DISCRIMINATING BETWEEN AFFERENT AND
EFFERENT CONTRIBUTIONS TO VISUAL AWARENESS IN AFTERIMAGES

A Thesis

Presented to

the Faculty of the College of Science and Technology

Morehead State University

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

by

Allen Lane Thomas

July 31, 2005
Accepted by the faculty of the College of Science and Technology, Morehead State University, in partial fulfillment of the requirements for the Master of Science degree.

Director of Thesis

Master's Committee

Date May 31, 2005
DISCRIMINATING BETWEEN AFFERENT AND EFFERENT CONTRIBUTIONS TO VISUAL AWARENESS IN AFTERIMAGES

Allen Lane Thomas, MS
Morehead State University, 2005

Abstract of Thesis

The purpose of this study was to discriminate between the contributions between efferent and afferent inputs into visual awareness. Utilizing after-imaging techniques, 96 college students were required to evaluate their perception of the size of afterimages in four different test conditions. Each test condition is conducted by inducing an afterimage and then removing all visual afferent input. All participants were to determine any variance of size in the induced afterimage in one of four test conditions. Condition one is with no motor activity, condition two is with movement induced by participants, condition three is with passive movement, and condition four is with attempted movement against restraint. By removing all afferent visual input, it is assumed that any
changes "seen " in the induced afterimage will be the results of central processing minus the visual afference.
AKNOWLEDGEMENTS

There are several people that I would like to acknowledge and say thank you to for giving me the opportunity to work and accomplish this academic endeavor. First and foremost I would like to give my heartfelt and sincere thanks to my advisor and mentor. Without the advice, assistance, knowledge, and direction of Dr. Dale Dickson this project would not have occurred. Dr. Dickson’s efforts, physical as well as monetary in the construction of the testing facility were enormous. Thank you Dr. Dickson. In addition, I would like to thank my advisory panel, Dr. Mattingly, Dr. Morgan, and Dr. Remillard for their contributions to this project.

Finally I would like to thank Porter Dwayne Jones, a life long resident of Morehead, Kentucky. Porter helped build and install the test fixture used in this study at no charge to anyone.

Morehead State University
# TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>Chapter</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>I. Introduction</td>
<td>1</td>
</tr>
<tr>
<td>Proposed Contribution of Muscular Afference to Visual Perception.......</td>
<td>3</td>
</tr>
<tr>
<td>Proposed Contribution of Muscular Efference to Visual Perception.......</td>
<td>7</td>
</tr>
<tr>
<td>Motor Activities And Afterimages</td>
<td>11</td>
</tr>
<tr>
<td>Afferent and Efferent Contributions of Non-Ocular Motor Systems.......</td>
<td>13</td>
</tr>
<tr>
<td>II. Method</td>
<td>19</td>
</tr>
<tr>
<td>Participants</td>
<td>20</td>
</tr>
<tr>
<td>Experimental Setting And Apparatus</td>
<td>20</td>
</tr>
<tr>
<td>Procedure</td>
<td>23</td>
</tr>
<tr>
<td>III. Results</td>
<td>25</td>
</tr>
<tr>
<td>IV. Discussion</td>
<td>32</td>
</tr>
<tr>
<td>References</td>
<td>44</td>
</tr>
<tr>
<td>Appendix A: Informed Consent</td>
<td>49</td>
</tr>
<tr>
<td>Figure</td>
<td>Description</td>
</tr>
<tr>
<td>--------</td>
<td>-----------------------------------------------------------------------------</td>
</tr>
<tr>
<td>1.</td>
<td>Block diagrams of the two rival theories of the interaction of motor command signals and afferent visual signal flow</td>
</tr>
<tr>
<td>2.</td>
<td>Test Apparatus Showing Black And White Stripped Background For Contrast</td>
</tr>
<tr>
<td>3.</td>
<td>Test apparatus showing flash strobe in relation to participants position during experiment</td>
</tr>
<tr>
<td>4.</td>
<td>Test Apparatus</td>
</tr>
<tr>
<td>5.</td>
<td>Comparison of reported experiences indicating a trend versus no trend (near larger or far larger) by experimental condition</td>
</tr>
<tr>
<td>6.</td>
<td>Frequency distribution of near larger and far larger categorizations by experimental condition</td>
</tr>
<tr>
<td>7.</td>
<td>Comparison of reported experiences within the trend (near larger or far larger) by experimental condition</td>
</tr>
<tr>
<td>8.</td>
<td>Comparison of response distributions regarding trend through use of a Two tailed analysis using fishers exact test of probability</td>
</tr>
</tbody>
</table>
CHAPTER 1

AN INTRODUCTION TO DISCRIMINATING BETWEENafferent AND efferent CONTRIBUTIONS TO VISUAL AWARENESS IN AFTERIMAGES

The ability to differentiate between observer movement and object movement is a fundamental requirement for vision because it affords us the ability to maintain a consistent world percept. In some fashion we need to be able to differentiate eye-movements, movements of our head and neck, and movement associated with locomotion from object movement as we travel through our environment.

During normal vision, the retinal images of objects in our environment tend to shift across the retina due to parallactic movements. Moreover, saccadic movements occur approximately every 200 to 800 milliseconds producing rapid displacements of images across the retina. In spite of the retinal displacements, we generally perceive objects in our environment as maintaining a constant existence and, under all but the most extreme conditions, they are correctly perceived as moving or stable relative to our position (Grusser, 1986). These types of observations have led to an assumption that during locomotion and gaze movement, visual afferent signals are modified during processing by other signals arising from processes of motor activity.

Consideration of signals that arise as part and parcel of motor activity leads to two potential sources, each of which may provide the necessary and sufficient information to modify the processing of visual afferent information appropriately. One potential source of information regarding motor activity is the constant outflow of motor commands to muscle groups. As depicted in Figure 1a, the interpretation of
object movement may be modified by a system that is constantly monitoring motor signals as they are issued from motor control centers of the brain. For example in this model, a command to shift one's gaze to the right at a certain velocity is taken into consideration when making attributions regarding image displacement on the retina. If a shift of equal velocity and similar direction across the retina (note: right-left reversal of retinal image) occurs, the object could be perceived as stationary with the image displacement attributed wholly to gaze movement. If, however, image displacement occurs in the absence of any command to shift gaze, the movement is attributed entirely to object movement. While these two scenarios represent the extremes, an algorithmic relationship could be easily derived to accommodate intermediate combinations of gaze control and image displacement. The critical element to note here is that the command issued to alter gaze provides all the information necessary to accurately interpret object movement in the face of potential observer-initiated movements.

