

# Asymmetric Transfer of Task Dependent Perceptual Learning in Visual Motion Processing

Sampada Charudatta Wakde  
*Marquette University*

---

## Recommended Citation

Wakde, Sampada Charudatta, "Asymmetric Transfer of Task Dependent Perceptual Learning in Visual Motion Processing" (2011).  
*Master's Theses (2009 -)*. Paper 111.  
[http://epublications.marquette.edu/theses\\_open/111](http://epublications.marquette.edu/theses_open/111)

ASYMMETRIC TRANSFER OF TASK DEPENDENT PERCEPTUAL LEARNING  
IN VISUAL MOTION PROCESSING

by

Sampada Wakde, B.S.

A Thesis submitted to the Faculty of the Graduate School,  
Marquette University,  
in Partial Fulfillment of the Requirements for  
the Degree of Master of Science

Milwaukee, Wisconsin

August 2011

ABSTRACT  
ASYMMETRIC TRANSFER OF TASK DEPENDENT  
PERCEPTUAL LEARNING IN VISUAL MOTION  
PROCESSING

Sampada Wakde, B.S.

Marquette University, 2011

The effects of perceptual learning (PL) on the sensory representation are not fully understood, especially for higher-level visual mechanisms more directly relevant to behavior. The objective of this research is to elucidate the mechanisms that mediate task dependent learning by determining where and how task dependent learning occurs in the later stages of visual motion processing.

Eighteen subjects were trained to perform a dual-2AFC visual discrimination task in which they were required to simultaneously detect changes in the direction of moving dots (task-1) and the proportion of red dots (task-2) shown in two stimulus apertures presented in either the left or right visual field. Subjects trained on the direction discrimination task for one of two types of motion, global radial motions (expansion and contraction) presented across stimulus apertures (global task), or an equivalent (local) motion stimulus formed by rotating the direction of motion in one aperture by 180°. In task-1 subjects were required to indicate whether the directions of motion in the second stimulus interval were rotated clockwise or counter-clockwise relative to the first stimulus interval. In task-2, designed to control for the spatial allocation of attention, subjects were required to indicate which stimulus interval contained a larger proportion of red dots across stimulus apertures.

Sixteen of the eighteen subjects showed significant improvement on the trained tasks across sessions ( $p < 0.05$ ). In subjects trained with radial motions, performance improvements transferred to the radial motions presented in the untrained visual field, and the equivalent local motion stimuli and untrained circular motions presented in the trained visual field. For subjects trained with local motion stimuli, learning was restricted to the trained local motion directions and their global motion equivalents presented in the trained visual field. These results suggest that perceptual learning of global and local motions is not symmetric, differentially impacting processing across multiple stages of visual processing whose activities are correlated. This pattern of learning is not fully coherent with a reverse hierarchy theory or bottom-up model of learning, suggesting instead a mechanism whereby learning occurs at the stage of visual processing that is most discriminative for the given task.

## **ACKNOWLEDGEMENTS**

**Sampada Wakde, B.S.**

As I write this acknowledgement, I remember all the ups and downs that happened to me since I came to Milwaukee. I started as a graduate student during fall'06 in Biomedical Engineering program. Over these years, I've been fortunate to be surrounded by my colleagues, friends and family, whom I want to acknowledge here. More than anything I owe a lot to my adviser Dr. Scott Beardsley for the patience he had in me and the encouragement and support he gave me throughout my graduate life. Throughout the project with him, we collected data over many human subjects at the cost of a few friends who really hated the experiments. I thank all the subjects who participated in our 'uncomfortable but not painful' experiments.

I thank all of my colleagues in the INSL lab Jain, Megan, David, and Prajakta. I am grateful to my committee members Dr.Scheidt and Dr.Libenthal along with my adviser Dr.Beardsley to be on my committee. My Husband, Mayank, has been really supportive and encouraging throughout the process of my thesis. My dearest friend Mukta always stood besides me even in my hard times, which I won't forget for lifetime. I take this opportunity to specially thank my dear friends Tushar, Priyanka S., Chintan, Vaibhav, and Promita who were always there for me.

Finally, I want to thank my parents, father-in-law and my younger sister for the mental support, and advice and financial support to be able to complete my

thesis. I would like to dedicate this thesis to my father Mr.Charudatta M. Wakde, who has been a role model and an immense source of inspiration throughout my academic career. And also my mother-in-law, Mrs. Mrunalini Sudhakar Rege without whom this accomplishment was impossible.

# Table of Contents

|  |           |
|--|-----------|
| ACKNOWLEDGEMENTS   | i         |
| LIST OF FIGURES  | v         |
| LIST OF TABLES   | ix        |
| <b><u>CHAPTERS</u></b>                                     |           |
| <b>1 INTRODUCTION &amp; SPECIFIC AIMS</b>                  | <b>1</b>  |
| <b>2 BACKGROUND AND SIGNIFICANCE</b>                       | <b>4</b>  |
| 2.1 PERCEPTUAL LEARNING                                    | 4         |
| 2.2 VISUAL MOTION PROCESSING                               | 7         |
| 2.3 SIGNIFICANCE   | 12        |
| <b>3 EXPERIMENTAL APPARATUS AND METHODS</b>                | <b>13</b> |
| 3.1 EXPERIMENTAL APPARATUS                                 | 13        |
| 3.1.1 <i>Human Subjects</i>                                | 13        |
| 3.1.2 <i>Stimuli</i>                                       | 13        |
| 3.1.3 <i>Experimental Setup</i>                            | 15        |
| 3.1.4 <i>Eye Tracker Calibration</i>                       | 20        |
| 3.1.5 <i>Visual Motion Tasks (Global vs. Local Motion)</i> | 22        |
| 3.2 EXPERIMENTAL PARADIGM                                  | 23        |
| 3.2.1 <i>Speed discrimination training paradigm</i>        | 26        |
| 3.2.2 <i>Threshold Tracking Paradigm</i>                   | 27        |
| <b>4 RESULTS</b>   | <b>30</b> |
| <b>5 DISCUSSION</b>  | <b>43</b> |

|   |           |
|---|-----------|
| 5.1 REVERSE HIERARCHY THEORY                    | 44        |
| 5.2 BOTTOM-UP THEORY OF PERCEPTUAL LEARNING     | 47        |
| 5.3 SENSITIVITY-SPECIFICITY THEORY (SST)        | 49        |
| 5.4 ALTERNATIVE THEORIES OF PERCEPTUAL LEARNING | 52        |
| <b>6 CONCLUSION</b>                             | <b>54</b> |
| <b>7 FUTURE DIRECTIONS</b>                      | <b>55</b> |
| <b>8 BIBLIOGRAPHY</b>                           | <b>56</b> |
| <b>9 APPENDIX</b>                               | <b>65</b> |
| 9.1 APPENDIX A1                                 | 65        |
| 9.2 APPENDIX A2                                 | 66        |
| 9.3 APPENDIX A3                                 | 67        |
| 9.4 APPENDIX A4                                 | 68        |
| 9.5 APPENDIX A5                                 | 69        |
| 9.6 APPENDIX A6                                 | 70        |

## List of Figures

- FIGURE 2-1. VISUAL PROCESSING PATHWAYS. (TOP) THE VISUAL PROCESSING HIERARCHY IS SHOWN DIAGRAMMATICALLY. (BOTTOM) ANATOMICAL PROJECTIONS BETWEEN VISUAL AREAS INCLUDING THOSE ASSOCIATED WITH VISUAL MOTION PROCESSING - ROCEPRIMARY VISUAL CORTEX), V2 (PRESTRIATE CORTEX), MT (MIDDLE TEMPORAL), MST (MIDDLE SUPERIOR TEMPORAL), VIP (VENTRAL INTRAPARIETAL), AREA 7A (THIS AREA IS INVOLVED IN VISUO-MOTOR COORDINATION).....8
- FIGURE 2-2. SCHEMATIC DIAGRAM ILLUSTRATING THE FUNCTIONAL HIERARCHY OF VISUAL MOTION PROCESSING BETWEEN THE MIDDLE TEMPORAL (MT) AND MEDIAL SUPERIOR TEMPORAL (MST) AREAS. THE VISUAL MOTION PROPERTIES OF MT/MST NEURONS ARE PORTRAYED IN SEPARATE LAYERS TOGETHER WITH THEIR RELATIVE RECEPTIVE FIELD SIZES. THE ARROWS BETWEEN LAYERS SHOW THE PRIMARY DIRECTION OF INFORMATION FLOW. MT NEURONS ARE TUNED TO DIRECTIONS OF MOTION WHILE NEURONS IN MST PREFERENTIALLY RESPOND TO MORE COMPLEX PATTERNS OF MOTION SUCH AS EXPANSION AND CONTRACTION. THE DOTTED CIRCLES IN THE VISUAL FIELD INDICATE THE RELATIVE SIZES OF THE RECEPTIVE FIELDS BETWEEN NEURONS IN MT AND MST..... 11
- FIGURE 3-1. SCHEMATIC DIAGRAM OF THE MOTION MECHANISMS ASSOCIATED WITH THE GLOBAL AND LOCAL MOTION TASKS. A GLOBAL MOTION TASK WAS USED TO ENGAGE COMPLEX MOTION MECHANISMS AND QUANTIFY SUBJECTS' ABILITY TO DISCRIMINATE CHANGES IN THE DIRECTION OF RADIAL MOTION ACROSS STIMULUS APERTURES. A LOCAL MOTION TASK, WHEREIN THE DIRECTION OF MOTION IN ONE APERTURE WAS ROTATED  $180^{\circ}$  TO REMOVE THE GLOBAL MOTION PERCEPT, WAS USED TO PREFERENTIALLY ENGAGE LOCAL MOTION MECHANISMS TO QUANTIFY THE SUBJECTS' ABILITY TO DISCRIMINATE CHANGES IN THE DIRECTION OF LOCAL PLANAR MOTION.....16
- FIGURE 3-2. EXPERIMENTAL SETUP. FIXATION ON THE SCREEN WAS PRESENTED EITHER ON THE LEFT OR RIGHT SIDE OF SCREEN TO MAXIMIZE THE VISUAL DISPLAY OF THE STIMULUS AND RESTRICT THE STIMULUS TO A SINGLE VISUAL FIELD. THE HEAD AND CHIN REST WAS USED TO WAS USED TO HOLD THE SUBJECTS HEAD IN A PLACE WHILE THE EXPERIMENT WAS CONDUCTED AND THE EYE TRACKER GOGGLES WERE ON AT THE SAME TIME TO TRACK THE PUPIL MOVEMENTS OF THE EYE..... 17
- FIGURE 3-3. SCHEMATIC ILLUSTRATION OF THE STIMULUS PRESENTATION SEQUENCE. TWO 500 MS STIMULI WERE PRESENTED (S1 AND S2), WITH A 500 MS INTER-STIMULUS INTERVAL. THE DOTTED LINES ARE SHOWN FOR REFERENCE AND WERE NOT PRESENT DURING TESTING. THE GREY SQUARE AT THE INTERSECTION OF THE ILLUSORY LINES IS THE FIXATION POINT AND THE ROTATED ARROWS IN STIMULUS S2 SHOW THE DIRECTION OF DOT MOTION ROTATED BY AN ANGLE  $\Phi_p$ ..... 18



