duration would be significantly longer for the No load condition than the Low load condition, and the Low load condition would be longer than the High load condition. While this precise relationship was not found, the principle influence of diverted-attention on MAE duration was found. That is, when attention was diverted the MAE was reduced relative to when attention was not diverted. Similar results using similar stimuli and tasks have been reported (Rees, Frith, & Lavie, 1997). When an observer engages in a significantly demanding visual attention task while viewing a moving pattern, the resultant gain of motion processing mechanisms is lowered relative to when attention is not diverted.

Performance in RSVP tasks.

The mean proportion of correct responses was 0.97 in the Low load condition (standard error of the mean was 0.01) and the mean was 0.79 (standard error of the mean was 0.01) in the High load condition. Because there was no task for the observer to perform in the No load condition, it was impossible for the observer to make an error. Therefore, performance in the No load condition was coded as one, which indicates perfect performance. The proportions of correct responses to the RSVP tasks were analyzed using an ANOVA for within-subjects designs. There was a single factor (attentional load) with three levels (No load, Low load, High load). Mauchly's Test of Sphericity was significant, $\chi^2(2)=6.89, p < 0.03$, necessitating a reduction of degrees of freedom with the Greenhouse-Geisser correction. The Greenhouse-Geisser corrected ANOVA revealed a significant change in performance across the different levels of the RSVP task, $F(1.3, 13.03) = 322.07, p < 0.001, MSe < 0.00$. Pairwise comparisons on performance were conducted for all combinations of the three RSVP tasks. Performance in the Low load condition was significantly lower than the No load condition (perfect performance), $p < 0.001$. Also, performance in the High load condition was significantly lower than in the No load condition, $p < 0.001$. There was also a significant reduction in performance in the High load condition relative to the Low load condition, $p < 0.001$.

These data show that the performance in the RSVP task declined with task difficulty. This means that the diverted-attention manipulation did have an effect on the observers that is commensurate with previous findings in the literature (Patterson, et al., 2005).

As expected, there was a reduction of MAE duration when a diverted-attention manipulation was introduced during adaptation. These results generally support the gain control explanation of the MAE. That is, motion adaptation appears to recalibrate the visual system which is then normalized when a test pattern is presented. Diverting visual attention during adaptation reduces the gain of motion adaptation. This means that the motion signal during adaptation is weaker under conditions of diverted-attention relative to when attention is not diverted. Consequently, when the test pattern is presented, the motion pathway normalizes more rapidly when attention had been diverted during adaptation relative to when attention had not been diverted during adaptation.

It was also expected that the High load condition would have the shortest MAE duration, Low load would have a longer MAE duration than the High load condition, but shorter than the No load condition, and the No load condition would have the longest MAE duration. While this exact relationship was not found, the key finding that diverting attention during adaptation results in a shorter MAE duration than when attention is not diverted was found. These results are very similar to the results of the fMRI study by Rees, et al., (1997). Those authors used the same RSVP tasks that were used in this experiment. They found that there was a significant reduction of neural activity associated with motion processing in area V5 as well as along the V1 and V2 border when observers participated in the High load RSVP task. These authors also found a reduced MAE duration in the High load condition. However there was no reduction of neural activity in the Low load condition nor was there a significant reduction of the MAE duration.

Experiment 2

The purpose of Experiment 2 was to expand the diverted-attention and MAE paradigm to include storage of the MAE. Specifically, Experiment 2 ensured that the use of a storage interval in the present paradigm exerted an effect that is consistent with effects previously reported in the literature (i.e., lengthened effective MAE duration which is interpreted as a slower recovery of gain). The design of Experiment 2 was identical to Experiment 1 except that a storage interval was added between the adapting pattern and the test pattern. During the storage interval the adapting pattern was replaced by the storage pattern. The RSVP task, if any, was ended at the onset of the storage interval. The observers viewed the storage pattern until the test pattern appeared during which time they indicated the duration of their MAE. It was expected that the MAE duration would be reduced when attention was diverted relative to when attention was not diverted—showing a similar pattern to that found for Experiment 1. Specifically as attentional load increases, the MAE duration should decrease. Therefore we expected that the shortest MAE duration would be found in the High load condition, a longer MAE duration would be found in the Low load condition than in the High load condition, and the longest MAE duration would be found in the No load condition. Such an effect would be consistent with the gain control explanation of the MAE. If attention reduces the gain of visual processing, there should be a weaker motion signal. This would result in less time needed for the motion processing units to normalize under conditions of diverted-attention relative to when attention is not diverted.

Method

Observers.

Fourteen observers participated in this experiment. Observer recruitment, characteristics, and compensation were the same as in Experiment 1.

Apparatus, stimuli and procedure.

The apparatus, stimuli and procedure were the same as in Experiment 1 except for the following. After experiencing one of the diverted-attention conditions during the motion adaptation, a storage interval was presented. The duration of the storage interval was determined for each observer through the averaging of a series of four baseline MAE durations (see Spiegel 1960, 1962a, 1962b). The baseline MAE trials were identical to the No load condition in Experiment 1. At the beginning of the storage interval, the RSVP task (Low load and High load conditions) ended and the storage pattern was presented. The storage pattern was identical to the test pattern, except that it was rotated 90 degrees either clockwise or counterclockwise about a central axis. The direction of rotation was randomized at the beginning of each trial. The probability of the storage pattern being rotated clockwise or counterclockwise was 0.5 on all trials. Immediately following the storage interval, the test pattern was presented continuously until the observer indicated that the MAE was no longer visible by depressing the spacebar on the keyboard.