Figure 1. Block diagrams of the two rival theories on the interaction of motor command signals and afferent visual signal flow.

Adapted from O.-J. Grüsser 1986
An alternative approach to the problem can be seen in Figure 1b. In this approach, inflow signals arising from sensory organs embedded in muscle groups are monitored in order to determine the current state of the muscle groups. This muscle-state information may subsequently be integrated with visual afference to develop an accurate representation of object movement in extrapersonal space. For example, proprioceptive signals may indicate that the superior rectus muscles are constricted. If, at the same time, visual afference indicates an upward displacement of a retinal image cast by a particular object, the image displacement would be attributed to gaze change as opposed to object movement. If, however, image displacement occurs absent any temporally contiguous change in muscle state, the image displacement would be attributed to movement of the object in the surrounding environment.

Theoretically, both models could provide the necessary and sufficient information to yield an accurate and useful representation of the visual scene as regards object movement. Of course each of these models place different requirements on the basic structure and function of the observer’s system. If outflow theories are to be supported, there must exist some mechanism for the actual monitoring of motor signals. On the other hand, if inflow models are correct, there must be some type of sensory apparatus that allows for the monitoring of muscle state in an ongoing fashion. While these models operate upon different bases, they are not mutually exclusive thus offering the potential for both models to contribute simultaneously to the interpretation of visual afference.
Proposed Contributions of 
Muscular Afference to Visual Perception

Investigations of the interaction of motor activity and visual afference have largely focused on the extraocular muscles. The coordinated interaction of twelve muscles, six muscles per eye, facilitates rapid, accurate eye movement.

One of the earliest mentions of a muscular influence on visual perception comes from Bain (1855; as cited in Coren 1986), when he indicated that “by a horizontal sweep, we take in a horizontal line, by a circular sweep, we derive the muscular impression of a circle” (p.236). While in this instance Bain is only addressing shape perception he also incorporated the concept of muscular consciousness into his general theory of perception by stating that muscular consciousness plays an indispensable, necessary and vital role in percept formation. Bain did not specify how we develop muscular consciousness, leaving the question of whether muscular consciousness originates from proprioceptors embedded in muscles or from commands sent to the muscles unanswered.

In a similar vein, Sherrington (1918) posited a theory of visual perception in which proprioceptive feedback from the extraocular muscles played an integral part in one’s perception of spatial layout. In support of his theory, he developed a hypothetical physiological organization that could account not only for extraocular muscle influences on visual perception but also a vestibular influence as well. The indication from Sherrington’s work is that afferent feedback from the extraocular muscles can be a contributor to space as perceived by the eye. Although Sherrington
was never able to specify actual anatomical structures underlying the proprioceptive capacity of the extraocular muscles, data from recent research (Mclean, 2002) indicates that the small cells in the central nuclei of extraocular muscles may mediate a kinaesthetic sense for the extraocular muscles, thus providing a physiological basis for Sherrington's model.

Even before Mclean’s identification of these neurons, the availability of extraocular muscle afference had been demonstrated behaviorally by Skavenski (1971; 1972). Skavenski has shown that participants could, in the absence of visual afference, accurately determine that the eye had been displaced when it was passively moved via a weight and pulley system. Not only could the displacement be discerned but the magnitude and direction also could be determined. This work effectively demonstrates the presence and availability of an afferent signal apparently originating in the extraocular muscles and also suggests that, at least under these experimental conditions, the signal may be utilized to determine eye position.

Further support for an inflow model comes from the studies of ocular position sense following saccadic eye movement. In order to change visual fixation from point to point, observers typically execute a series of saccadic movements. Saccadic movements are ballistic by nature and once initiated they come to completion without modification. While effective in general, saccadic movements are most often slightly inaccurate with the observer either undershooting or overshooting the intended fixation point, an error that is quickly noted through visual afference and resolved by a second, corrective saccade. Furthermore visual afference is suppressed during the
course of the saccadic movement. Shibelske (1976) capitalized upon these slight inaccuracies as well as the suppression of visual information in a study in which he required participants to fixate a single point and quickly shift their fixation to a second point. During saccadic movement when visual afference is suppressed, the second point was removed and a third point was placed either in the same place or to the right or left of the second point. The participants simply had to indicate the location of the third point relative to the second point. Since the second point was removed during the initial saccade, no corrective saccade could occur thus participants were forced to rely upon the felt position of the eye in order to make an appropriate judgment of location. Under these conditions, participants accurately identified the relative location of the third point thus providing support for the viability of an inflow model.

Hansen and Skavenski (1977) conducted three experiments to investigate the accuracy of eye position information as it is relayed to the motor control system. Participants were tasked with returning their eyes to a reference point after saccadic and nystagmus movements, while in the dark. The participants could complete this task reasonably well suggesting that the ocular motor system received high quality, accurate information about saccadic movements as well as smooth pursuit movements. Based on these studies, afferent extraocular information is judged to have an accuracy of approximately 0.5 degrees of arc. Moreover, this information appears to be available for the guidance of limb movements as indicated through ballistic pointing studies as well as subsequent eye movements.
While there is data that supports a role for muscle afference, experimental evidence to the contrary does exist. Brindley and Merton (1960) conducted studies that involved passive manipulation of the participant’s eye by the experimenter. Displacements were accomplished by grasping the insertions of the lateral and medial rectus muscles. When the occluded eye was displaced, the participants failed to acknowledge its movement. When the participants attempted to move their eye as it was held steady by the experimenter, they tended to report that the movement had occurred. Moreover, when visual afference was made available under these conditions, the participants resolved the subjective feeling of eye movement with the absence of visual image displacement by reporting that the scene appeared to shift in concert with the eye movement. Clearly this line of investigation calls into question the existence of any position sense in the eye.