- FIGURE 3-4. ARRINGTON BINOCULAR EYE TRACKER CAMERA AND EYE IMAGE ON RIGHT WITH CORNEAL REFLECTION (GLINT). ARRINGTON BINOCULAR EYE TRACKER CAMERA (LEFT) THE TWO SMALL PROTRUSIONS NEAR THE EYES ARE THE IR-ILLUMINATORS AND CAMERAS. THE SMALL CUBE ON THE FOREHEAD BAND OF THE GOGGLES IS THE HEAD CAMERA. THE GOGGLES ALSO HAVE A TIGHTENING STRAP AT THE BACK, WHICH HELPS SUPPORT THE GOGGLES ON THE SUBJECT'S FOREHEAD. THE EYE IMAGE WITH A CORNEAL REFLECTION (GLINT) FROM ONE EYE OBTAINED BY THE IR-ILLUMINATOR AND CAMERA USED TO PERFORM THE PUPIL-GLINT LOCALIZATION IS SHOWN ON THE RIGHT. .... 20
- FIGURE 3-5. THE EYE SPACE WINDOW WITH THE ADVANCED CALIBRATION SETTINGS. EYE TRACKER CALIBRATION. CALIBRATION POINTS WERE PRESENTED AT 16 POINTS SPANNING THE DISPLAY. IN THE DEFAULT CONFIGURATION (USED HERE) THE AUTO CALIBRATION SEQUENCE PRESENTED THE CALIBRATION POINTS IN RANDOM ORDER, EACH FOR ~5 SEC.....21
- FIGURE 3-6. EXPERIMENTAL PARADIGM FOR THE GLOBAL MOTION TASK (EXP.1) AND LOCAL MOTION TASK (EXP. 2). DURING THE PRE, POST AND RET SESSIONS ALL EIGHT COMBINATIONS OF MOTION TASK (GLOBAL VS. LOCAL), VISUAL FIELD (LEFT OR RIGHT) AND MOTION DIRECTION (RADIAL VS. CIRCULAR) WERE TESTED. THE TC (TRAINED CONDITION) BLOCKS IN RED DASHED FRAME DENOTE DIFFERENT TASKS SELECTED IN TRAINING SESSIONS WHERE 'N' WAS BASED ON SUBJECTS LEARNING THRESHOLDS. SUBJECT WAS TRAINED ON DUAL TASK PARADIGM (SPEED TASK WITH DOT DISCRIMINATION AS SEEN IN SPEED DISCRIMINATION TRAINING PARADIGM) BEFORE THE MAIN EXPERIMENT TO TRAIN THE SUBJECTS ON PERFORMING THE DUAL TASK.....24
- FIGURE 3-7. EXPERIMENTAL CONDITIONS TESTED BEFORE AND AFTER TRAINING. EIGHT EXPERIMENTAL CONDITIONS WERE CONSISTED BEFORE AND AFTER TRAINING CORRESPONDING TO ALL COMBINATIONS OF MOTION TASK (GLOBAL VS. LOCAL), VISUAL FIELD (LEFT OR RIGHT) AND MOTION DIRECTION (RADIAL VS. CIRCULAR). THRESHOLDS ARE COLLECTED ON THESE CONDITIONS BEFORE TRAINING (PRE), AFTER TRAINING (POST) AND RETENTION (RET) IN THE EXPERIMENTAL PARADIGM (FIGURE 3-6).....25
- FIGURE 3-8. THE THRESHOLD TRAINING PARADIGM SESSION (~1 1/2 HOURS IN ONE DAY) IS DIAGRAMMATICALLY REPRESENTED USING THE FLOW CHART. DURING ONE SESSION OF THRESHOLD PARADIGM TRAINING THE SUBJECTS HAS TO PERFORM A STAIRCASE PARADIGM ON THE TASK TO BE TRAINED AND WE GET THE PERFORMANCE MEASURE IN TERMS OF THRESHOLD ( $T$ ) AND STANDARD DEVIATION ( $\Sigma$ ). THESE TERMS  $T$  AND  $\Sigma$  ARE USED TO FORM THREE LEVELS FOR ONE RUN IN CONSTANT STIMULUS PARADIGM. AS THE PERCENTAGE CORRECT PERFORMANCE OF THE SUBJECT FOR RUN1  $\geq 80\%$ , THEN THE LEVELS ARE REDUCED BY  $\Sigma$  FOR RUN2 AND SO ON. EVERY SESSION HAS NINE RUNS IN TOTAL AND 3 RUNS TOGETHER COMPRISE OF A BLOCK. HENCE EVERY SESSION HAS 3 BLOCKS AND THESE BLOCKS FURTHER FROM ALL THE TRAINING SESSIONS ARE COMPILED

|  |    |
|--|----|
| TOGETHER TO PLOT THE THRESHOLD CURVE FOR EVERY SUBJECT USING THE WEIBULL PSYCHOMETRIC FIT.....   | 29 |
| FIGURE 4-1. DIRECTION DISCRIMINATION THRESHOLDS AS A FUNCTION OF TRAINING BLOCK FOR SUBJECTS TRAINED ON THE GLOBAL MOTION TASK. DISCRIMINATION THRESHOLDS (79% CORRECT) ARE SHOW FOR SUBJECTS S1-S9 AS A FUNCTION OF TRAINING BLOCK. A NONLINEAR LEAST-SQUARE EXPONENTIAL FIT WAS APPLIED TO EACH SUBJECTS' PERFORMANCE (RED DASHED LINE) TO CHARACTERIZE THE TIME COURSE OF LEARNING. THE BEST-FIT PARAMETERS FOR EACH SUBJECT ARE SHOWN IN TABLE 4-1.....  | 31 |
| FIGURE 4-2. PERCENT CORRECT PERFORMANCE ON THE (TASK2) DOT DISCRIMINATION TASK AS A FUNCTION OF TRAINING BLOCK FOR SUBJECTS TRAINED ON THE (A) GLOBAL MOTION AND (B) LOCAL MOTION TASKS. PERFORMANCE IS REPORTED WITHIN EACH GROUP AS THE MEAN ACROSS SUBJECT'S $\pm$ 1 SE.....  | 36 |
| FIGURE 4-3. GROUP AVERAGED DIRECTION DISCRIMINATION THRESHOLDS ACROSS EXPERIMENTAL CONDITIONS. (A) PRE- AND POST-TRAINING PERFORMANCE AND (C) POST-TRAINING AND LEARNING RETENTION (ONE WEEK AFTER TRAINING) FOR SUBJECTS TRAINED ON THE GLOBAL MOTION TASK. (B) PRE- AND POST-TRAINING PERFORMANCE AND (D) POST-TRAINING AND LEARNING RETENTION (ONE WEEK AFTER TRAINING) FOR SUBJECTS TRAINED ON THE LOCAL MOTION TASK. PERFORMANCE IS REPORTED AS THE MEAN $\pm$ SE. THE SINGLE ASTERISK DENOTES CONDITIONS THAT WERE SIGNIFICANTLY DIFFERENT ( $P < 0.05$ ). .....   | 38 |
| FIGURE 4-4. DIAGRAMMATIC COMPARISON OF STATISTICALLY SIGNIFICANT TRAINING-INDUCED CHANGES IN DIRECTION DISCRIMINATION THRESHOLDS ACROSS EXPERIMENTAL CONDITIONS. VISUAL FIELDS WERE CLASSIFIED AS TRAINED AND UNTRAINED, BASED ON THE CONDITIONS THE SUBJECTS WERE TRAINED ON. <u>COLOR REPRESENTATION</u> : BLUE DENOTES THE TRAINED TASK AND CONDITION. ORANGE INDICATES SIGNIFICANT IMPROVEMENT IN POST (VERSUS PRE-) TRAINING THRESHOLDS ( $P < 0.05$ ). WHITE INDICATES NO SIGNIFICANT CHANGE IN THRESHOLDS BEFORE AND AFTER TRAINING. <u>CONDITION ANNOTATIONS</u> : THE TASK CONDITION ANNOTATIONS CORRESPOND TO THE TASK AND MOTION TYPE PRESENTED DURING TRAINING (GR: GLOBAL-RADIAL, GC: GLOBAL-CIRCULAR, LR: LOCAL-RADIAL, LC: LOCAL-CIRCULAR)..... | 41 |
| FIGURE 5-1. COMPARISON OF EXPERIMENTAL RESULTS WITH PREDICTIONS FROM A TASK-SPECIFIC ATTENTION DRIVEN INTERPRETATION OF REVERSE HIERARCHY THEORY (RHT). THE COLOR REPRESENTATION AND DESIGNATION OF EXPERIMENTAL CONDITIONS FOLLOWS THE CONVENTION DETAILED IN FIGURE 4-4.....   | 45 |
| FIGURE 5-2. COMPARISON OF EXPERIMENTAL RESULTS WITH PREDICTIONS FROM A TASK-DIFFICULTY DRIVEN INTERPRETATION OF REVERSE HIERARCHY THEORY (RHT). THE COLOR REPRESENTATION AND DESIGNATION OF EXPERIMENTAL CONDITIONS FOLLOWS THE CONVENTION DETAILED IN FIGURE 4-4.....   | 47 |

|  |    |
|--|----|
| FIGURE 5-3. COMPARISON OF EXPERIMENTAL RESULTS WITH PREDICTIONS FROM A BOTTOM-UP THEORY OF PERCEPTUAL LEARNING. THE COLOR REPRESENTATION AND DESIGNATION OF EXPERIMENTAL CONDITIONS FOLLOWS THE CONVENTION DETAILED IN FIGURE 4-4.....   | 49 |
| FIGURE 5-4. COMPARISON OF EXPERIMENTAL RESULTS WITH PREDICTIONS FROM A SENSITIVITY-SPECIFICITY THEORY OF PERCEPTUAL LEARNING. THE COLOR REPRESENTATION AND DESIGNATION OF EXPERIMENTAL CONDITIONS FOLLOWS THE CONVENTION DETAILED IN FIGURE 4-4.....                                     | 51 |
| FIGURE 5-5. COMPARISON OF EXPERIMENTAL RESULTS WITH PREDICTIONS FROM A COMBINATION OF SENSITIVITY-SPECIFICITY THEORY AND BOTTOM-UP THEORY OF PERCEPTUAL LEARNING. THE COLOR REPRESENTATION AND DESIGNATION OF EXPERIMENTAL CONDITIONS FOLLOWS THE CONVENTION DETAILED IN FIGURE 4-4..... | 52 |

## List of Tables

- TABLE 4-1. PARAMETERS FOR BEST FIT EXPONENTIAL TO SUBJECTS' DISCRIMINATION THRESHOLD WITH TRAINING ON THE GLOBAL MOTION TASK. LEAST SQUARES ESTIMATES OF SUBJECTS' PRE-TRAINING THRESHOLD ( $F_{PRE}$ ),  $B= 1/TIME$  CONSTANT ( $T$ ), AND POST-TRAINING THRESHOLDS ( $F_{POST}$ ) ARE SHOWN TOGETHER WITH THEIR 95% CONFIDENCE INTERVAL (IN BRACKETS) FOR EACH SUBJECT. THE NEGATIVE TIME CONSTANT OBTAINED FOR S2 INDICATES THE SUBJECT WAS A NONLEARNER (HIGHLIGHTED IN GRAY). ..... 33
- TABLE 4-2. PARAMETERS FOR BEST FIT EXPONENTIAL TO SUBJECTS' DISCRIMINATION THRESHOLD WITH TRAINING ON THE LOCAL MOTION TASK. LEAST SQUARES ESTIMATES OF SUBJECTS' PRE-TRAINING THRESHOLD ( $F_{PRE}$ ),  $B= 1/TIME$  CONSTANT ( $T$ ), AND POST-TRAINING THRESHOLDS ( $F_{POST}$ ) ARE SHOWN TOGETHER WITH THEIR 95% CONFIDENCE INTERVAL (IN BRACKETS) FOR EACH SUBJECT. THE NEGATIVE TIME CONSTANT OBTAINED WITH S11 INDICATES THE SUBJECT WAS A NONLEARNER (HIGHLIGHTED IN GRAY). ..... 34
- TABLE 4-3. GROUP ANALYSES OF PRE- VERSUS POST-TRAINING DIRECTION DISCRIMINATION THRESHOLDS ACROSS EXPERIMENTAL CONDITIONS AS SHOWN IN TABLE ON LEFT FOR SUBJECTS TRAINED WITH (A) GLOBAL RADIAL MOTIONS AND (B) LOCAL RADIAL MOTIONS. DIFFERENCE IN PRE VERSUS POST-TRAINING THRESHOLDS WERE EVALUATED ACROSS SUBJECTS USING PAIRED T-TESTS WITH SEVEN DEGREES OF FREEDOM. TEST CONDITIONS HIGHLIGHTED IN GREY SHOWED STATISTICALLY SIGNIFICANT DECREASES IN DISCRIMINATION THRESHOLDS FOLLOWING TRAINING. 40

## 1 INTRODUCTION & SPECIFIC AIMS

Previous research has shown that perceptual abilities in adults can be developed through practice or experience (Ahissar and Hochstein, 1997; Doshier and Lu, Z.L.1998; Vidyasagar and Stuart, 1993; Gilbert et. al; 2001; Snowden and Milne, 1996; Bex and Mehta, 1998; Pleger, 2003). The ability to improve ones capability or skills with practice to detect changes in the features that define a sensory stimulus is referred to as perceptual learning (Gilbert et. al; 2001). This property, assumed to reflect plasticity at different levels of sensory processing, has been shown to occur across a wide range of sensory attributes (Doshier and Lu, Z.L., 1998; Ahissar, M. and Hochstein, S., 1997). In the visual system, hyper-acuity (Poggio et al., 1994; Kapadia et al., 1994; Fahle and Morgan, 1996), orientation discrimination (Shiu and Pashler, 1992; Vogels, R., 2010), direction discrimination (Ball and Sekuler, 1982, 1987), and object segregation using textural cues (Karni and Sagi, 1991, 1993) can all be improved with practice. There are two types of perceptual learning, task dependent (or task relevant) and task independent (or task irrelevant). In task dependent learning subject attends to the stimulus features, while in task independent learning subject does not attend to the stimulus features.