Results and Discussion

Motion aftereffect duration.

The mean storage interval duration was 15475.62 milliseconds and the standard error of the mean was 1485.04. The MAE durations for each of the diverted-attention conditions are presented in Figure 3. As is evident in Figure 3, the pattern of MAE durations are similar to those found in Experiment 1. Specifically, there is a reduction of the MAE duration when attention is diverted relative to when attention is not diverted.

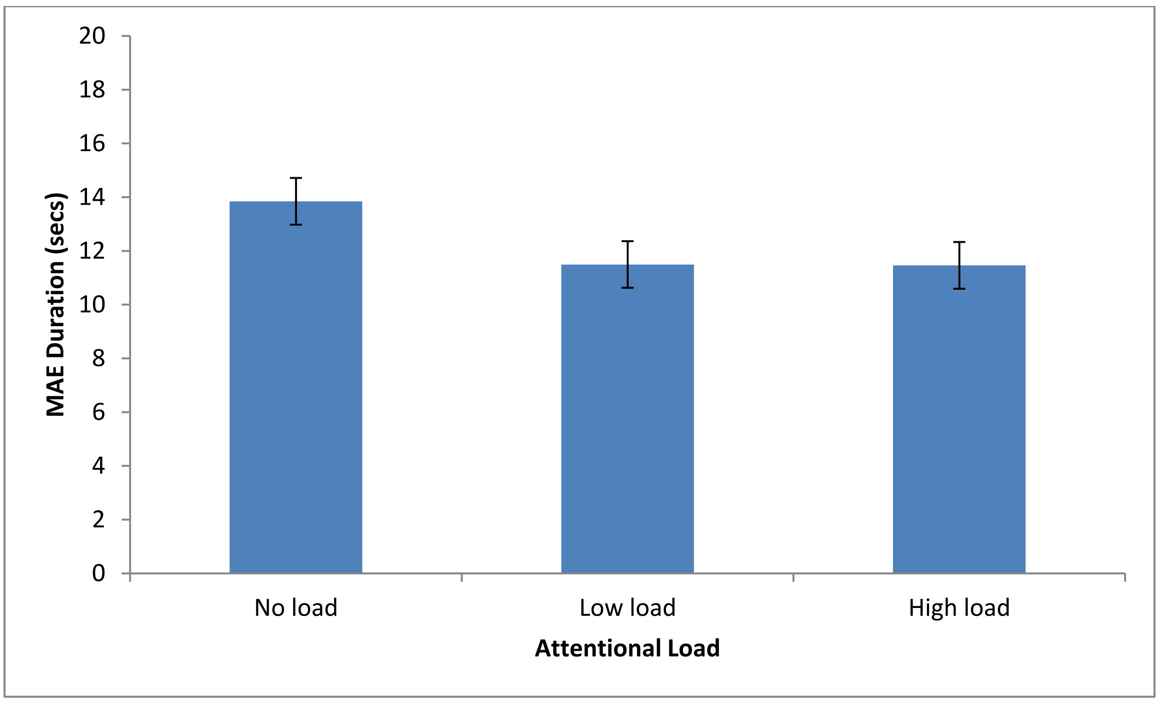

Figure 3. Results of Experiment 2. The motion aftereffect duration obtained under the three diverted-attention conditions (No load; Low load; High load). Attention was diverted during adaptation with the RSVP tasks in the Low load and High load conditions. Each bar represents the mean of fourteen observers. Error bars represent +/- one within-subjects standard error of the mean.

An ANOVA for within-subjects designs was conducted to analyze the effect of diverted-attention on MAE duration. There was a single factor (attentional load) with three-levels (No load, Low load, High load). Mauchly's Test of Sphericity was significant, $\chi^2(2) = 7.21$, $p < 0.03$, necessitating a reduction of degrees of freedom in the ANOVA of the MAE duration results by using a Greenhouse-Geisser correction. The Greenhouse-Geisser corrected ANOVA revealed a significant effect of diverted-attention on the MAE duration, $F(1.38, 17.91) = 4.17$, $p < 0.05$, $MSe = 9104342.684$. The within-subject standard error of the mean was 868.06. Pairwise comparisons on effect of diverted-attention on the MAE duration revealed that the Low load condition MAE duration was significantly less than the No load condition MAE duration, $p < 0.01$, which is consistent with predictions of gain control theory. However, the comparison of the No load condition and the High load condition was not significant, $p < 0.07$, nor was the comparison between the Low load condition and the High load condition, $p < 0.97$.

Again, these results generally conform to the previous literature regarding diverted-attention and the MAE. When visual attention is diverted during motion adaptation, there is a reduction of the MAE duration. What is novel in this experiment is the addition of a storage interval. There has not been previous research in which attention was diverted during adaptation followed by storage of the MAE. According to the gain control explanation of MAE storage, the gain of the motion pathway slowly normalizes during the storage interval. The incorporation of a diverted-attention manipulation during motion adaptation reduced the gain of the motion pathway, necessitating less normalization during the storage interval. This in turn resulted in a reduced MAE duration when attention was diverted during motion adaptation relative to when attention was not diverted during motion adaptation.

Performance in RSVP tasks.