Extraocular afferent organs have been identified in humans. For instance, Ruskell (1978) has studied the structure and output of myotendinous cylinders embedded in extraocular muscle fibers. These sensory organs, however, are associated with non-twitch fibers that appear to generate tonic rather than phasic contractions (Lewis & Zee, 1993) thus passive stretch of the extraocular muscles would seem to provide a poor stimulus for myotendinous activation (Lewis & Zee, 1993; Ruskell, 1978).

Fiorentini, Maffei, Cenni, and Tacchi, (1985) found indirect evidence from animal research supporting the idea that afference is utilized in distance perception. Poor distance discrimination was shown in deaffrentated cats. Trotter, Beaux, Pouget,
and Imbert (1991) have shown additional evidence supporting the previously mentioned results in that the removal of afferent feedback by unilateral and bilateral deafferentation of young cats results in deficits of the distance perception mechanisms.

While there seems to be overwhelming evidence for the existence of an inflow signal indicating eye position, the function of this signal remains quite unclear. Some have proposed that the inflow signal does not contribute to object localization of movement perception but rather to the execution and control of smooth pursuit (Brindley & Merton, 1960; Hansen & Skavenski, 1977; & Skavenski 1971; 1972)

Proposed Contributions of Motor Efferent Signals to Visual Perception

Sir Charles Bell appears to be the first researcher to formally suggest that a relationship exists between the perception of visual direction and control of the extraocular muscles (Wade, 1978). Helmholtz (1909/1962) followed Bell's lead in developing his theory of an efferent contribution to the perception of direction and extent. In essence, his theory suggests that the information derived from the monitoring of motor commands to the extraocular muscles contributes greatly to visual perception. Support for Helmholtz’ theory comes from several experiments that involved active and passive ocular movement. For example Helmholtz found that the passive movement of one eye while viewing a stationary object with both eyes resulted in a double image, however the passive movement of a single eye with the other eye occluded resulted in apparent movement of the object. Helmholtz also
found that afterimages appeared to remain stationary when the eye is passively moved but appear to move when the eye is allowed to move actively and naturally. Moreover, Helmholtz found that unsuccessful attempts to move a paralyzed eye gave rise to apparent motion. This last finding was later replicated in an experiment by Mach (1914) when he achieved paralysis of an eye by packing putty into the orbit to prevent any rotation of the eye. As was reported by Helmholtz and Brindley, Merton and Mach found that any attempt to rotate the paralyzed eye gave rise to perceived motion in the direction of the intended but unsuccessful eye movement.

Further support for an efference model comes from Festinger and Canon (1965). These investigators had participants engage in either saccadic eye movements or smooth pursuit tracking movements to localize targets. When a target was localized and tracked through smooth pursuit movements, participants were only able to provide accurate information about the target’s direction and velocity of movement. When required to make a single saccadic movement from the target’s initial position to its final position, participants could identify the target’s final position with greater accuracy. Under both smooth pursuit and saccadic conditions, participants’ eyes came to rest in roughly the same location, thus muscular afference would have been approximately equivalent. With regard to the motor commands associated with the two conditions, a significant distinction arises. Whereas smooth pursuit movements require only relative movements with regard to the target’s momentary location guided by visual afference, saccadic movements require the specification of an absolute position corresponding to the target’s final location. When the motor command
incorporates an absolute position, subsequent localization of the target’s position is
more accurate.

Skavenski, Haddad and Steinman (1972) conducted an experiment that
allowed the afferent and efferent signals to be manipulated independent of each other.
Participants were directed to maintain focus on a fixation point as weight was applied
to passively rotate the eye via a pulley system attached to the contact lens developed
by Skavenski (1972). The purpose was to maintain a constant afferent signal while
varying the efferent signal in response to the weight applied to the eye. The
consensus of the participants was that the point of fixation appeared to be displaced in
a direction opposite to the pull induced by the weights. This indicates that the
efferent output is interpreted by the participant as a subjective change of the fixation
point in space when in fact there had been no motion at all. The more weight that
was placed on the contact lens the greater force necessary to counteract the weight
resulting in a greater amount of perceived motion. Skavenski, Haddad and Steinman
take these results to indicate that the extraocular efferent signal is dominant when an
afferent-efferent conflict in vision arises.

Festinger, Ono, Burnham and Bamber (1967) capitalized on the different
requirements for actively guided movements and passively guided movements to
study the role of centrally issued motor commands in the organization of the
perceptual world. Participants fitted with prismatic lenses viewed either an
objectively curved edge as a straight edge or an objectively straight edge as being
curved. To promote active guidance, one group of participants were instructed to
move a stylus along the edge, being careful not to actually touch the edge. The second group was told to press the stylus against the edge firmly as they moved, thus their hand was passively guided by the edge. Results indicated that participants who actively guided the stylus displayed a greater degree of perceptual adaptation than those making passively guided movements. Under these conditions the issuance of efferent commands appears to have been critical in the organization of the perceptual world of the participants. Similar results have been reported by Bairstow and Lazlo (1979) using active and passive exploration of complex patterns.

Bridgeman and Stark, (1991) modified the efferent and afferent signal by covering one eye (to modify the afferent signal) and applying pressure with a finger to the seeing eye (to modify the efferent signal), it was found that both caused a perceived shift in the direction of the target.

In order to further investigate the role played by efferent motor commands in the organization of visual space, Stevens, Emerson, Gerstein, Kallos, Neufield, Nichols, & Rosenquist, (1976) administered curare to a single participant. As an anticholinergic agent, curare effectively paralyzes muscle fibers while sparing the proprioceptive apparatus associated with the muscle. Since curare's action occurs through an inhibition of activity at the motor end plate, the motor neurons remain unaffected. This methodology produces a disassociation of motor efference from muscle afference. Attempted movements of the eyes in this state of paralysis gave rise to the subjective experience of visual field displacement. Furthermore, these experiences were found to be dosage dependent. This robust effect remained even
when cocaine was used to desensitize the front of the eye and the eyelid thus further isolating the activity of extraocular muscle proprioceptors, prompting the investigators to "conclude that the spatial system that the spatial system, with the corollary discharge and information from the retinal mosaic can produce a perceptually stable spatial world" (pp. 98).