Though perceptual learning for complex visual motion processing has been widely reported (Gilbert et. al; 2001), it still remains uncertain how the underlying mechanisms determine where in the sensory system learning is suppose to occur. At which stage of information processing does perceptual

learning occur? Is there a hierarchy to the perceptual learning mechanism? The extra-striate visual cortex areas suitable for analysis of perceptual learning hierarchy in visual motion are MT (middle temporal) and MST (middle superior temporal).

Reverse Hierarchy Theory (RHT) suggests that task-dependent learning is a top-down guided process, which starts at later stages of sensory visual processing, and when these are not sufficient, progresses backwards to initial stages of processing, which have a better signal-to-noise ratio (Ahissar, M. and Hochstein, S. 1997a, 1997b, 1999, 2004). In task dependent learning, attention is focused on the stimulus to be learnt. Alternatively learning can occur from the bottom-up when the stimulus feature falls outside the focus of attention. Watanabe and colleagues have referred to this form of plasticity as task irrelevant learning (Watanabe et. al., 2002; Seitz and Watanabe 2005). A recent study by Nishina, Kawato and Watanabe suggests that in the visual motion system learning of motion patterns associated with self-motion is based on changes in local rather than global motion processing (Nishina, S., Kawato, M., and Watanabe, T. 2009).

This research seeks to further characterize the mechanisms that mediate task-dependent learning by identifying the specific stages of visual processing at which task dependent learning occurs. We propose two coupled experimental studies designed to identify the visual motion mechanisms modulated during training by contrasting psychophysical performance in tasks designed to dissociate local motion (orthogonal motion, in this particular motion the neurons

are tuned to the planar motions) direction mechanisms from the global motion (expansion, contraction, radial and circular etc., in this particular motion the neurons are tuned to complex motions) pattern percept.

**SPECIFIC AIM 1:** *Identify the stage(s) within the visual motion processing hierarchy at which task dependent learning for global and local motions occur.*

We compare psychophysical performance in two visual motion tasks designed to determine the stage of visual processing at which learning occurs - at the level of motion direction mechanisms that operate within an aperture versus complex motion mechanisms that operate across apertures. The disparity in the degree of motion direction and complex motion mechanisms extending into the ipsilateral hemi-field, in combination with the increase in spatial scale observed across successive stages of visual motion processing is used to identify where in the visual processing hierarchy learning occurs.

**SPECIFIC AIM 2:** *To characterize the mechanisms that mediate task dependent perceptual learning across multiple stages of visual processing. The patterns of task-specific improvement in visual motion discrimination between visual hemi-fields and across task conditions will be tested against two prominent theories of perceptual learning (Ahissar, M. and Hochstein, S. 1997a, 1997b, 1999, 2004; Nishina, S.; Kawato, M. and Watanabe, T., 2009), to identify the mechanisms that mediate task-specific improvements in visual motion processing.*

## 2 BACKGROUND AND SIGNIFICANCE

### 2.1 Perceptual Learning

Enhancement in perceptual skills and behavior with practice or experience to sensory stimuli is referred to as perceptual learning. The enhancement of performance with exposure and/or training is fundamental to our ability to adapt to changes in the environment and the ease with which our perception adapts to task-relevant changes in the environment illustrates that learning is a fundamental part of the normal perception.

Perceptual learning displays an important relationship with the practiced stimulus as the transfer of learning has been shown to involve functional and structural changes to the sensory cortex (Recanzone et. al, 1993; Fahle, Edelman and Poggio, 1994; Gilbert et. al., 2001; Schwartz et. al., 2002; Pleger et. al, 2003; Vogels, 2009). Training-based improvements in discrimination for visual features, such as direction discrimination (Ball and Sekuler, 1982, 1987, orientation (Shiu and Pashler, 1992; Vogels, R., 2010) and spatial frequency are typically task-specific and have been shown to be spatially limited to a certain area in the visual field, suggesting plasticity within visual (or more generally sensory) processing areas of the brain - a hallmark of perceptual learning.

The dynamics of learning can be difficult to evaluate since the measured parameter, performance, can be affected by a variety of factors. Learning, attention, training, and memory can improve performance while cortical



impairment, lack of attention and fatigue, can adversely affect performance (Schnupp and Kacelnik, 2002; Dawson and Reid, 1997).

Physiological studies have shown training related improvements in the responses of individual neurons (Recanzone et al. 1992, 1993; Ghose, 2002; Yang and Maunsell, 2004). Functional imaging studies suggest similar task-dependent changes in the representation of sensory information in the human brain (Schwartz et al., 2002; Pleger et. al, 2003; Logothetis, 2002; Logothetis et. al, 2002) across a wide variety of areas and sensory stimuli including the cortical representation and training induced changes in activity in somatosensory cortex in response to tactile coactivation of skin (Pleger et al., 2003).

In a series of studies Ahissar and Hochstein (Ahissar, M. and Hochstein, S. 1997a, 1997b, 1999, 2004) showed that that task-dependent learning in a visual pop-out task is a top-down guided process; beginning first at later stages of visual processing, and when these do not suffice, progressing backwards through the processing hierarchy to earlier stages of processing, which have a better signal-to-noise ratio. Based on these results they proposed a learning mechanism wherein easy task conditions are learned at later stages of sensory processing, where receptive fields generalize across position and orientation. As task difficulty increases, perceptual learning systematically shifts toward earlier stages of processing where receptive fields are more specific to both retinal position and orientation (Ahissar, M. and Hochstein, S. 2004).

Attention in particular has been shown to play an important role in perceptual learning (Goldstone, 1998; Karni and Sagi, 1993). Learning effects are typically limited to the attended, task-relevant, features and are typically absent or very limited for task-irrelevant and unattended features. In such cases, attention provides a selection mechanism, restricting learning to those pieces of information considered to be of importance. Watanabe and colleagues have shown that 'task irrelevant' learning can occur in the absence of focused attention to the learned feature (Watanabe et. al, 2002; Seitz and Watanabe, 2005). However, task-irrelevant learning was only found for stimulus attributes (e.g., motion direction) that were correlated temporally with the task (Seitz and Watanabe, 2005). Hence the study by (Watanabe et. al, 2002) also shows improved sensitivity to local motion directions and also showed that task irrelevant motion was processed at lower levels in visual system, showing bottom-up mechanisms are active during task-irrelevant learning.

A study by Watanabe and colleagues indicates that perceptual (task dependent) learning of global pattern motion occurs on the basis of local motion processing (Nishina, S., Kawato, M., and Watanabe, T. 2009). The study suggests that perceptual learning of motion at least according to their experimental settings is highly likely to be based on changes related to local motion rather than global motion, although the task was to detect global motion.

## 2.2 Visual Motion Processing

The visual motion system is a fundamental part of our actions and perception of the environment and perceptual learning has been demonstrated across a variety of visual motion attributes (Ball, K., & Sekuler, R. 1982, 1987; Seitz, A. and Watanabe T. 2003; Sundareshwaran and Vaina, 1995; Wakde and Beardsley, 2009; Liu and Weinshall, 2000). Coupled with the hierarchical organization of the visual motion system (Van Essen and Maunsell, 1983; Van Essen and Gallant, 1994), perceptual learning of visual motion processing provides a well-characterized model system within which to determine where learning occurs. Thus, this research focuses on perceptual learning in the visual motion system as a convenient sensory sub-system within which to more fully characterize the mechanisms that mediate task-dependent learning.

The anatomical and physiological pathways that mediate visual motion processing have been characterized in considerable detail (Maunsell and Van Essen, 1983; Deyoe and Van Essen, 1988; Andersen, R.A. 1997; Felleman and Van Essen, 1991), and are shown in Figure 2-1. The visual scene is encoded on the retina and subsequently transmitted to primary visual cortex (V1) via the optic nerve and lateral geniculate nucleus (LGN).



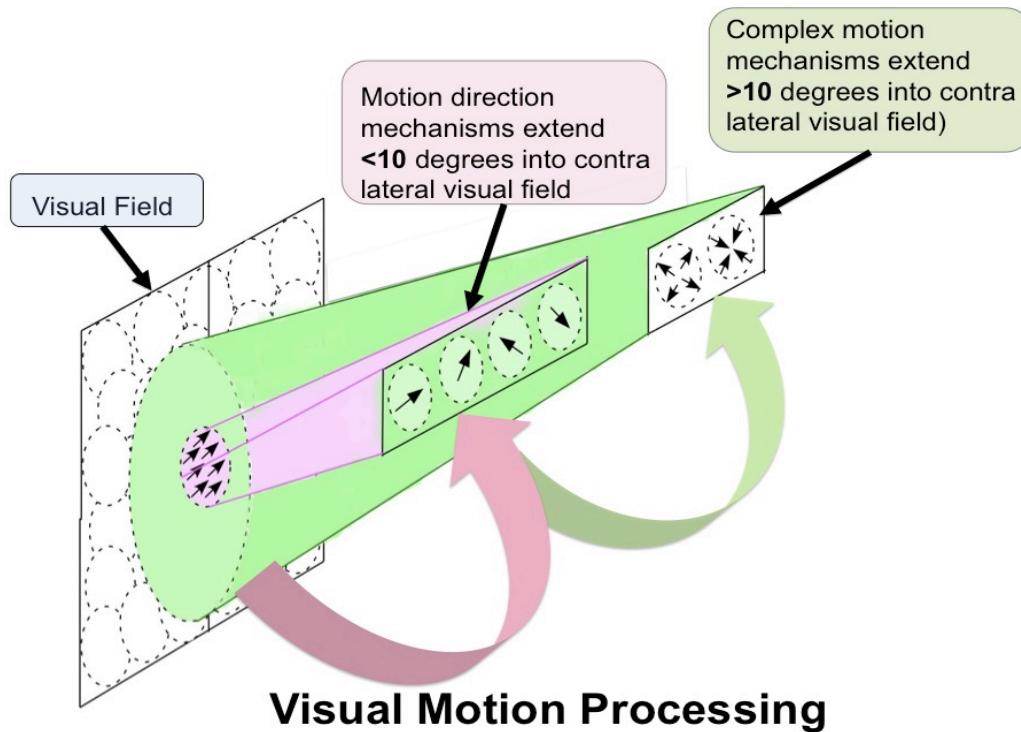
Cells in V1 encode a wide range of basic visual attributes including, luminance, contrast, disparity, and spatiotemporal frequency, which are combined at successive stages of visual processing (including V2, V3, etc.) to represent the complex visual features that together characterize the visual scene. The analysis of visual stimuli that begins in V1 and V2 continues through two major visual processing streams. One, the ventral pathway, extends to the temporal lobe and is associated with the representation of objects. The second, the dorsal pathway, extends to the parietal lobe and is associated with the processing of motion and spatial location.