The mean proportion of correct responses was 0.98 in the Low load (standard error of the mean was 0.01) and was 0.79 in the High load condition (standard error of the mean 0.02). Because there was no task for the observer to perform in the No load condition, it was impossible for the observer to make an error. Therefore, performance in the No load condition was coded as 1.0, which indicates perfect performance. The proportion of correct responses to the RSVP tasks were analyzed using an ANOVA for within-subjects designs. There was a single factor (attentional load) with three-levels (No load, Low load, High load). Mauchly's Test of Sphericity was significant, $\chi^2(2) = 27.11$, $p < 0.001$, necessitating a reduction of degrees of freedom with the Greenhouse-Geisser correction. The Greenhouse-Geisser corrected ANOVA revealed a significant change in performance across different levels of the RSVP task, $F(1.06, 13.72) = 127.43$, $p < 0.001$, $MSe = 0.01$. Pairwise comparisons on performance were conducted for all combinations of the three RSVP tasks. A significant reduction in RSVP task performance was found in the Low load condition relative to the No load condition, $p < 0.001$, and a reduction in RSVP task performance in the High load condition relative to the No load condition, $p < 0.001$. There was also a significant reduction in RSVP task performance in the High load condition relative to the Low load condition, $p < 0.001$. The performance data has a similar pattern of results as in Experiment 1. That is, performance in the RSVP task declined with increased task difficulty. Again, this shows that the diverted-attention manipulation did have an effect on the observers.

As expected, there was a reduction of MAE duration when a diverted-attention manipulation was introduced during adaptation. These results generally support the gain control explanation of the MAE storage. That is, motion adaptation appears to recalibrate the visual system and the introduction of a storage interval allows the gains to slowly normalize. Diverting visual attention during adaptation reduces the gain of motion adaptation and thereby produces a weaker motion signal during adaptation. The introduction of a storage interval following adaptation paired with a diverted-attention manipulation during adaptation normalizes more quickly relative to when attention was not diverted during adaptation because the motion pathway does not have to recalibrate the gain as much in order to fully normalize.

It was expected that the MAE duration would be reduced most in the High load condition. Instead, the MAE duration in the Low load condition was significantly reduced relative to the No load condition. It may be possible that the observers paid more attention to the Low load RSVP task than the High load RSVP task. If you look at the performance differences in the RSVP tasks, the observers performed better overall in the Low load task (greater proportion correct) and were more consistent (lower standard error) than in the High load condition. If the observers were paying more attention to the Low load task, then they would have had fewer resources to devote to attending to the background motion. Consequently the motion signal would have been weaker and therefore produced a shorter MAE duration.

Experiment 3

The purpose of Experiment 3 was to test the gain control explanation of storage of the MAE. Experiment 3 was similar to Experiment 2 except that the diverted-attention manipulation was applied during the storage interval rather than during adaptation. If storage of the MAE involves a gain recovery process (normalization), then diverted-attention during storage (Low and High load RSVP tasks) should weaken the normalization process, resulting in a longer effective MAE than during the No load condition during which attention was not diverted. Specifically, the longest MAE duration should be found in the High load condition and the second longest MAE duration should be found in the Low load condition. The shortest MAE duration should be found in the No load condition.

Method

Observers.

Sixteen observers volunteered to participate in this experiment. One of the observers had no MAE and was excluded from the study, leaving fifteen observers that participated in this experiment. Observer recruitment, characteristics, and compensation were the same as in Experiment 1.

Apparatus, stimuli and procedure.

The apparatus, stimuli and procedure was similar to Experiment 2 except that the three RSVP diverted-attention tasks (No load, Low load, and High load) were presented during the storage interval and were not presented during motion adaptation.

Results and Discussion

Motion aftereffect.

The mean storage interval duration was 14350.06 milliseconds and the standard error of the mean was 859.3. The MAE durations for each of the diverted-attention conditions are presented in Figure 4. The pattern of MAE duration results appears flat indicating that there was no significant impact of diverted visual attention during the storage interval. An ANOVA for within-subjects designs was conducted to analyze the effect of diverted-attention on MAE duration. There was a single factor (attentional load) with three-levels (No load, Low load, High load). No significant differences between conditions were found.