Matin, Picoult, Stevens, Edwards, Young, & MacArthur, (1982) used a similar procedure as utilized by Festinger, Ono, Burnham and Bamber, and found that their participant experienced oculoparalytic illusions that were dosage-dependent. For example, under the influence of curare he experienced errors in localizing eye-level-horizontal and median planes. These findings are consistent with efference theory, but not afference theory, because curare does not affect the sensory receptors or nerve fibers, only the influence of neural signals on muscle contraction.

Lewis, Gaymard, and Tamargo (1998) have shown by unilateral or bilateral deafferentiation the extraocular muscles of rhesus monkeys produced no significant error in pointing at a visual target. The monkeys were trained prior to deafferentiation and it was ascertained that no acute of gradual change existed after surgery. The efferent copy of the extraocular muscles was sufficient to allow accurate acquisition of a visual target. These researchers recognize that an adaptive mechanism may compensate for the lack of muscular afferent or alternatively, that the afferent and efferent inputs may complement each other in a system that is redundant.
Afferent and Efferent Contributions of Non-Ocular Motor Systems

The most apparent contributions to our visual perceptual awareness appears to be extraocular afference and efference. Other contributors have also been examined, and some of these contributors are the efferent and afferent signals that are derived from our non-ocular motor systems. Bairstow, and Laszlo (1979) researched the precision of afferent and efferent signals, and the precision of the information was assessed by monitoring the active and passive movements of the hand and arm. It was demonstrated that active movement of the arm and hand around intricate patterns that were not known to the participants was better for visual recognition than were passive movements. Through this cross-modal approach it was shown that active kinesthesis conveys more information than does passive kinesthesis, especially in the absence of visual input. Vierck (1978) suggest that one reason for this is may be that even though most kinesthetic information is transmitted along the same route as tactile stimulation, the two types of information are kept separately and possibly processed via different routes.

It is argued that afterimages are a central phenomena instead of a peripheral phenomena, which some evidence indicates, based on efferent input of convergence and divergence of the eyes.

Gregory, Wallace and Campbell (1959) Observed unusual occurrences with afterimages that were viewed in the complete absence of light, to prevent any visual afference, it was determined that movements of the participant’s body allowed changes in the perceived afterimage to viewed. By having the participant move their
head, even a few centimeters, toward the object the size of the afterimage decreased, and by moving their head backwards the size of the afterimage increased. This is the first indication that the afterimage may not be a retinal phenomenon, but it was a phenomenon of central processing. If the phenomena were retinal in nature then the changes induced by body movement should have had no effect on the image. However changes did occur even though no explanation was forthcoming from the investigators.

Other work was done following the Gregory et al. demonstration on the effects of motor input and its impact on the appearance and duration of afterimages by Davies (1973a). By inducing a positive afterimage in participants by using a photoflash and then varying the complexity of the afterimage by varying the proportion of the participants body that they were able to see in the afterimage. The participants were able to view nothing, one hand, or both hands. Davies believed that he was varying the complexity of the induced afterimage and the complexity of the task that the participants were involved with. The more of the participants body in the field of vision during the photoflash, the greater the complexity of the afterimage. The more involved the participant was with moving versus the intricacy of the afterimage the greater the complexity of the task. A positive correlation was shown with duration of the afterimage as the complexity of the scene, as well as the complexity of the task increased. The data gathered from this experiment supports the hypothesis that when the visual input is restricted to one sample; conflicting input from different sources may affect what we perceive in that one sample, such as an
Davie (1973b) further investigated the effect of motor activity when it was demonstrated that the movement of a participant in relation to the afterimage caused an increase in the duration of the afterimage, as well as qualitative changes. Davies had the participants either stand still and observe the afterimage, turn right or left through 90 degrees and observe the afterimage, or walk along an afterimaged corridor. The participants reported walking through an afterimage while walking down a corridor. Davies concluded that the afterimage was not solely a product of photochemical processes. The fact that they were subject to modification in appearance, as well as duration indicates that the afterimages are products of higher level processing and are a central phenomenon.

Davies (1973c), has shown that the idea that an afterimage is a central phenomenon is also supported by a third study that he conducted, as well as a case study that Davies (1995) conducted on himself by intentionally creating a scotoma by firing a powerful flash gun directly into one eye. He concluded from information that he gathered from his scotoma that prolonged afterimages are probably not retinal in origin, but of central storage. Based on Davies three studies in 1973, which is supported by his 1995 case study, he proposed a framework for a hypothesis that a central processing mechanism is utilized that uses afferent and efferent cues in order to process our visual perception of the environment. This work is consistent with Urist, (1958) who demonstrated changes in size of afterimages that are projected on walls at various distances from the participant. Convergence is associated with the
image being perceived as being larger and divergence is associated with the perceived image becoming smaller. It is seen as being evidence that efferent input from the extraocular muscles during convergence and divergence having the results of changing the size of the afterimage.

Hayhoe and Williams (1984) conducted research that supports the idea that afterimages are a central processing phenomena by producing positive afterimages in the periphery of a participant's field of view. After the image is created the participant is required to rotate their eyes in a manner that would put the afterimage in a position that would lie outside of the normal field of vision. When the afterimage is located outside of the normal field of view, the image would vanish when located in impossible viewing space. Prior to the information gathered in these combined studies it was thought that afterimages were of retinal origin, the product of photochemical processes in the eye (Brindley, 1959, 1963), researchers today understand that there are more processes involved than retinal processes, and can be utilized to study the central portion of our visual perception.

Dickson (2000) manipulated the percept of afterimages, and causing qualitative changes in the complete absence of visual afference and has demonstrated that non-ocular input does change what we perceive in the afterimage. Dickson varied bodily efference and afference while holding visual afference constant. He used four test conditions, Static, dynamic, observed, and contact condition. The participants initiated no movement in the static condition, but did move one of their hands during the dynamic condition. In the observed condition an afterimage of the
The experimenter’s hands were created and the participant was verbally informed of the movements that the experimenter was making. In the contact condition the participants had an afterimage created and then the experimenter gave the participant haptic cues by moving his hand on the surface of the participants arm either towards or away from the participant. The haptic cues provided during the contact condition did not have an effect due to the possibility that tactile feedback is kept separate and processed differently from kinesthetic information, as was discussed previously by Vierck (1978). Eye movement did not contribute to these findings due to the monitoring of eye movements during the experiment. The changes were contributed to bodily afference as being a sufficient condition to modify our precept and have the precept conform to Emmert’s law.