The ability to perceive motion and moving objects is a critical visual sub-modality that relies on changes in luminance, color, texture, and disparity over time to identify and segment motion within the visual field. Each region in visual cortex is characterized by neurons whose receptive fields increase across successive stages of processing and whose encoded visual motion attributes become increasingly complex.

Motion information in V1 is represented by spatiotemporal frequencies over small regions of the visual field ( $\sim 1^\circ$ ). Neurons in middle temporal cortex (MT), provide the earliest representation of motion direction which is combined across subsequent parietal areas including the medial superior temporal area (MST), ventral intraparietal area (VIP), and superior temporal polysensory area (STP) to represent more complex forms of motion of progressively larger regions of the visual field (Maunsell and Van Essen, 1983; Deyoe and Van Essen, 1988; Andersen, 1997), (Figure 2-1). Functionally, these regions are largely in

agreement between monkey neurophysiology and human fMRI studies (Vanduffel et. al., 2001).

Visual motion processing between areas MT and MST has a hierarchical structure such that neurons in MT are selective to the speed and direction of translation (local) motion, while neurons in MST are selective to more complex patterns of motion, including radial, circular and spiral (global) motion (Saito et. al., 1986; Meese and Harris, 2001). Neurons in MST, exhibit preferred responses to radial, rotational and translational motions formed by spatially integrating local motions across the visual field to obtain a global motion percept (Clifford et. al., 1999; Morrone et. al., 1995; Beardsley and Vaina, 2005; Burr et. al., 1998; Snowden and Milne et. al., 1996; Meese et. al., 2001).



**Figure 2-2.** Schematic diagram illustrating the functional hierarchy of visual motion processing between the middle temporal (MT) and medial superior temporal (MST) areas. The visual motion properties of MT/MST neurons are portrayed in separate layers together with their relative receptive field sizes. The arrows between layers show the primary direction of information flow. MT neurons are tuned to directions of motion while neurons in MST preferentially respond to more complex patterns of motion such as expansion and contraction. The dotted circles in the visual field indicate the relative sizes of the receptive fields between neurons in MT and MST.

In MT, neurons are tuned for motion direction, have receptive fields that span ( $\sim 10^\circ$ ) and are confined largely to the contra-lateral visual field; extending less than  $10^\circ$  into the ipsilateral visual field. Neurons in MST have larger receptive fields ( $\sim 61^\circ$ ) that extend more than  $10^\circ$  into the ipsilateral visual field (Duffy and Wurtz, 1991a; Duffy and Wurtz, 1991b). Consistent with the known anatomy (Maunsell and Essen, 1983; Ungerleider and Desimone, 1986), MST motion selectivity assumes input from a range of MT cells (Bex et. al., 1998)

(Figure 2-2). Tanaka and Saito proposed that motion pattern tuning in MST neurons results from the combined inputs of MT cells whose directional tuning and receptive fields coincide with the directions of motion that form the MST neurons preferred motion (Tanaka and Saito, 1989).

### **2.3 Significance**

This study seeks to characterize the mechanisms that mediate perceptual learning by determining how learning progresses through particular stages of sensory processing. In the near term, the techniques developed here are expected to provide insights into the mechanisms that mediate task-dependent learning. Over the long term, improved understanding of how learning occurs and the extent to which the sensory representation is modulated by training could impact neurorehabilitation facilitating development of more effective rehabilitation strategies in patients suffering from stroke or neurodegenerative diseases in areas such as virtual reality (Marians et. al., 2006) and robot aided sensorimotor rehabilitation (Volpe et. al. 2001). Understanding how the brain dynamically adapts to changes in the environment (including the percept of self) could impact the design of adaptive closed-loop prosthetic systems, e.g., neuroprosthetics, visual neuroprosthetics (Piedade, 2005), and cochlear implants (Rouger et. al, 2007), by providing insight into the physiological adaptive processes that operate with (or against) man-made adaptive controllers.



### **3 EXPERIMENTAL APPARATUS AND METHODS**

#### **3.1 Experimental Apparatus**

##### **3.1.1 Human Subjects**

A total of 18 subjects (7 females and 11 Males; age range: 23.83 years with SEM of  $\pm 2.81$ ) with normal or corrected to normal vision participated in the experiment. Prior to participation in the study written informed consent was obtained from all subjects in accordance with Institutional Review Board at Marquette University. During their participation in the study, the pattern of subjects' sleeping habits, recorded via questionnaire, was taken into consideration when setting up training and test sessions to maximize attention to the tasks. Throughout the study, subjects were trained and tested at the same time of day to control for diurnal (active during daytime) effects on attention (Babkoff, H. and Zukerman, G. et al.; 2005). The quality and amount of sleep was evaluated using a short self-assessment questionnaire (Pittsburg sleep quality index (PSQI)) prior to each test/training session.

##### **3.1.2 Stimuli**

Visual stimuli were generated in Matlab© 2007b, using Psychtoolbox v.3 for stimulus presentation and Bravitoolbox v.2008.9.25 for experimental design, and presented on a calibrated NEC Accusync 120 CRT display with a resolution of 1024 x 768 pixels. During testing subjects fixated on a grey square with a pen

width of 4 minutes of visual angle and luminance of  $59.98 \text{ Cd/m}^2$ . The stimulus was presented on a grey background with luminance of  $20.12 \text{ Cd/m}^2$ , as shown in Figure 3-2. The fixation square defined the center of the stimulus with respect to the subjects' visual field, such that stimuli were presented either in the left or right visual field.

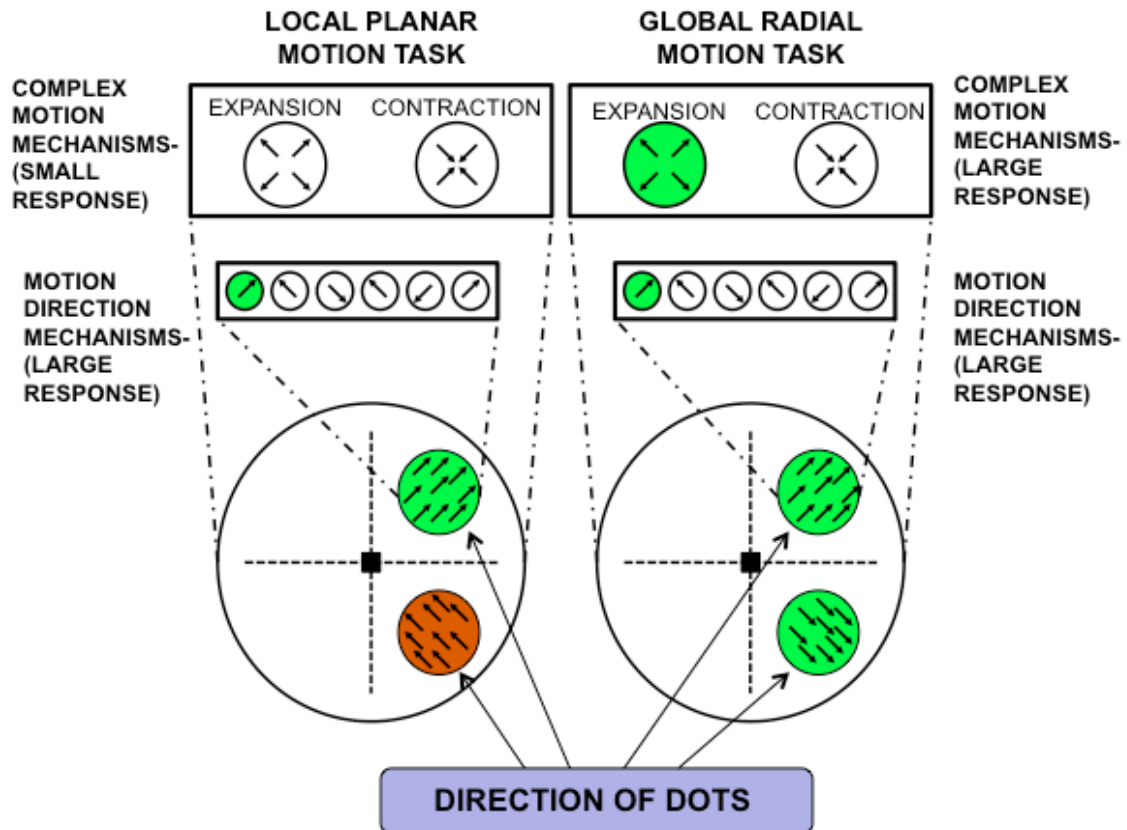
Stimuli consisted of random dot kinematograms (RDK's) presented in two circular apertures,  $8^\circ$  in diameter, located in either the left or right visual field. The stimulus apertures, which were illusory, were presented  $14^\circ$  to the left or right of the vertical midline through the fixation mark presented on the display. For stimuli presented in the right visual field, the stimulus apertures were located at  $35^\circ$  and  $325^\circ$ , relative to the horizontal midline through fixation, at an eccentricity of  $17.17^\circ$ . For stimuli presented in the left visual field the apertures were located at  $145^\circ$  and  $215^\circ$  relative to the horizontal midline.

Dots were randomly positioned in each aperture with a density of 2 dots/degree<sup>2</sup>. At stimulus onset, the dots moved for 500 ms with a constant speed of 4 deg/sec in directions consistent with an expanding or contracting motion or local planar motion (See Figure 3-3). During testing, expansion and contraction stimuli were counterbalanced across trials to minimize adaptation to a single type of motion, e.g., expansion. A proportion of the dots in each aperture were colored red ( $87.31 \text{ Cd/m}^2$ ) and the remaining dots were grey ( $79.92 \text{ Cd/m}^2$ ), as part of a dot density discrimination task (see Section Experimental Paradigm). When dots exceeded their lifetime or moved beyond the stimulus boundaries,

they are assigned new positions and trajectories consistent with the specified motion (Clifford, C., Beardsley, S.A. and Vaina, L.M; 1999).

### **3.1.3 Experimental Setup**

In the experiments outlined below we use perceptual learning in a dual-task paradigm to identify the visual motion mechanisms modulated during training by contrasting psychophysical performance in tasks designed to dissociate local motion direction mechanisms from the global motion pattern percept. Subjects participated in two perceptual tasks used to determine the cortical level where perceptual learning occurs. A “Global Motion Task” was used to quantify subjects’ ability to discriminate changes in the direction of radial motion (motion of dots away from or towards the center of the display) across stimulus apertures (Figure 3-1). A “Local Motion Task” was used to quantify subjects’ ability to discriminate changes in the direction of local planar motion within stimulus apertures (Figure 3-1). Task dependent learning on the visual motion tasks was examined using a threshold tracking paradigm, in which pre-session threshold estimates and within-session adjustment criteria were used to maintain comparable levels of task difficulty across training sessions (See Section Threshold Tracking Paradigm).



**Figure 3-1.** Schematic diagram of the motion mechanisms associated with the global and local motion tasks. A Global Motion Task was used to engage complex motion mechanisms and quantify subjects' ability to discriminate changes in the direction of radial motion across stimulus apertures. A Local Motion Task, wherein the direction of motion in one aperture was rotated  $180^\circ$  to remove the global motion percept, was used to preferentially engage local motion mechanisms to quantify the subjects' ability to discriminate changes in the direction of local planar motion.