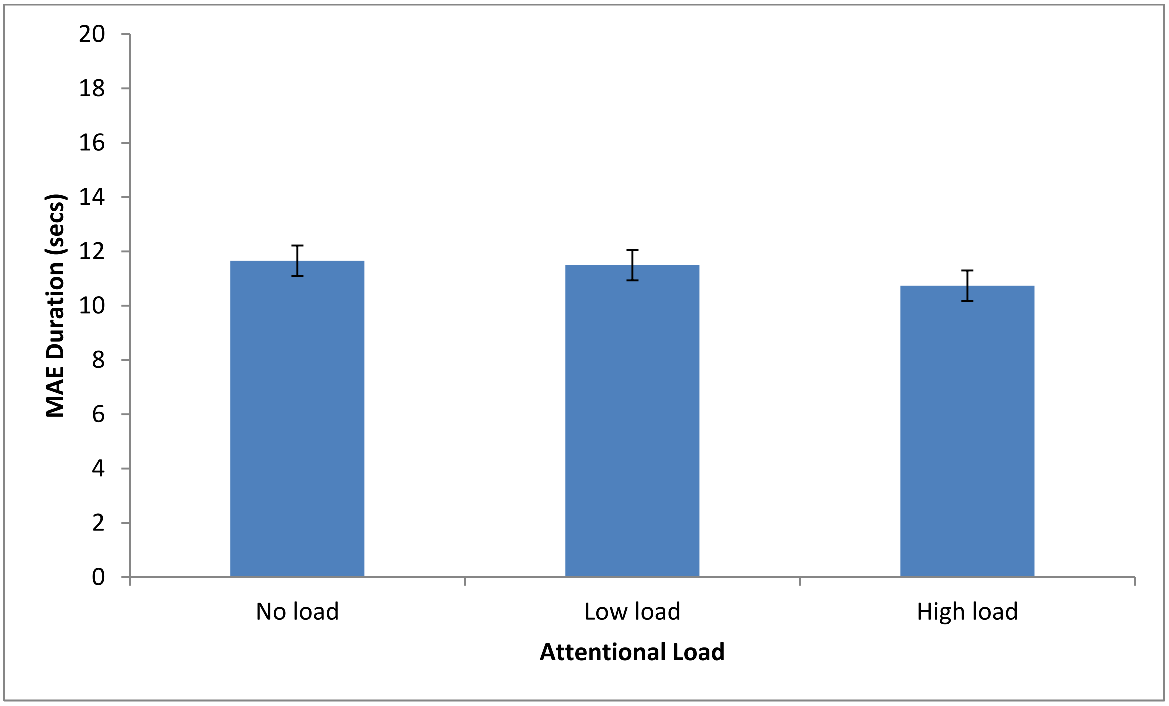

Figure 4. Results of Experiment 3. The motion aftereffect duration obtained under the three diverted-attention conditions (No load; Low load; High load). Attention was diverted during storage with the RSVP tasks in the Low load and High load conditions. Each bar represents the mean of fifteen observers. Error bars represent +/- one within-subjects standard error of the mean.

In contrast to the assumptions underlying the gain control explanation of MAE storage, we failed to find a lengthening of the MAE under conditions of diverted-attention (Low-load and High load RSVP tasks) relative to the No load condition, during which attention was not diverted.

Performance in RSVP Tasks.

The mean proportion of correct responses was 0.94 (standard error of the mean was 0.01) in the Low load condition and was 0.78 (standard error of the mean was 0.03) in the High load condition. Because there was no task for the observer to perform in the No load condition, it was impossible for the observer to make an error. Therefore, performance in the No load condition was coded as 1.0, which indicates perfect performance. The proportions of correct responses to the RSVP tasks were analyzed using an ANOVA for within-subjects designs. There was a single factor (attentional load) with three-levels (No load, Low load, High load). Mauchly's Test of Sphericity was significant, $\chi^2(2) = 17.73, p < 0.001$, necessitating a reduction of degrees of freedom with the Greenhouse-Geisser correction. The Greenhouse-Geisser corrected ANOVA revealed a significant change in performance across different levels of the RSVP task, $F(1.15, 16.05) = 45.46, p < 0.001, MSe = 0.01$. Pairwise comparisons on performance were conducted and found to be significant for all combinations of the three RSVP tasks, $p < 0.001$ for each test.

The RSVP performance data has a similar pattern of results to that of Experiments 1 and 2. That is, performance declined as the difficulty of the task was increased. This shows that this visually based diverted-attention task did have an effect on the observers, although not in terms of influencing their MAE duration.

It is possible that the diverted-attention manipulation was simply too weak to exert an influence. If the tasks were not demanding enough, then the normalization process would not be affected. Experiment 2 had a statistically weak effect that only detected a reduction of the MAE in the Low load condition but not in the High load condition. This suggests that a more difficult task may be more effective at diverting attention and may therefore be more effective at influencing the normalization process. In order to test that, Experiment 4 was developed. Experiment 4 is the same as Experiment 3 except that attention was diverted using a task that is more challenging.

Experiment 4

The aim of this experiment was to assess whether participating in a more difficult diverted-attention task during storage would have an impact on the gain normalization process. Experiment 4 was very similar to Experiment 3 except that attention was diverted non-visually during the storage interval by having observers count backwards aloud. As in Experiments 1, 2, and 3 there were three conditions based upon the diverted-attention load (No load, Low load, High load). The No load condition was the same as the No load condition in Experiment 3. In the Low load condition observers were asked to count backwards aloud by an interval of one. In the High load condition observers counted backwards aloud by an interval of three. This diverted-attention manipulation is known to be a highly demanding task which tends to produce a high central load by taxing working memory (Houghton, Macken, & Jones, 2003; Peterson & Peterson, 1959).

Method

Observers.

Eleven observers participated in this experiment. The description of the observers is the same as in Experiment 1. Observer recruitment, characteristics, and compensation were the same as in Experiment 1.

Stimuli, apparatus, and procedure.

Experiment 4 was identical to Experiment 3 except that attention was diverted non-visually by having observers count backwards aloud during the storage interval. As in Experiment 3 there were three conditions (No load, Low load, High load) based upon the degree of attentional load that was imposed during the storage interval. The No load condition was the same as the No load condition in Experiment 3. In the Low load and High load conditions, observers were asked to count backwards aloud during the storage interval. At the beginning of the storage interval, a randomly determined three-digit number ranging from 300-999 appeared for 750 ms. The observers were asked to count backwards from the three-digit number aloud once per second for the duration of the storage interval.