Bross (2000) has shown that bodily afference derived from haptic cues can be used for size-distance scaling but it has limitations involving how well established the object is that is to be scaled, due to limits that are imposed on the ability to accurately assess size-distance scaling.

The present study follows along in the same thought as the Dickson study. There are four conditions, static, dynamic, passive, and resistance. The control condition is the static condition due to the there being no efferent or afferent flow. In the dynamic condition, where the participant moves their own hand, they have actively initiated the efferent command and received the muscle afference after movement. The passive condition allows for the participant to be moved, but not initiate a signal for the movement. The final condition is utilized to allow for the
participant to initiate a command to move the arm but not receive a signal back telling the participant that the arm has moved. By comparing these four conditions, we in essence are comparing the results of situations that have efference or afference, to a condition that have both efference and afference (static), a condition that has both efference and afference (dynamic), a condition that has afference only (passive), and a condition that has efference only (resistance). By creating these four conditions and observing the effect that the four different conditions have on the observed afterimage, it can be established to what extent efference or afference plays a part in our perception of the world.
CHAPTER II

METHOD
Participants

The present study utilized 96 undergraduate students at Morehead State University, including 57 females and 39 males. The average age of the participants was 24.1 years of age. Participation was restricted to individuals with normal or corrected to normal vision. In return for their participation, students received course credit. All participants were naïve as to the nature and purpose of the research.

Experimental Setting and Apparatus

Testing took place in a darkened room that was painted flat black. The internal dimensions of the room were 4.88 meters by 2.44 meters. The participant sat at a specially constructed desk (figure 1) that had extensions that their arms were secured to. The extensions were on a metal rod that allowed movement of 22.5 degrees in either direction from the perpendicular. Full range of motion for both arms was 45 degrees. A professional photographer's flood flash (AC Studio Strobe, model SP 250) that delivered a 250 watt-second flash, mounted from the ceiling directly behind the participant (see figure 2), was utilized to create all afterimages. The flood flash was mounted in this manner so that a shadow would not be created during the creation of the afterimage.

Two red lights were placed in the darkened room so that participant's could safely maneuver about the room upon entering the dark room. A bank of switches on the wall controlled power to all lights and apparatus. A pull switch allowed the red light to be extinguished and a plunger switch was utilized to activate the flood flash.
Figure 2. Test Apparatus Showing Black And White Stripped Background For Contrast.
Figure 3. Test Apparatus Showing Flash Strobe In Relation To Participants Position During Experiment.
Procedure

Twenty-four groups of 4 participants were tested, each participant was tested individually. Each participant was assigned to a randomized test condition. The test conditions were the static condition (participant stays still), dynamic condition (participant moves hands), passive condition (experimenter moves hands), and the resistance condition (participant tries to move hands against resistance).

Participants entered the experimental room and were seated at the test desk and underwent approximately ten minutes of dark adaptation. The ten minute period was not long enough to allow for complete dark adaptation, but was long enough to allow for adaptation of cone-mediated vision. This allowed for the enhancement of the quality of positive afterimages that the participants experienced. During the dark
adaptation period the directions and instructions were read to each participant, as they reflected each test condition that the participants were participating in. Prior to the flash flood being flashed all participants were asked if they were ready, as a warning that the flash was to be used. When a proper afterimage had developed for the experimenter he asked the participants to perform the required task as the condition that the participant was assigned to dictated, either static, passive, dynamic, or resistance. When the appropriate instructions were followed the participant was asked to determine if the image of the hand to their left or the image of the hand to their right appeared larger. When the response had been delivered, the dark rooms red light condition was restored and another ten-minute dark adaptation period was experienced and information concerning the nest trial were gone over with the participant. The order of hand movements was randomized for each participant.
CHAPTER III

RESULTS
Results

A Fisher's exact two tailed analysis was used for data analysis. Fisher's Exact Test is a procedure that you can use for data in a two by two contingency table. Fisher's Exact Test is based on exact probabilities from a specific distribution (the hypergeometric distribution). Fisher's exact test is utilized for categorical data. All tests had alpha set at 0.05. The responses of each participant were categorized into one of three categories based upon the frequency with which the image of the hand nearest to the face or farthest from the face was reported as larger. Using the four reports that were received from participants, there were three combinations possible. If three or four reports were that the near hand was larger it was categorized as \textit{near larger}. If three or four reports were that the far hand was larger it was categorized as \textit{far larger}. If two of the reports were that the far hand was larger and two were that the near hand was larger then it was classified as \textit{no trend}. Figure 2 shows the results of a trend versus no trend in each of the four test conditions.
The static condition, which represents the control condition, shows that the near hand is clearly larger. The resistance condition shows a trend for the near hand to be larger but it is not statistically significant difference. In the dynamic condition and the passive condition participants obviously show a preference for the image of the far hand to be larger.
Figure 6. Comparison of reported experiences within the trend (near larger or far larger) by experimental condition.

Table 1 exhibits the results in a two-step process. It is divided into two sections, the left side shows the trend analysis. This analysis is only concerned with a trend and not the direction of the trend. The right side takes the direction of the trend into consideration.

By far the greatest number of responses given by participants in the static condition displayed an extremely high tendency towards an expected trend when tested against a hypothesized chance level of .20. A hypothesized chance level of .2 was used due to the possibility of 5 different response sets being possible and in order for a no trend condition to be seen by any participant there was only 1 of 5 combinations that would allow that observation to be made.

This near hand being larger is expected in the static condition because the
amount of space on the retina during the afterimage is constant, with the nearer hand actually casting a larger image on the retina. In the absence of movement of the hands there is no conflicting afferent input or efferent output to suggest that any movement has taken place and the initial afterimage stands with no conflict. The only input was an initial visual afferent signal with no afferent signals and no efferent signals to conflict with the initial formation of an afterimage.