Prior to the experiment subjects were fitted with an Arrington Research Systems, Binocular Eye Frame Mounted Scene Camera System (resolution =  $0.3^\circ$ ), to track eye movements during testing. During the experiment subjects were comfortably seated in front of a 40 x 30 cm computer display (NEC Accusync 120 CRT display), at a distance of 60 cm such that their line of sight was perpendicular to the display. A custom-made head and chin rest mounted on

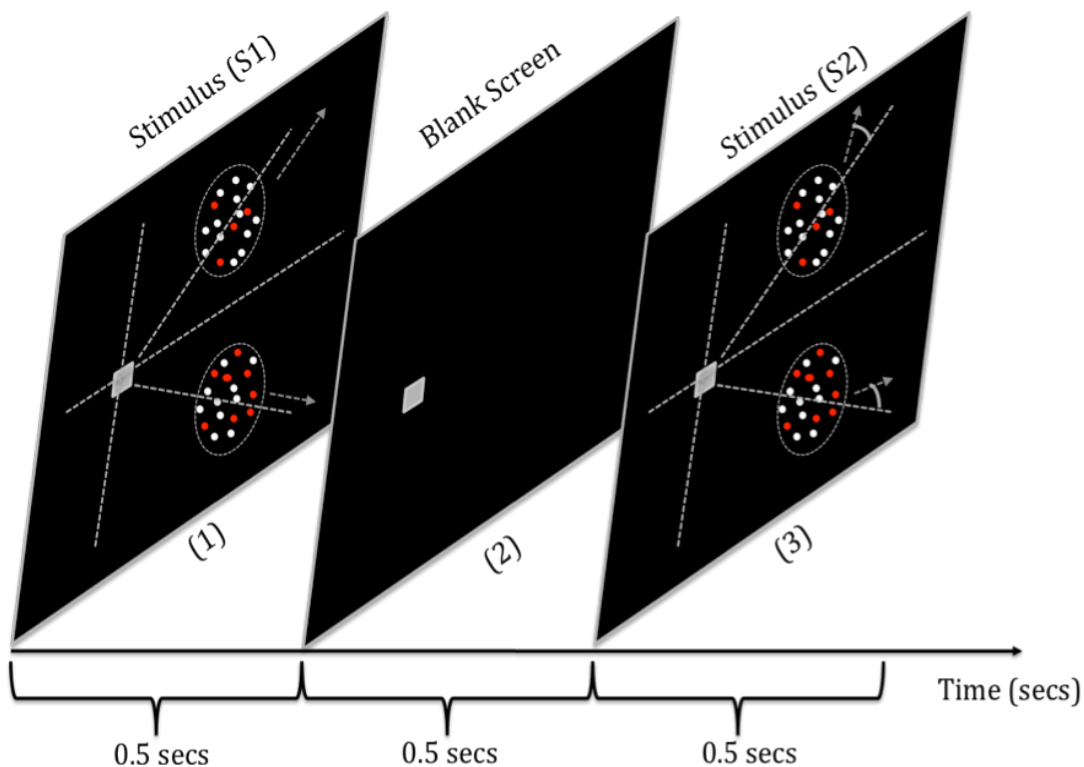
a small table placed in front of the subject was used to reduce head motion and maintain a fixed distance from the screen. All experiments were performed in a quiet darkened room.



**Figure 3-2.** Experimental Setup. Fixation on the screen was presented either on the left or right side of screen to maximize the visual display of the stimulus and restrict the stimulus to a single visual field. The head and chin rest was used to hold the subjects head in a place while the experiment was conducted and the Eye tracker goggles were on at the same time to track the pupil movements of the eye.

During testing, subjects fixated at a pre-defined point (fixation) on the display while being presented with sequences of visual stimuli (Figure 3-2). Following each stimulus presentation subjects responded to changes in the visual properties of the stimuli by pressing a pre-defined key on a computer keypad. Subject responses were recorded via key press by the testing computer and stored for offline analysis. A second computer continuously monitored eye movements to ensure that subjects maintained proper fixation during the task. If

the subject's eye position deviated more than  $2^\circ$  from the fixation mark, the stimulus presentation was aborted until subjects resumed fixation. When a trial was aborted, a new trial containing the same stimulus was inserted at the end of the test sequence.



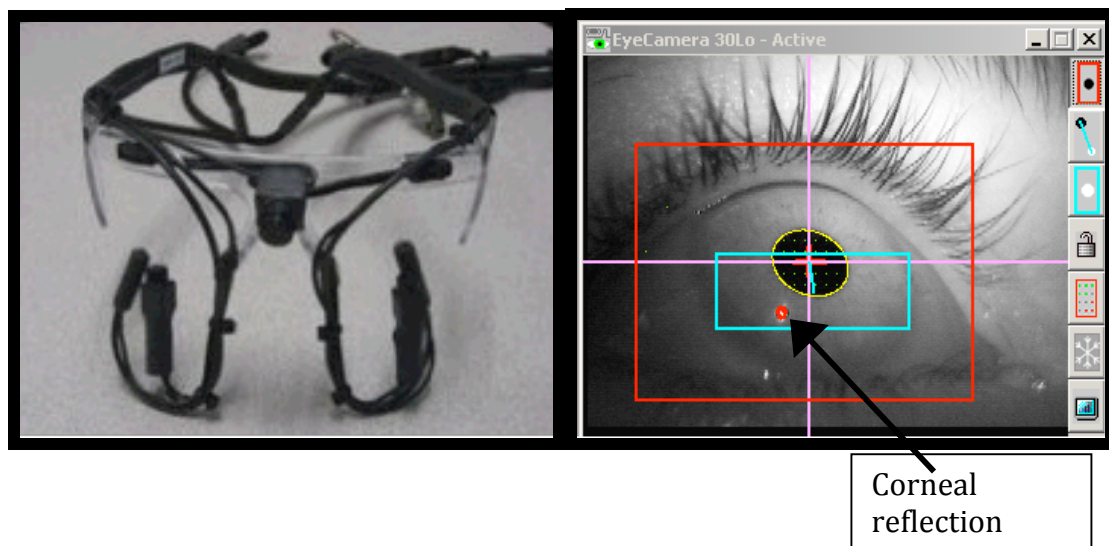
**Figure 3-3.** Schematic illustration of the stimulus presentation sequence. Two 500 ms stimuli were presented (S1 and S2), with a 500 ms inter-stimulus interval. The dotted lines are shown for reference and were not present during testing. The grey square at the intersection of the illusory lines is the fixation point and the rotated arrows in stimulus S2 show the direction of dot motion rotated by an angle  $\Phi_p$ .

During each trial, dots in both apertures move radially with respect to the fixation in one of the two stimulus intervals (Figure 3-3). In the other stimulus interval the direction of dot motion was perturbed coherently by an angle  $\pm\Phi_p$  with respect to the radially oriented motion. Following each paired stimulus presentation; subjects were required to provide two responses via key press for the dual task. The subjects' tasks were (1) to indicate whether the motion in the second stimulus was rotated clockwise (CW) or counter-clockwise (CCW) relative to the first stimulus (2) and to indicate which stimulus interval contained a larger proportion of red dots across both stimuli. The keys used to indicate subjects' perceptual judgments are shown in APPENDIX A4. Subjects' response times were recorded relative to the beginning of the second stimulus interval.

### **3.1.3.1 Monitoring eye movements**

An Arrington Research Systems BS007 Binocular Eye Frame Mounted Scene Camera System was used to monitor eye movements as subjects performed the task (Figure 3-4). The Eye tracker was interfaced with a Windows XP platform of PC through the View-Point Eye Tracker® software. Eye position was measured via pupil deflection sampled at 60 Hz. Following an initial calibration, the eye tracking software automatically recorded eye position and eye velocity on the display. The values of eye position were then streamed to the computer running the visual tasks to verify eye position in real time.

The eye tracker used a Glint pupil vector method to locate the pupil. This approach is robust to x-axis or y-axis movements (in the plane of the subject's head), but is more sensitive to the movement of head away from the camera. Hence we used a head-fixed calibration technique and physically strapped the subject's head to the head and chin rest.



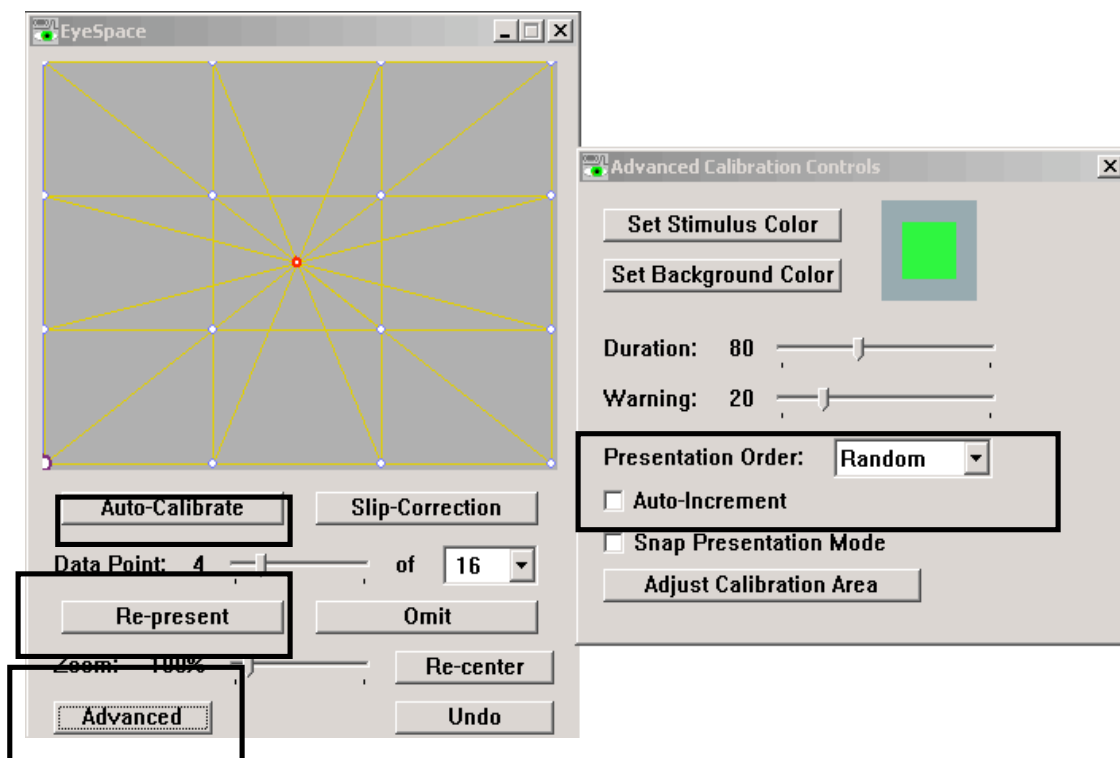
**Figure 3-4.** Arrington binocular eye tracker camera and eye image with corneal reflection (glint). Arrington binocular eye tracker camera (left) The two small protrusions near the eyes are the IR-illuminators and cameras. The small cube on the forehead band of the goggles is the head camera. The goggles also have a tightening strap at the back, which helps support the goggles on the subject's forehead. The eye image with a corneal reflection (glint) from one eye obtained by the IR-illuminator and camera used to perform the pupil-glint localization is shown on the right.

### 3.1.4 Eye Tracker Calibration

At the beginning of each test session, the eye tracker was calibrated using the Glint-Pupil Vector method to calculate the pupil position. The calibration



region encompassed the visual display and was normalized from (0.00,0.00) to (1.00,1.00). Calibration was performed by having subjects make saccades to a sequence of 16 targets arrayed in a circle around the screen center (Figure 3-5). During the calibration sequence, subjects fixated on a central square. When a target was presented subjects were instructed to shift their gaze to the target and maintain fixation on the target for a period of 5 sec. For each target location the pupil-center/corneal-reflection relationship was recorded and used together with the target location in the normalized display space to map eye position to (x, y) coordinates on the screen.



**Figure 3-5.** The Eye Space Window with the Advanced Calibration settings. Eye tracker calibration. Calibration points were presented at 16 points spanning the display. In the default configuration (used here) the Auto calibration sequence presented the calibration points in random order, each for ~5 sec.

### 3.1.5 Visual Motion Tasks (Global vs. Local Motion)

During the experiment, subjects performed a dual-task paradigm to determine the cortical level where perceptual learning occurs. The subject's consisted of a either a Global or Local motion task (Figure 3-6; task-1) in which they were required to indicate whether the motion in the second stimulus interval was rotated clockwise (CW) or counter-clockwise (CCW) relative to the first stimulus interval. In task-s, subjects were required to indicate which stimulus interval contained a larger proportion of red dots across both stimuli. The time course of the events during the 2-TAFC task for the Global and Local motion tasks is shown in Figure 3-3.