The step size by which they counted backwards was varied according to the condition. In the Low load condition, observers were asked to count backwards aloud by a step-size of one. In the High load condition observers counted backwards aloud by a step-size of three. The computer emitted a 600 Hz tone for 200 ms every second for the duration of the storage interval. This simulated the timing and sound of a metronome that was used to cue observers to count backwards. Counting backwards continued throughout the duration of the storage interval. At the end of the storage interval, the observer stopped counting backwards aloud and the storage pattern was replaced by the test pattern.

Once the test pattern appeared, the observer stopped counting backwards and the experimenter noted the final number that was uttered by the observer. As in Experiments 1, 2, and 3, the test pattern was presented continuously until the observer indicated that the MAE was no longer visible by pressing the spacebar on the computer keyboard. The computer then wrote the duration of the MAE in milliseconds to a data file. At this time, the experimenter was able to enter the last number reported by the observer into a data entry field in the experiment control software. The experiment control software then wrote the entered number as well as the randomly generated 3-digit number from the start of the storage interval to the datafile. All observers experienced four trials of each of the three conditions. The order of the trials was randomized for each observer.

Results and Discussion

Motion aftereffect duration.

The mean storage interval duration was 15457.41 milliseconds and the standard error of the mean was 1315.03. The MAE durations for each of the diverted-attention conditions are presented in Figure 5. The pattern of MAE duration results for Experiment 4 appears to be similar to the MAE duration results of Experiment 1 and 2. The graph shows that the No load condition had the longest MAE duration. The Low load and High load conditions were roughly equivalent and reduced relative to the No load condition.

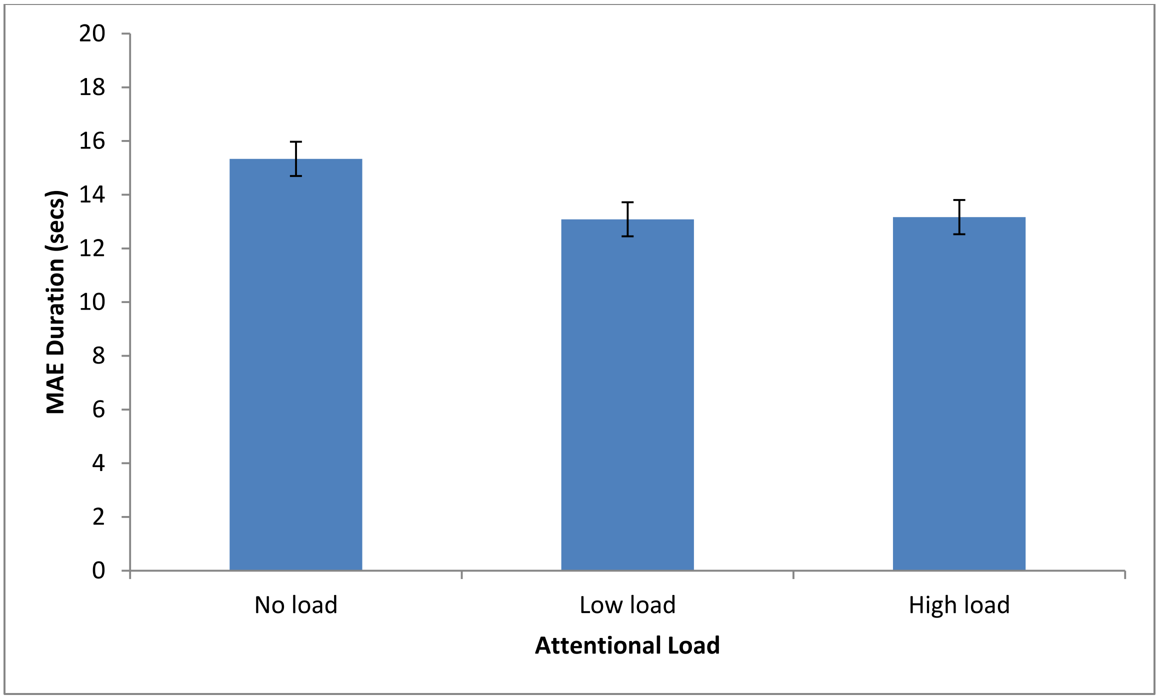

Figure 5. Results of Experiment 4. The motion aftereffect duration obtained under the three diverted-attention conditions (No load; Low load; High load). Attention was diverted during storage with the backwards counting task in the Low load and High load conditions. Each bar represents the mean of eleven observers. Error bars represent +/- one within-subjects standard error of the mean.

An ANOVA for within-subjects designs was conducted to analyze the effect of diverted-attention on MAE duration. There was a single factor (attentional load) with three-levels (No load, Low load, High load). Mauchly's Test of Sphericity was significant, $\chi^2(2) = 8.4, p < 0.02$, necessitating a reduction of the degrees of freedom in the ANOVA by using a Greenhouse-Geisser correction. The Greenhouse-Geisser corrected ANOVA revealed a significant effect of diverted-attention on the MAE duration, $F(1.25, 12.45) = 4.55, p < 0.05, MSe = 6315866.15$. The within-subject standard error of the mean was 636.25. Pairwise comparisons on the effect of diverted-attention during storage on the MAE showed a significant reduction of MAE duration in the High load condition relative to the No load condition, $p < 0.04$. The comparison between the No load condition and Low load condition was not significant, $p < 0.06$, nor was the comparison between Low load and High load significant, $p < 0.86$.