The participant's responses in the dynamic condition and the passive condition were statistically significant when compared to the static condition as far as the trend is concerned.

Table 1. Number of participants displaying a trend in their responses and the direction of the trends by condition

<table>
<thead>
<tr>
<th>Presence if a Response Trend</th>
<th>Direction of Trend</th>
</tr>
</thead>
<tbody>
<tr>
<td>Condition</td>
<td>Trend</td>
</tr>
<tr>
<td>Static</td>
<td>24</td>
</tr>
<tr>
<td>Dynamic</td>
<td>20</td>
</tr>
<tr>
<td>Passive</td>
<td>12</td>
</tr>
<tr>
<td>Resistance</td>
<td>20</td>
</tr>
</tbody>
</table>

Participants in the majority of the static conditions reported trends that were in line with expectations in that all, except two cases, of the participants reported the near hand larger. The resistance condition also reported the majority of observations
to indicate that the near hand was larger. However the difference between reports
that the near hand larger or the far hand was larger was not significant. This is
noteworthy in that Helmholtz’s (1866/1896) theory where he suggest that the mere
effort of will is sufficient to cause a resulting change in consciousness so that even in
the absence of sensory feedback an appropriate observation would occur. This is also
contrary to the out-flow models theory that an efferent copy signal would have
enough influence to cause a change in perception (Grüsser 1986). No variations of
the afferent signals were available in the resistance condition, to suggest that
movement had occurred, so it appears that any efferent copy signals from the motor
system were not strong enough to influence the outcome of the resistance condition.

Among individuals that exhibited a trend in the dynamic and passive
condition it seems that the far hand is perceived to be larger and when compared to
the static condition (control condition) both conditions are significant when tested at
the .05 level with the hypothesized chance level of performance at .5. The resistance
condition exhibited a trend for the near hand to be perceived as larger. This suggest
that the efferent signal may have an effect on the perceived size of the participants
hand, but insufficient for the effect to be statistically significant. While it was not
statistically significant it is interesting to note that the trend is reversed from the
dynamic condition as well as the passive condition. One difference in this reversal
trend is that an afferent signal from the muscles is not being sent to the brain to
suggest that the arm has moved.
Table 2. Comparison of response distributions regarding trend through use of a two tailed analysis using Fishers Exact Test of Probability.

<table>
<thead>
<tr>
<th></th>
<th>Static</th>
<th>Dynamic</th>
<th>Passive</th>
<th>Resistance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Static</td>
<td>------</td>
<td>&lt;.0001</td>
<td>.0010</td>
<td>.0121</td>
</tr>
<tr>
<td>Dynamic</td>
<td>------</td>
<td>-------</td>
<td>1.0</td>
<td>.1053</td>
</tr>
<tr>
<td>Passive</td>
<td>------</td>
<td>-------</td>
<td>-------</td>
<td>.1467</td>
</tr>
<tr>
<td>Resistance</td>
<td>------</td>
<td>-------</td>
<td>-------</td>
<td>------</td>
</tr>
</tbody>
</table>
DISCUSSION

Participants responses in the present study were presumably based upon information available to them at the time of their response. Under normal viewing conditions, this information may arise from a variety of sources including visual afference, muscle afference, motor efference, and expectancy. While all of these sources may provide the observer with useful information it is altogether unclear which of these sources are actually utilized in the formation and interpretation of the visual percept. By manipulating the informational sources available at the time of visual percept formation and interpretation, the present study has helped to clarify the interplay of these sources. This will at the same time distinguish the different cues proposed to play a role by the conflicting models of outflow theory and inflow theory.

Certainly visual afference plays a dominant role in percept formation under normal viewing conditions, however visual afference alone is unlikely to provide sufficient information for the fast and accurate interpretation of observer initiated movement (Festinger, Ono, Burnham, & Bamber, 1967). Information related to observer initiated movement, must be integrated with visual afference. In an effort to examine the potential contributor, visual afference was held constant through use of afterimages. In essence this afforded the opportunity to create disassociations between visual afference, muscular afference, motor efference, and observer expectancy.
The static condition was unique in this experiment because it was the only condition in which muscle afference, motor efference, and observer expectancy were in complete agreement with visual afference at the time of percept formation. Therefore the static condition served as a control against which all other experimental conditions were compared.

The phenomena experienced by participants in the present experiment are not instantaneous but rather take place over time, with the duration varying slightly from observer to observer. Two distinct periods that deserve attention include the moment at which the photoflash was activated, thus providing the observer with visual afference, and the time at which the observer made a decision regarding the relative sizes of the images of their hands. The latter period is important because it is assumed that if muscle afference or motor efference contribute to the observers’ percepts, the afferent and/or efferent signals are monitored during this final period. Any change in position of the hands during the interim between flash and decision may lead to discrepancies between muscle afferent, motor efferent, and visual afferent information.

Examining the events that occur in the resistance condition we find that at the time of the flash all putative cues were in agreement. However when the participant attempted to move one of their hands a discrepancy was created between motor efference and the rest of the cues. For example when the participant began the trial with their hands extended outward, muscle afference would indicate that their hands were extended outward, and motor efference would indicate that their hands were
extended. Moreover during the flash they saw their hands were extended out in front of them. However when the participants attempted to move their hand toward their face the motor efferent signal would have indicated that the hand was approaching their face. Due to the restraints the hand did not approach their face, thus the muscle afferent signal would have indicated that the hand remained in an extended position. Given this discrepancy inflow theory and outflow theory would make different predictions about the effect of this attempted movement. Outflow theory, being based on the efferent motor command, would suggest that the hands would be perceived as being at different distances and therefore the images cast by the hands would be of different sizes. In contrast inflow theory, being based upon the muscle afferent signal, would indicate that the hands were equidistant from the observer, therefore the images cast by the hands would be equal in size. This latter prediction was supported by the empirical data in that there was an almost even split between the “near” and “far” hands being judged as casting a larger image.