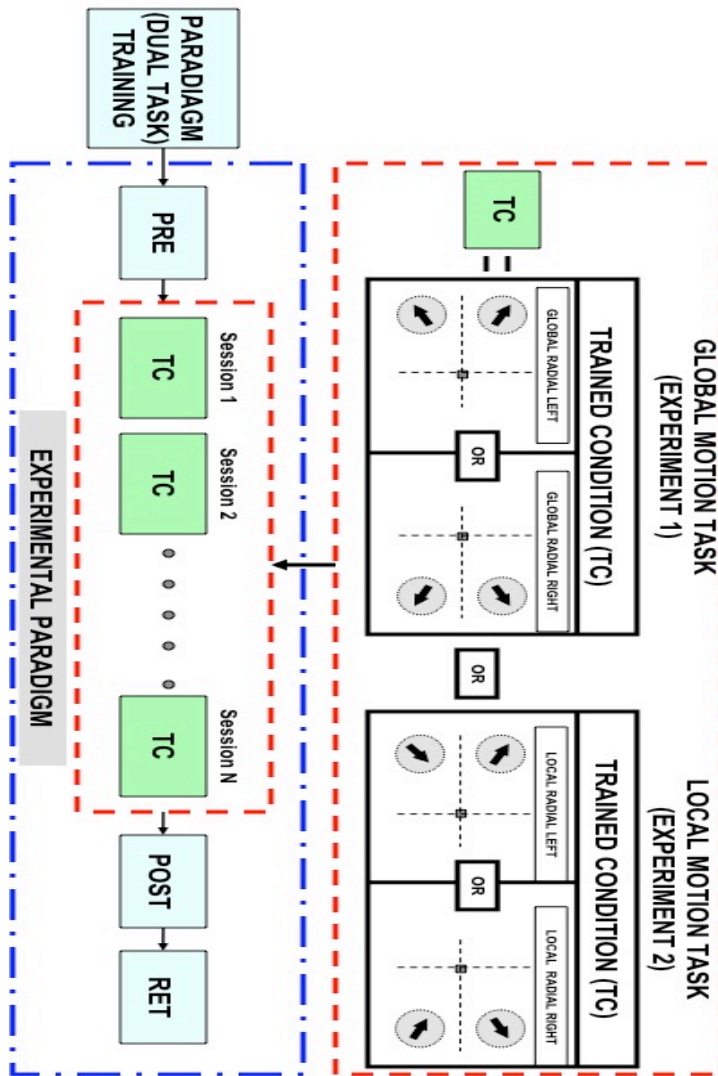
The **Global Motion Task (Experiment 1)** was a 2-TAFC (Two temporal alternative forced choice) task which, quantified subjects' ability to discriminate changes in the direction of radial motion (Figure 3-1) along with the dot discrimination task. Within each aperture, the dots moved in a constant direction either radial motion or circular motion to a line connecting the fixation mark and stimulus aperture. During the task, subjects were presented with pairs of stimuli and required to discriminate changes in the direction of the radial motion or circular motion presented across stimulus apertures. Within each trial, the direction of dot motion in the test stimulus S2 was rotated CW or CCW by an angle  $\Phi_p$ , relative to a comparison stimulus S1 (Figure 3-1).

The **Local Motion Task (Experiment 2)** was also a 2-TAFC (Two temporal alternative forced choice) task which, quantified subjects' ability to discriminate changes in direction of local planar motion (Figure 3-1) along with the dot discrimination task. The stimulus was identical to Exp (1) with the exception that the direction of motion in one aperture was rotated  $180^\circ$ , to remove the global motion percept (e.g. expansion-contraction). The resulting dot motion was inconsistent with a simple radial motion, while maintaining the same local directions of motion across trials. During the task subjects were presented with test and comparison stimuli and required to discriminate changes in the direction of the local planar motion across stimulus apertures. The CW/CCW change in the direction of dot motion, by  $\Phi_p$ , was applied within each aperture in the same way as the Global Motion Task (Experiment 1).

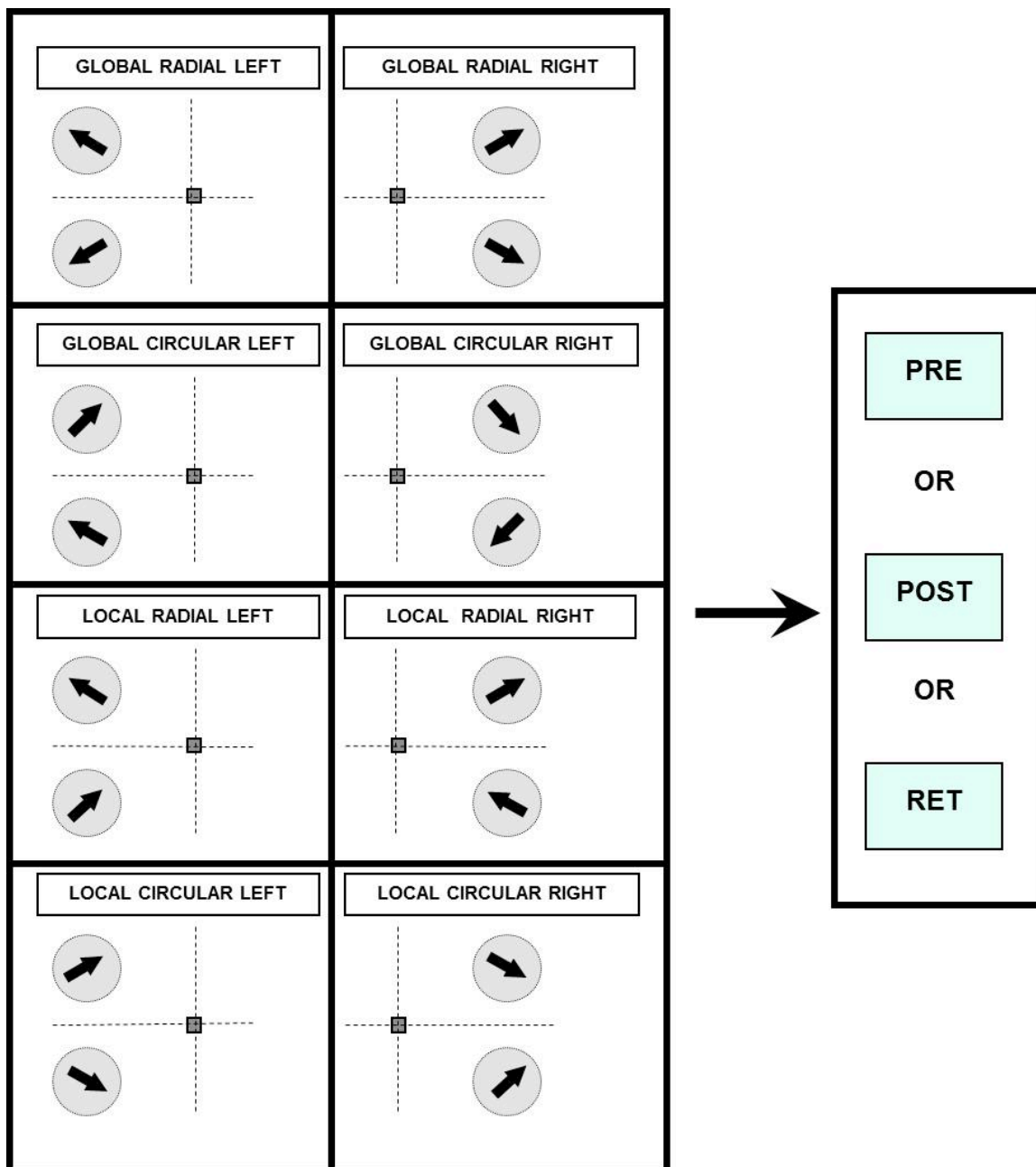
### **3.2 Experimental Paradigm**

Prior to testing subjects were divided into two groups corresponding to the motion direction stimuli (Global or Local) presented during training. Figure 3-7 shows the eight experimental conditions on which all subjects were tested before and after training. Nine subjects were trained to discriminate changes in the direction of radial motion (expansion and contraction). Similarly, nine were trained to discriminate changes in the direction of the equivalent local planar motion stimuli. Five subjects in each group were trained with stimuli presented in

the right visual field and the remaining subjects were trained with stimuli presented in the left visual field.



**Figure 3-6.** Experimental Paradigm for the Global motion task (Exp.1) and Local motion Task (Exp. 2). During the PRE, POST and RET sessions all eight combinations of motion task (global vs. local), visual field (left or right) and motion direction (radial vs. circular) were tested. The TC (Trained condition) blocks in red dashed frame denote different tasks selected in training sessions where ‘N’ was based on subjects learning thresholds. Subject was trained on dual task paradigm (speed task with dot discrimination as Seen in *speed discrimination training paradigm*) before the main experiment to train the subjects on performing the dual task.



**Figure 3-7.** Experimental conditions tested before and after training. Eight experimental conditions were consisted before and after training corresponding to all combinations of motion task (global vs. local), visual field (left or right) and motion direction (radial vs. circular). Thresholds are collected on these conditions before training (pre), after training (post) and retention (ret) in the experimental paradigm (**Figure 3-6**)

### 3.2.1 Speed discrimination training paradigm

Before training on the direction discrimination task, subjects were trained on the dual-task paradigm to control for the effects of learning to perform the dual-discrimination task. During this phase, a speed discrimination task was used in conjunction with the dot density task to provide the same image statistics used in the actual experiment while minimizing the likelihood of improvements in direction discrimination. The speed discrimination task had the same frame-wise image properties as the direction discrimination task used in the main experiment except that the directions of motion for each dot were chosen randomly on every stimulus frame.

In a Two temporal alternative forced choice (*2-TAFC*) task, subjects were presented with pairs of random motion stimuli and required to indicate which of the two stimuli contained the faster motion (task-1). The second task (task-2), was to identify which of the two stimuli had a larger number of red dots across stimulus apertures. Task-2 was an attention task, which was included with task-1 to ensure that the observer attended to both apertures during stimulus presentation. In task-2 (dot discrimination) the red dots were distributed across both stimulus apertures such the number of red dots in a single aperture was uncorrelated with the task-1 judgment across trials.

Following the presentation of each stimulus pair, subjects were instructed to respond first, to task-1 (in this case speed discrimination), and then to task-2. During testing a constant stimulus paradigm was used with task-1 levels

corresponding to either [28, 30, 32] deg/sec or [20, 22, 24] deg/sec differences in speed based on subject's performance with 20 trials per stimulus level. For task-2, the constant stimulus levels were set to [80, 95] % change in red dot density. When an observer's percent correct performance was  $\geq 80\%$  for the smallest change in speed and  $\geq 80\%$  for the dot density task, they were enrolled in the perceptual learning study.