The Experiment 4 MAE duration results are different than those of Experiment 3; there was a reduction of MAE duration when attention was diverted during storage using the backwards-counting tasks instead of the RSVP tasks. It is thought that the backwards-counting diverted-attention manipulation used in Experiment 4 is more challenging than in the RSVP tasks that were used in Experiment 3. This, in turn, created a central load that strongly utilized working memory resources in order to influence the normalization process.

Performance in backwards counting tasks.

Task performance was measured by analyzing deviation scores. The deviation scores were obtained by subtracting the last number the observer reported from what they should have reported if they counted correctly. The No load condition had no diverted-attention manipulation and was therefore treated as perfect performance (i.e., a deviation score of 0 was used). The mean deviation scores were 7.36 (standard error of the mean was 3.65) in the Low load condition and 44.36 (standard error of the mean was 9.46) in the High load condition. On average, the size of the error in the High load condition was six times that as in the Low load condition. The deviation scores were analyzed using an ANOVA for within-subjects designs. There was a single factor (attentional load) with three-levels (No load, Low load, High load). Mauchly's Test of Sphericity was significant, $\chi^2(2) = 11.63, p < 0.01$, necessitating a reduction of the degrees of freedom in the ANOVA by using a Greenhouse-Geisser correction. The Greenhouse-Geisser corrected ANOVA revealed a significant change in performance across different levels of the backward-counting tasks, $F(1.16, 11.59) = 21.91$, $p < 0.00$, $MSe = 489.6$. Pairwise comparisons on performance were conducted for all combinations of the backwards counting tasks. There was a significant reduction in task performance between the No load condition and the High load condition, $p < 0.01$. There was also a reduction in task performance between the Low load condition and the High load condition, $p < 0.00$. No significant difference was found between the No load condition and the Low load condition, $p < 0.07$.

Performance for the backwards counting diverted-attention conditions show the same general pattern as visually based diverted-attention conditions (RSVP tasks) in Experiments 1, 2, and 3. The performance data show that performance declined with increased task difficulty. In contrast to Experiment 3, these results suggest that diverted-attention does affect the normalization process. Surprisingly, the results of Experiment 4 have a remarkable similarity to Experiments 1 and 2. It is clear that introducing a diverted-attention manipulation during the storage interval can significantly influence the subsequent MAE duration. What is surprising is that the MAE duration was reduced instead of increased when attention was diverted during storage. According to the logic outlined above, it was expected that diverting attention during storage would attenuate the normalization process and produce a longer MAE duration than when attention was not diverted. Instead, the results of Experiment 4 show that the normalization process is clearly accelerated as task difficulty increases. Experiment 4 therefore does not support the gain control explanation of MAE storage in its current form. The differential reduction of MAE durations found across different conditions of attentional load necessitates modification of the gain control explanation of MAE storage.

GENERAL DISCUSSION

In this project we tested the gain control explanation of the motion aftereffect (MAE) storage phenomenon by implementing diverted-attention manipulations during the storage interval. The logic behind this manipulation was that diverted-attention should interact with gain control mechanisms in the motion pathway. In Experiments 1 and 2 we found support for the gain control explanation of the MAE when visual attention was diverted during adaptation. However, in Experiment 3, we failed to find support for the gain control explanation of MAE storage when visual attention was diverted during storage. Moreover, in Experiment 4, we failed to find support for the gain control explanation of MAE storage when non-visual attention was diverted during storage. Surprisingly, the results of Experiment 4 were opposite to what would be predicted by gain control theory as it is currently described in the literature. However, a modified version of gain control theory that incorporates the notion of interference would be supported by the results of Experiment 4.

Experiment 1 supports gain control theory and mirrors the existing body of the MAE literature by replicating its general findings. According to gain control theory (van De Grind, et al., 2003; van De Grind, et al., 2004; Verstraten, et al., 1994), motion adaptation lowers the gain, or sensitivity, of motion processing units that are tuned to the direction of motion stimulation. Subsequent viewing of a static test pattern normalizes the motion processing units. Because the outputs from multiple directional pathways are combined to produce the perception of movement in a given direction, the combination of signals from adapted plus non-adapted pathways induces an illusory perception of motion in a direction opposite to the direction of adaptation when a stationary test pattern is viewed. During the viewing of the test pattern the gain of the motion processing units is becoming normalized. The illusion continues until the normalization process is complete because the signals coding the opposite direction of motion are now relatively stronger.

Experiment 1 also mirrors the existing body of the diverted-attention MAE literature by replicating its general findings. In this case, when attention was diverted during the observation of a moving pattern, the subsequent MAE was reduced relative to when attention was not diverted. Chaudhuri (1990) found that when observers engaged in a character recognition task during motion adaptation, the duration of the subsequent MAE was reduced relative to when they did not engage in a character recognition task. Rezec, et al. (2004) asked observers to either attend to a moving pattern while ignoring a RSVP stream or to attend to a RSVP stream and recognize when vowels were presented while ignoring background motion. They found that the subsequent MAE was reduced when the observers attended to the RSVP vowel recognition task and concluded that attention affects the adaptation gain of motion processing mechanisms. Thus, in cases in which the observer attends to motion, the gain of motion processing mechanisms is increased; when attention is diverted away from motion, the gain of motion processing units is lowered. In studies that used the same RSVP tasks during adaptation that were used in this study, it was found that increased diverted-attention load reduced any subsequent MAE duration (Patterson, Fournier, Wiediger, Vavrek, Becker-Dippman, & Bickler, 2005; Rees, Frith, & Lavie, 1997). This has been attributed to the automatic gain-control process in which diverted-attention affects the adaptation gain (Patterson et al., 2005, p. 2606).