In the passive condition, all cues to hand position were in agreement at the time of photoflash activation. In this condition all movements of the participants’ hands were initiated and controlled by the experimenter thus relieving the participants of any need to generate a motor efferent signal. In the absence of any efferent signal, a purely outflow theory would suggest that the hands would be perceived to have remained in the locations they occupied at the time of the flash, that is, equidistant from the observer’s face. With regard to the perceived sizes of the images of the hands, outflow theory would predict that they should be perceived as congruent, thus
yielding an even split between the objectively near and far hands as being reported as larger. Since passive movement of the observers’ hands would not interfere with one’s ability to utilize muscle afferent signals, inflow theory makes a very different prediction than outflow theory in this experimental condition. Inflow theory suggests that as the hand is moved by the experimenter, the participant would receive a continual stream of signals concerning the hands’ location relative to the rest of the body. As the hands come to rest in their final locations, the signals would indicate to the observer that the two hands were at different distances from the point of observation, therefore the images associated with the two hands should be perceived as being different in size. Examination of the obtained results suggest that the images of the hands were perceived to be different in size with the far hand reported as casting a larger image than the near hand by a three-to-one margin.

While the perceived differences in image size of the two hands conform to and ultimately support the prediction of inflow theory, the actual distribution of responses may seem quite perplexing because far objects usually cast smaller images than near objects. This pattern of responses however is in line with Emmert’s law which states that the perceived size of an afterimage is directly related to the distance through which it is projected. That is, afterimages will appear to increase in size as the plane upon which they are projected increases in distance from the observer.

The fact that observers’ experiences conform to Emmert’s law is particularly advantageous for it weakens any arguments concerning observer expectancy. While it is certainly true that one’s expectation to see a particular phenomenon may augment
the likelihood of actually seeing the phenomenon, it is highly unlikely that a group of nine unrelated individuals would have formed expectancies in direct contrast to their life-long experiences. On a daily basis these individuals have experienced the images of objects decreasing in size as the objects become more distant and increasing in size as the objects get closer. The possibility that these individuals had built up expectations in exact opposition to their daily experience seems highly unlikely.

In the dynamic condition, all cues at the time of flash were in agreement with hand position. The dynamic condition is the only condition in which the participants were in complete control of the initiation and coordination of movements. In the dynamic condition the participants generated a motor efferent signal to initiate movement and presumably received a muscle afferent signal to indicate that the motion was in progress or completed. Since inflow and outflow theories both suggest that their associated signals would be sufficient to establish that the hands have come to rest at different distances from the eye, both theories predict that the images of the hands will appear different in size. The predictions of both inflow theory and outflow theory are supported by the results obtained in the dynamic condition; the images of the two hands did appear to be of different sizes. By a three-to-one margin the image of the far hand was seen as being larger than the image of the near hand. The three-to-one ratio is identical to the ratio of responses obtained in the passive condition. The two conditions differ only in the number of participants exhibiting a trend in their responses and hence categorically presented as displaying either a near larger or far larger response trend. Whereas 12 of 24 participants in the passive condition
displayed a reliable trend, 20 of 24 participants in the dynamic condition displayed a reliable trend in their responses.

Expectancy cannot play an explanatory role in the dynamic condition for the same reasons as in the passive condition. If expectancy were to play a role then the image of the near hand should have been chosen as being larger but this was not the case; in the dynamic condition the image of the far hand is clearly preferred. Participants’ responses once again conformed to Emmert’s law in the dynamic condition.

The purpose of this study was to discriminate between the contributions of efferent outflow and afferent inflow to visual perception. In order to differentiate the different levels of contribution that efference and afference have in vision several issues must be addressed. The present study seems to shed light on a number of these issues.

The first issue addresses the general nature of afterimages. Although Brindley (1959, 1963) described afterimages as purely retinal phenomena, the present study clearly suggests that they are centrally processed phenomena. This position is consistent with Gregory, Wallace and Campbell (1959) reports of qualitative changes in afterimages as a result of participants’ movements. Davies (1972a, 1973b) has shown that the duration of an afterimage is contingent upon such non-visual attributes as motor task complexity, observer initiated movements, and degree to which one’s own body is included in the afterimaged scene. Further evidence of the role of central processing was given by Hayhoe and Williams (1984), when they showed that
afterimages will disappear when they were projected to locations normally occluded by the orbit of the eye or the nose. By utilizing the Ames distorted room Dwyer (1990) has demonstrated that afterimages are influenced by distance cues and does not always adhere to Emmert’s law.

Given that a growing body of evidence seems to suggest that afterimages are centrally processed in a manner similar to “normal” visual afference, their potential usefulness in the study of “normal” visual processes is that they allow the experimenter the ability to hold visual afference constant while potential nonvisual influences upon visual perception are manipulated and observed.

Building upon the foundational assumption that the perceptual processes during an afterimage closely approximate the perceptual processes during normal vision, the present experiment has addressed the possibility that non-visual information concerning observer movement may influence the appearance of afterimages and, by extension, the appearance of the visual percept in normal vision. The present study clearly demonstrates that observer movement does induce changes in the appearance of afterimages. This position seems to have broad support in the field. For example Gregory, Wallace and Campbell (1959) have shown that movement of the body relative to the point of observation and movement of the body, including the point of observation, relative to the environment produces systematic changes in the appearance of the afterimage. Similarly, Davies (1973b) has shown that as participants’ walk down as afterimaged hallway, they experience a sense of optic flow consistent with movement through the afterimaged scene. Bross (2000),
Cowan, Dickson, and Misceo (1998), and Dickson (2000) have demonstrated that in the absence of visual afference, movement of an afterimaged hand produces changes in the afterimage that are consistent with the executed movement. A review of the literature fails to find any evidence to contradict these observations.