### 3.2.2 Threshold Tracking Paradigm

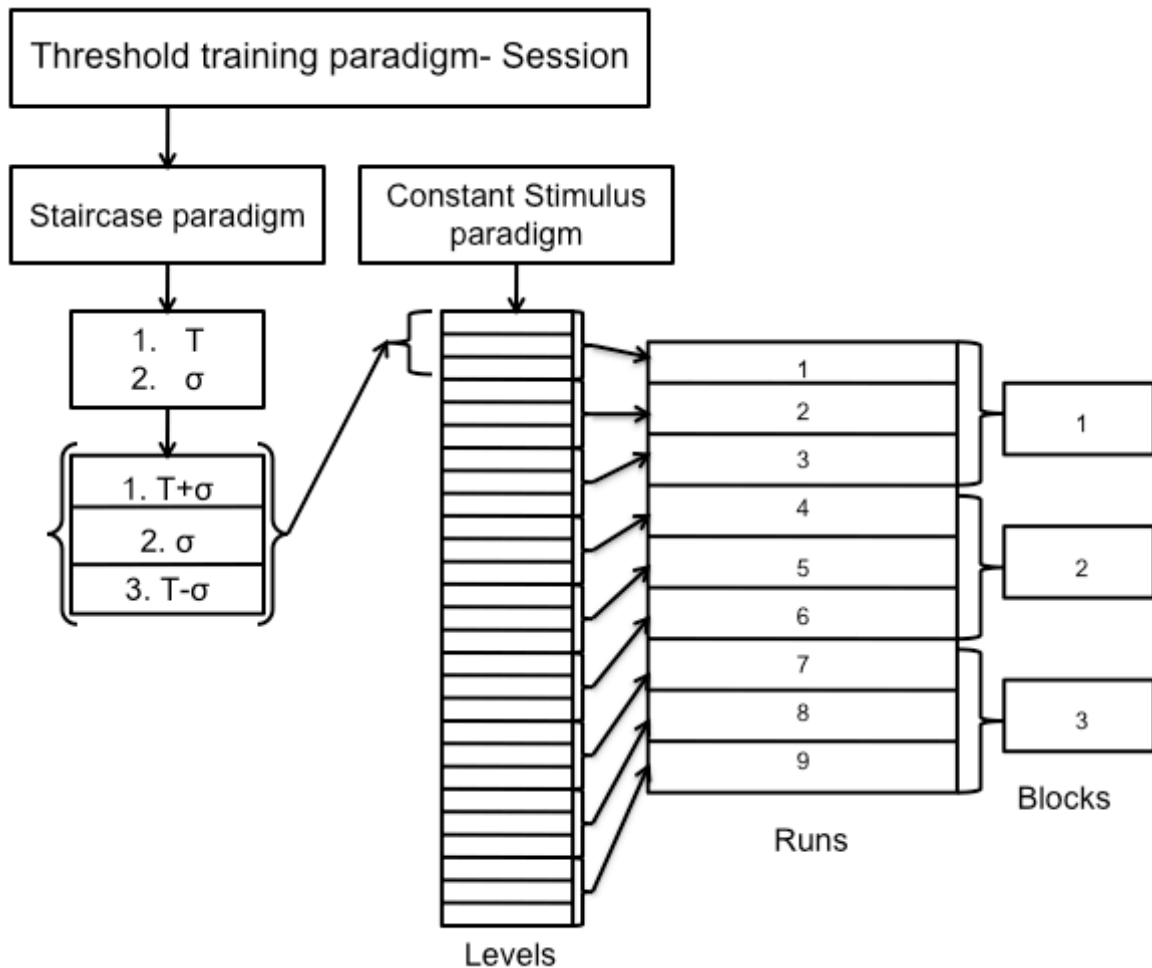
During training on the direction discrimination task, a threshold-tracking paradigm was used to maintain a constant level of task difficulty. During the first experimental session, observer thresholds ( $T_s = 79\%$  correct) were estimated for all training and control tasks using an adaptive staircase pattern. Each training session consisted of nine training blocks (constant stimulus runs), where each block contained 60 trials (20 trials per level). During the first experimental session, observer thresholds ( $T = 79\%$  correct) were estimated for all training and control tasks using an adaptive staircase paradigm.

For each observer the threshold estimate and standard deviation ( $\sigma$ ) obtained from the staircase procedure were used to select three task-specific levels of difficulty for subsequent constant stimulus training during the session  $[(T - \sigma), T, (T + \sigma)]$ . If an observer's percent correct performance for the  $(T - \sigma)$  level of difficulty exceeded 80%, the training levels were adjusted downward by  $\sigma$

to span the range  $[(T - 2\sigma), (T - \sigma), T]$ . Training was concluded and post-training data collected when the thresholds stabilized over 'N' sessions (Figure 3-8). Subjects' thresholds were considered to have stabilized when the number of blocks tested was greater than four time constants as defined by an exponential fit to discrimination thresholds across training blocks. Subjects were trained on consecutive or alternating days over a period of approximately ~1-2 weeks (~4-12 sessions).

During the first and last test sessions subjects' staircase thresholds on the training and control conditions (e.g. to the opposite field of view and the untrained task (or in this case it is the circular task)), were collected to quantify the degree of learning transfer and identify the cortical level at which perceptual learning occurs. Task retention thresholds following training were quantified after 7-10 days via repetition of the post-training test and control conditions.





**Figure 3-8.** Diagrammatic representation of the threshold training paradigm. During a test session subjects were first tested with a staircase paradigm on the training task to obtain estimates of subjects' threshold ( $T$ ) and standard deviation ( $\sigma$ ), which were subsequently used to specify the three constant stimulus levels to be used for the first run. If the subject's percent correct performance for the lowest level  $\geq 80\%$  on a run, then the levels were reduced by  $\sigma$  for the next run. Each test session consisted of nine runs, which were subsequently grouped into three blocks (of three runs each). Discrimination thresholds were estimated for each block using a least-squares curve-fit to a Weibull function.

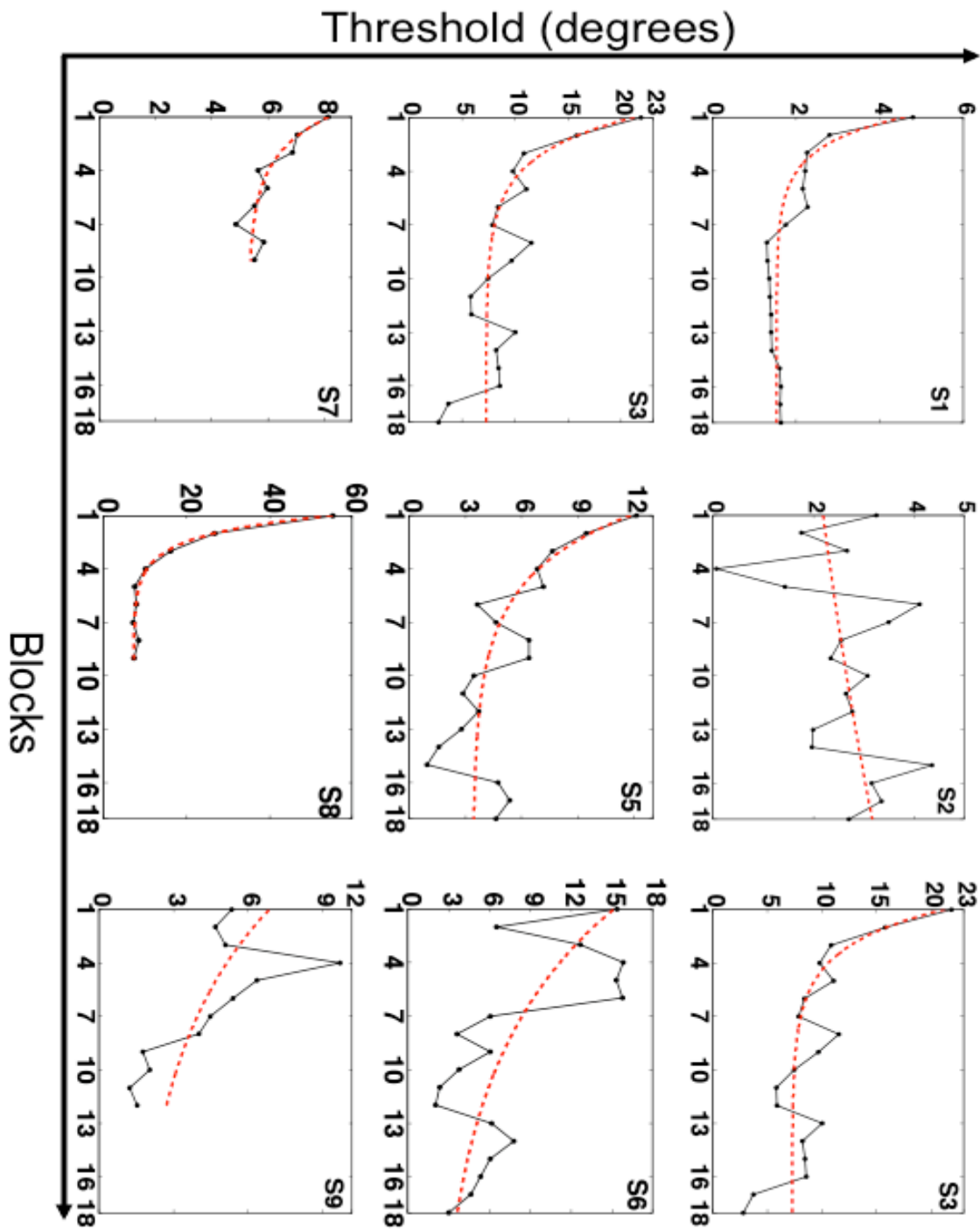
## 4 RESULTS

Between the two training groups, i.e. training with local or global motion, initial (before –training or pre-training) direction discrimination thresholds varied widely (4 – 35 degrees) across subjects. Of the 18 subjects trained between the two task conditions, 16 showed significant improvements in direction discrimination thresholds with practice (paired t-test;  $p < 0.05$ , See Table 4-3). Two subjects, S2 and S11 (one from each training group), showed no significant improvement in performance with training (paired t-test;  $p > 0.05$ ). Two subjects, one from each training group (S2 with time constant ( $\tau$ ) = -50 and S11 with time constant ( $\tau$ ) = -100) also had negative time constants, indicating that their thresholds did not improve with training (See Table 4-1 and Table 4-2). These subjects were hence classified as non-learners and excluded from all subsequent analyses of learning effects.

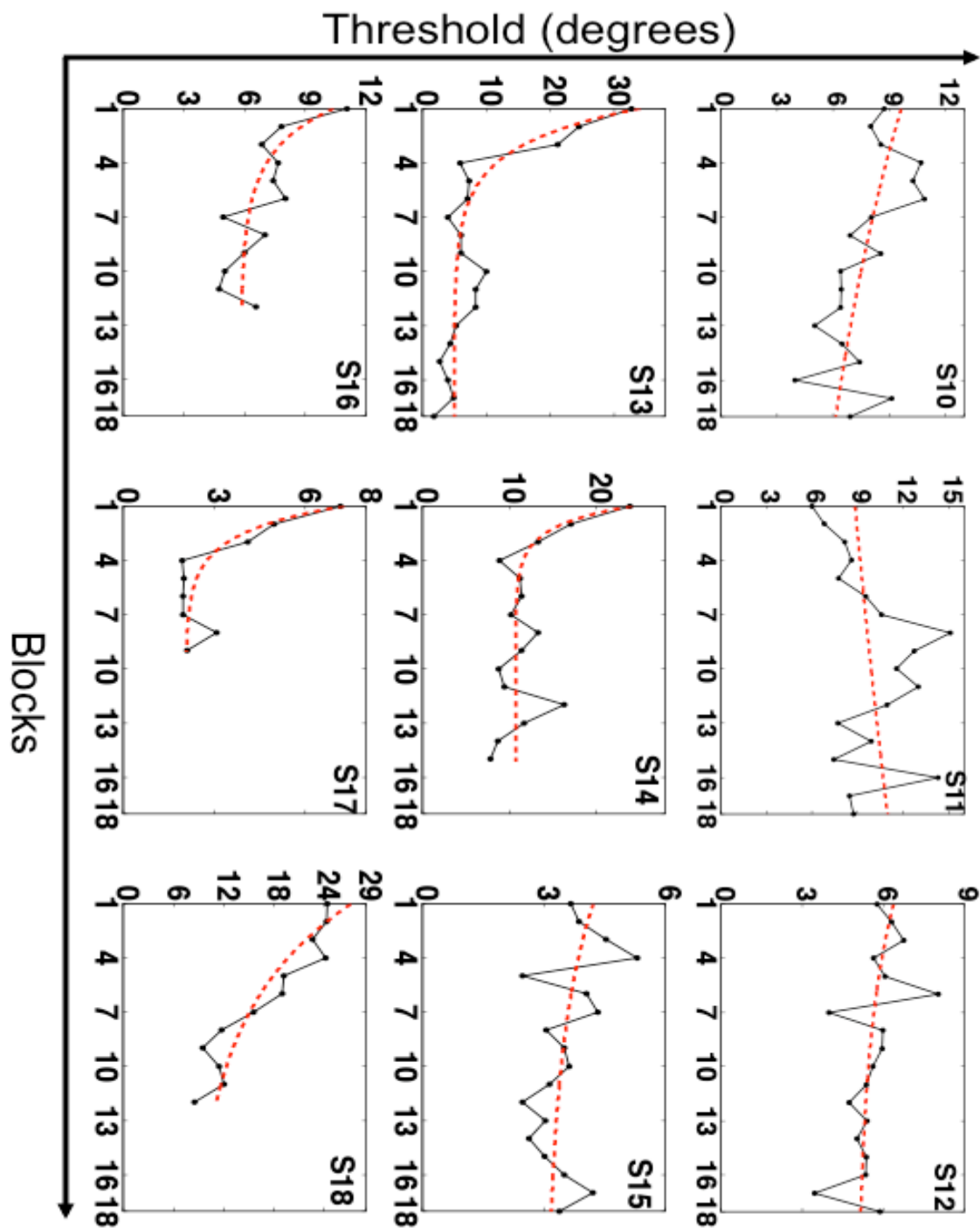
Figure 4-1 and Figure 4-2 show direction discrimination thresholds on the trained condition as a function of training block for the global-radial and local-radial motion training groups respectively. In each case threshold performance ( $\phi_{th}$ ) was fit to a decaying exponential to characterize the time course of learning