Experiment 2 mirrors the existing body of the MAE storage literature by replicating the general findings. The general finding of the MAE storage literature is that interposing an unrelated storage pattern between motion adaptation and the viewing of a non-moving test pattern effectively lengthens the overall MAE. Spigel (1960; 1962a; 1962b) interposed a contour-free period between the viewing of the adapting pattern and the test pattern. He found that the decay of the MAE was delayed by the imposition of the contour-free period. Verstraten, et al. (1994) showed that the imposition of a pattern containing spatially orthogonal lines to the adapting pattern and test pattern also delays the decay of the MAE. He argued that motion adaptation recalibrates the gain of the visual system and that viewing a test pattern normalizes the gain of the visual system. The viewing of an orthogonal storage pattern, according to Verstraten, et al. (1994), delays the normalization process due to a lack of motion information. The gain control explanation of MAE storage was further elaborated by van De Grind and colleagues (van De Grind, Lankheet, & Tao, 2003; van De Grind, van Der Smagt, & Verstraten, 2004). They argued that the normalization process proceeds at a slower rate when a storage pattern is viewed relative to when a test pattern is viewed.

Turning now to the results of Experiment 3, we failed to find support for a gain control explanation of MAE storage. In Experiment 3, visual attention was diverted during the storage interval using RSVP tasks with word stimuli. To date there is no other study in which a diverted-attention manipulation was imposed during the storage interval. It was expected that introducing a diverted-attention manipulation during the storage interval would retard the normalization process due to the lowering of the gain of the visual system (Hillyard, Vogel, & Luck, 1998; Ling, Liu, & Carrasco, 2009; Rezec, Krekelberg, & Dobkins, 2004; van De Grind, Lankheet, & Tao, 2003; van De Grind, van Der Smagt, & Verstraten, 2004; Verstraten, Fredericksen, Grüsser, & van De Grind, 1994). However, the results of Experiment 3 failed to show any influence of attention modulating the normalization process during MAE storage. Of course, it is difficult to interpret any lack of experimental effect, and in this case it is possible that the diverted-attention manipulation used in Experiment 3 may have been a relatively weak manipulation which exerted no effect on the normalization of process during the storage interval. To address this issue, Experiment 4 used a different, and stronger, diverted-attention manipulation during the storage interval.

In Experiment 4, the observers participated in backwards-counting tasks instead of using the RSVP tasks that were used in Experiments 1, 2, and 3. The backwards-counting task is thought to be very difficult and produces a strong central load because of the demands it places on working memory. If the current gain control explanation of MAE storage was correct, there should have been an increase of MAE duration under conditions of diverted-attention relative to when attention was not diverted. Instead, the opposite trend occurred. There was a reduction of the MAE duration under conditions of diverted-attention relative to when attention was not diverted. This shows an accelerated normalization process instead of a retarded normalization process when attention was diverted during storage. Because of this trend, the current gain control explanation of MAE storage as described in the literature (van De Grind, Lankheet, & Tao, 2003; van De Grind, van Der Smagt, & Verstraten, 2004; Verstraten, Fredericksen, Grüsser, & van De Grind, 1994) cannot be not supported. Instead, appears as though there is some form of signal interference that is occurring between the maintenance of the MAE and the backwards-counting task. The reason that the Low load and High load conditions had equivalent MAE durations despite the attentional load differences is that the backwards-counting task utilized the same neural substrates that were used in maintaining the MAE during storage. More explicitly, once there was more than one task, the neural resources were biased in their allocation to maintaining the attended task.

In Experiment 4, the observers had to maintain a recollection of what number came next in the sequence while they were counting backwards. As such, there was a strong working-memory component during the task. It is likely that the observers visualized a number line to help maintain a memory of the relationship between the last number they uttered and what number would come next in the sequence. As such, the visualization of the mental number line would not change between conditions of load so long as there was backwards-counting taking place. Because the backward-counting task likely required the use of visualization, and that visualization was the same between Low load and High load, the same neural substrates that are normally used for maintenance of the MAE were recruited. This resulted in a reduced MAE duration because of signal interference between the attended task and the maintenance of the MAE. As such, the gain of the visual system was normalized more rapidly when the observers participated in a backwards counting task.

The current description of gain control theory treats normalization as a passive process which proceeds automatically to adjust the sensitivity of the motion pathway. This process utilizes low-level automatic gain control mechanisms that are early in the visual pathway. During the normalization process, the gain of the motion pathway slowly and passively drifts to the normal set-point (van De Grind, Lankheet, & Tao, 2003; van

De Grind, van Der Smagt, & Verstraten, 2004). The evidence presented in this study is contrary to the current gain control explanation of MAE storage. The rapid normalization under conditions of increased cognitive load during storage demonstrates that there are higher-level mechanisms which can actively, rather than passively, return the gain of the motion pathway to the normal set-point. This likely is due to a sharing of neural substrates for multiple tasks. If two tasks utilize the same neural substrates, there will be some competition, or interference, of the signals associated with the maintenance of those tasks. When attention is diverted toward one task, such as counting backwards, the activity of shared neural substrates will be biased towards the maintenance of the attended task. As such, the gain mechanisms along the motion pathway will be actively normalized in order to free resources (i.e., neural substrates) for the maintenance of the attended tasks. As a consequence, the gain control mechanisms return to their normal set-point at an accelerated rate and the MAE duration is reduced. Support for the notion of signal interference and the sharing of neural substrates come from a number of neuroimaging studies.