If motor activity is sufficient to produce qualitative changes in an afterimage, the next logical issue to address concerns the source of the information that drives these changes. The efferent motor command, if somehow monitored by the perceptual apparatus, could provide the necessary information, however, the current experimental data suggest otherwise. When a motor command was issued to move an afterimaged hand and the hands' movement was physically restrained, participants did not report any consistent change in the size of the hand that would be indicative of the efferent command's ability to alter an afterimage. Similarly, Dickson (2000) found that executed movements that were consistent with an efferent command did not yield a more robust effect than was observed with muscle afference alone. While Skavenski (1972) and Shebilske (1976) have argued strongly that muscle afference and not motor efference are utilized in determining the position of the eye in the orbit, there are some reports in the literature that are inconsistent with the findings of this study. For example, Coren (1986) has demonstrated that movements of the eyes, actual or intended, were sufficient for the prediction of errors in estimation of linear extent. Similarly, Festinger and Canon (1965) have found that the localization of a target is achieved with greater accuracy when the judgment is based upon saccadic movement rather than smooth pursuit movements. Festinger, Ono, Burnham, and
Bamber, (1967) demonstrated that active arm movement resulted in a greater change in the visual percept than passive, afference guided movements. Using curare to paralyze the eye and thus produce a static muscle afferent signal, Matin, Picout, Stevens, Edwards, Young, and MacArthur (1982) found that illusions of environmental movement were experienced following an attempted movement of the paralyzed eye. While this disagreement over the role of the motor efferent signal in visual perception will need to be addressed through further research, it should be noted that the studies supporting a role for the efferent signal focused primarily on oculomotor activity while the present study and others questioning a significant role for the efferent signal have focused on non-ocular motor activity.

If motor efference is not the major causal factor of perceived change of afterimages in the present study, then an examination of muscle afference and it's contribution to visual perception is in order. The current research indicates that passive movement of the observer's hand does lead to changes in the perceived size of the afterimaged hand. Addressing the contribution of muscle afference to visual perception, Dickson (2000) found that movement of the experimenter's hand along an observer's arm can produce changes in the size of the afterimaged hands. Similarly, Bross, (2000) found that passive movements resulting in muscle afference did give rise to size change in afterimaged hands. Inconsistencies with this point do exist in the literature. Festinger and Canon (1965) felt that oculomotor afference during smooth pursuit movements was insufficient for accurate target localization. Furthermore the work of Festinger, Ono, Burnham, and Bamber (1967) suggest that
afferent information associated with passive guidance of arm movements does not
affect the visual percept as evidenced by a lack of adaptation aftereffects. In a much
more direct test of the utility of muscle afference, Brindley and Merton (1960) found
that passive movement of the eye does not lead to a sense of eye movement but rather
to an experience of environmental movement.

Neither an afferent inflow model nor an efferent outflow model seems to
satisfactorily explain the data from the current experiment and the amassed findings
of other researchers. Perhaps applying a synthetic model, which combines the
afferent inflow model and efferent outflow model, may provide a more complete
explanation of the range of data in this area of research. The addition of a consistent
efferent signal to an accurate afferent signal seems to yield a synergistic effect,
wherein the tendency to report phenomena consistent with Emmert’s law becomes
more probable. Although this increase has not been demonstrated to be statistically
reliable, both the present study and Dickson (2000) have shown that active movement
of the hand tended to produce a greater effect than passive movement.

If, as the current study suggests, muscle afferent signals are sufficient to drive
changes in the appearance of afterimages, one might wonder why so many
participants failed to experience a clear trend across the four experimental
afterimages. This issue is best addressed through a phenomena that Davies (1973a)
described as “crumble” effects. Davies found that when several of his participants
moved their hands while viewing an afterimage of their hands, the image of the
moved hand tended to disintegrate and/or disappear altogether. Post experimental
interviews in the present study found that approximately 25% of the participants experienced some type of crumble phenomenon. Moreover, the crumble effect was almost exclusively associated with the moved hand. This poses an interesting problem in the present study because when the participants are asked to indicate whether the image of the hand to their right or left appears larger, they may be forced to choose between an unchanged image of the unmoved hand and a disintegrated, crumbled image of the moved hand. Given that the unmoved hand is the near hand in two afterimages and the far hand in the remaining two afterimages, one would expect a pattern of response that yields a categorization of no trend.

While the present line of research leaves several questions unanswered, it also seems to provide at least partial answers to a number of questions. Through this study we found that despite the traditional view of afterimages as stabilized images, afterimages are in fact centrally processed percepts that are malleable to alternate inputs. Furthermore we have found that the primary alternate input appears to be muscle afference. This afferent signal seems to be capable of being augmented by a consistent motor efferent signal, however it should be noted that when muscle afference and motor efference are in conflict, the afferent signal dominates.
REFERENCES


Physiology Optics, 17. 225-231.

Graziano, M. S. A. (1999). Where is my arm? The relative role of vision and proprioception in the neuronal representation of... Proceedings of the National Academy of the United States of America, 96, 10418-10421.


Matin, L., Picoult, E., Stevens, J. K. Edwards, M. W., Young, D., & MacArthur, R.


APPENDIX A

INFORMED CONSENT
Informed Consent

The Department of Psychology and the Institutional Review Board at Morehead State University supports the practice of protection for human subjects participating in research. Your willingness to help us is greatly appreciated.

In this study you will be asked to experience a number of afterimages and report on their general nature and appearance. You may also be asked to engage in some simple hand movements or placements during the afterimage and to answer specific questions concerning the effects that these movements or placements have upon your experience. The experiment will take approximately one hour to complete. Although I cannot tell you the exact purpose of the study at this time, I will explain what I am investigating after you have finished. You will be receiving extra credit in your psychology course for assisting me in my research, however, if you decide not to participate in this experiment, other ways will be available to earn the same amount of extra credit.

This study has been reviewed by the Institutional Review Board of Morehead State University to determine that it poses little or no risk of harm to you. If, for any reason, at any point in your participation, you wish to withdraw, you may do so. If you choose to withdraw, you will still receive any credit promised to you in exchange for your participation.

You will be assigned an arbitrary participant number to assist in data collection, therefore any information obtained from you will be kept strictly confidential. We assure you that neither your name nor participant number will be
associated in any way with any reportable results. All information collected from you will be kept in a locked cabinet. The researchers are obliged to tell you as much as you care to know about the study after your part in the study is complete.

All persons who take part in this study must be at least 18 years old and must sign an Informed Consent Form. Your signature upon this form indicates that you have been informed of your rights as a participant and you have agreed to participate on that basis.