For example, in a review of visuospatial working memory, Slotnick (2004) reported that, in PET and fMRI research, the same neural substrate is used to represent visual memory and visual perception. Specific to a link between working memory and motion processing, it was found that maintaining a memory of a particular motion direction could bias the perception of direction of a moving stimulus at a later time. Moreover, Mendoza, Schneiderman, Kaul and Martinez-Trujillo (2011) dissociated and then later combined visual-attention and working memory in a series of experiments which used pulses of visual movement as the main stimuli. They concluded that feature attention serves to enhance the gain of desired features (such as visual movement) but that exposure to brief visual motion would place a demand on visual working memory that interferes with the recall of previously seen visual movement. Houghton, Macken and Jones (2003) explored the topic of a central cognitive load affecting the duration of the MAE. They used the backwards-counting diverted-attention manipulation that was used during the storage interval in Experiment 4, except that they employed it during adaptation and there was no storage interval employed in their research. They found that the implementation of the backwards counting diverted-attention manipulation resulted in a reduction in the MAE duration relative to when there was not a diverted-attention manipulation.

Evidence from fMRI research shows that mental imagery activates the same areas associated with vision (Ganis, Thompson, & Kosslyn, 2004; Slotnick, Thompson, & Kosslyn, 2005). Ganis, et al. (2004) asked observers to study several line drawings of common objects. The observers were then asked to visualize the pictures they had previously studied while undergoing fMRI. The observers then saw the same images displayed while undergoing fMRI. It was found that the same brain regions became active whether the observer was imagining or actually seeing the picture of the object. Slotnick, et al. (2005) conducted a similar study to the Ganis, et al. (2004) study except that the observers studied and imagined moving checkerboard patterns. Again, they found the same areas became active whether the observer was seeing or imagining the moving checkerboard pattern. Similarly, Kosslyn, et al. (1993) found that visualizing letters and actually seeing letters activated the same cortical regions.

It has been suggested that mathematical operations utilize a mental number-line that recruits visuospatial resources (Dehaene & Cohen, 1995; Dehaene, Spelke, Pinel, Stanescu, & Tsivkin, 1999). Dehaene, Tzourio, Frak, Raynaud, Cohen, Mehler, and Mazoyer (1996) asked participants to conduct multiplication and number comparison tasks during a PET scan. The researchers found that there was bilateral activation of the occipital lobes. In a fRMI study of cortical areas involved in mathematical operations, Rickard, Romero, Basso, Wharton, Flitman, and Grafman (2000) found bilateral activation of the occipital and parietal lobes, or more simply, areas associated with vision. The Dehaene, et al. (1996) and Rickard, et al. (2000) findings show that mental operations involving numbers utilize the same areas that are used for visual processing.

Neuroimaging evidence has also shown a reduction of the motion signal strength when attention is diverted during adaptation. Rees, et al. (1997) found that activity of area V5 and the V1 and V2 border was attenuated under the High load diverted-attention condition. This shows that diverting attention lowered the gain of motion processing and thereby produced a weaker motion signal. As a consequence, the MAE duration was reduced when attention was diverted relative to when attention was not diverted. In a similar fMRI study (Somers, Dale, Seiffert, & Tootell, 1999), a letter identification RSVP task was used to spatially isolate attention. The researchers found that when attention was allocated to the RSVP task the BOLD signal strength throughout all visual areas was weaker. In a similar study using both auditory and visual diverted-attention manipulations during motion adaptation, Berman and Colby (2002) found that the activity of area MT was reduced when attention was diverted. Again, the reduced activity of area MT meant that the motion signal was weaker due to the gain changing effects of diverted-attention.

Similarly, Treue and Maunsell (1996) conducted single-cell recordings using macaque monkeys and found that the signal strength of motion sensitive cells in areas MT and MST was weakened when attention was diverted.

It would seem then, that the accumulation of evidence from PET scans and fMRI on the topics of working memory, mental imagery, and mental counting and math operations, as well as the motion literature indicate that all of these activities utilize common neural substrates. As such, the results of this study can be explained as signal interference: when attention is diverted with a sufficiently demanding task, it interferes with maintaining the signal strength of motion processing units. If attention is diverted during motion adaptation, the gain is lowered resulting in reduced motion signal strength. If attention is diverted during storage, it accelerates the normalization process because the diverted-attention task recruits the same neural substrates that maintain the MAE. As a consequence, the MAE is reduced regardless whether attention is diverted during adaptation or storage.

Previous authors who have investigated the MAE storage phenomenon have treated it as a passive normalization process that proceeds automatically. These results as well as results from drawn from other topics tell a different story: normalization is an active process, which interacts with cognitive resources rather than just visual resources. Currently underway is an investigation utilizing mental imagery to accentuate interference effects during MAE storage and to further demonstrate that storage of the MAE is actually an active process.

More generally, even relatively simple adaptation aftereffects involving early visual mechanisms are affected by high-level attention processes. The influence of attentional processes on early visual mechanisms produces interference such that the attended task receives greater signal strength.

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APPENDIX

IRB Approval

Human participant use for this study was approved by the State University of New York Institute of Technology (SUNYIT) Institutional Review Board under the title of "Gain Mechanisms of the Optic Flow Motion Aftereffect."