$$\phi_{th} = \phi_{pre} * e^{-bt} + \phi_{post}$$

where  $\phi_{pre}$  is the threshold before training ( $\phi_{pre} > 0$ ),  $b$  is the rate of decay ( $= 1/\tau$ , where  $\tau$  is the time constant), and  $\phi_{post}$  is the threshold following training.



**Figure 4-1.** Direction discrimination thresholds as a function of training block for subjects trained on the Global Motion Task. Discrimination thresholds (79% correct) are shown for subjects S1-S9 as a function of training block. A nonlinear least-square exponential fit was applied to each subject's performance (red dashed line) to characterize the time course of learning. The best-fit parameters for each subject are shown in Table 4-1.



**Figure 4-2.** Direction discrimination thresholds as a function of training block for subjects trained on the Local Motion Task. Discrimination thresholds (79% correct) are shown for subjects S10-S18 as a function of training block. A nonlinear least-square exponential fit was applied to each subject's performance (red dashed line) to characterize the time course of learning. The best-fit parameters for each subject are shown in Table 4-2

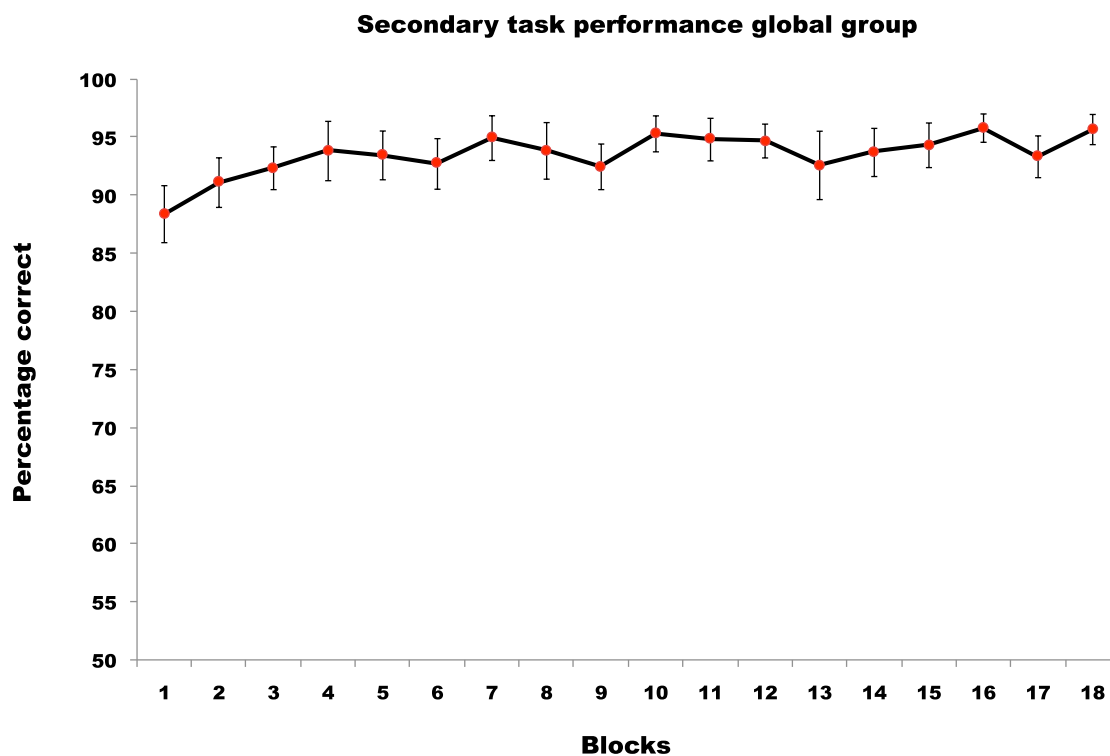
| Subjects  | $\phi_{pre}$            | $b= 1/\tau$ (blocks)          | $\phi_{post}$           |
|-----------|-------------------------|-------------------------------|-------------------------|
| <b>S1</b> | 5.63<br>(3.79, 7.48)    | 0.6083<br>(0.3826, 0.8341)    | 1.53<br>(1.36, 1.70)    |
| <b>S2</b> | 1.94<br>(-73.57, 77.45) | -0.02361<br>(-0.7666, 0.7194) | 0.21<br>(-76.62, 77.03) |
| <b>S3</b> | 22.56<br>(10.90, 34.22) | 0.4777<br>(0.1599, 0.7955)    | 7.26<br>(5.72, 8.80)    |
| <b>S4</b> | 3.59<br>(-0.34, 7.51)   | 0.3916<br>(-0.2267, 1.01)     | 2.92<br>(2.22, 3.63)    |
| <b>S5</b> | 11.32<br>(6.59, 16.05)  | 0.292<br>(0.0754, 0.5085)     | 3.39<br>(2.00, 4.78)    |
| <b>S6</b> | 15<br>(4.51, 25.49)     | 0.1181<br>(-0.1628, 0.3989)   | 1.84<br>(-11.75, 15.42) |
| <b>S7</b> | 4.54<br>(2.11, 6.98)    | 0.46<br>(-0.0035, 0.9235)     | 5.31<br>(4.49, 6.13)    |
| <b>S8</b> | 90<br>(fixed at bound)  | 0.7709<br>(0.6812, 0.8606)    | 6.83<br>(4.87, 8.80)    |
| <b>S9</b> | 10.66<br>(4.01, 17.31)  | 0.1199<br>(-0.0073, 0.2472)   | 2<br>(fixed at bound)   |

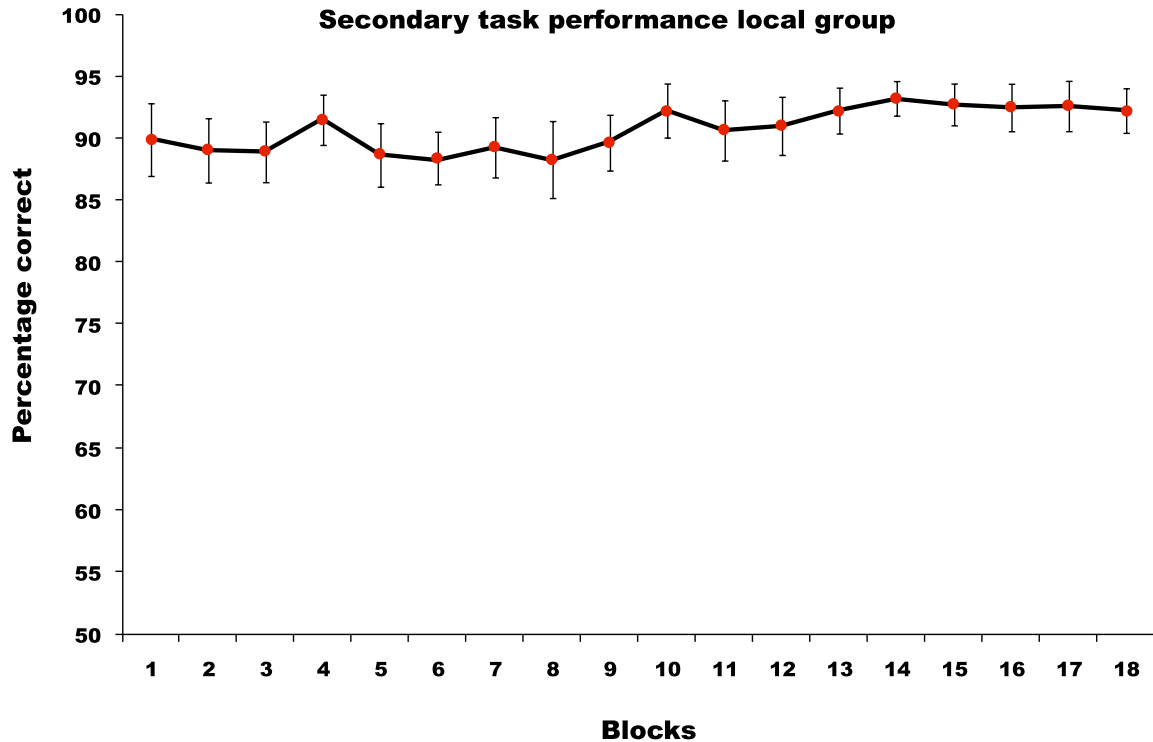
**Table 4-1.** Parameters for best fit exponential to subjects' discrimination threshold with training on the Global Motion Task. Least squares estimates of subjects' pre-training threshold ( $\phi_{pre}$ ),  $b= 1/\text{time constant } (\tau)$ , and post-training thresholds ( $\phi_{post}$ ) are shown together with their 95% confidence interval (in brackets) for each subject. The negative time constant obtained for S2 indicates the subject was a nonlearner (highlighted in gray).

| Subjects   | $\phi_{pre}$            | $b=1/\tau$ (blocks)                  | $\phi_{post}$          |
|------------|-------------------------|--------------------------------------|------------------------|
| <b>S10</b> | 7.18<br>(-30.09, 44.45) | 0.0417<br>(-0.2925, 0.3759)          | 2.75<br>(-36.69, 42.2) |
| <b>S11</b> | 7.70<br>(5.18, 10.22)   | <b>-0.01418</b><br>(-0.0426, 0.0143) | 1<br>(fixed at bound)  |
| <b>S12</b> | 1.56<br>(0.43, 2.70)    | 0.1256<br>(-0.0089, 0.26)            | 5<br>(fixed at bound)  |
| <b>S13</b> | 47.6<br>(31.52, 63.68)  | 0.49<br>(0.2798, 0.7002)             | 4.90<br>(2.85, 6.94)   |
| <b>S14</b> | 33.2<br>(1.16, 65.23)   | 0.9017<br>(0.1007, 1.703)            | 10.7<br>(9.09, 12.32)  |
| <b>S15</b> | 1.34<br>(-0.40, 3.07)   | 0.1259<br>(-0.4431, 0.694)           | 3.04<br>(0.86, 5.23)   |
| <b>S16</b> | 6.98<br>(1.49, 12.47)   | 0.4213<br>(-0.130, 0.9727)           | 5.81<br>(4.38, 7.24)   |
| <b>S17</b> | 10.18<br>(4, 16.35)     | 0.666<br>(0.1502, 1.182)             | 2.05<br>(1.15, 2.96)   |
| <b>S18</b> | 22.79<br>(16.85, 28.72) | 0.1666<br>(0.1036, 0.2296)           | 8<br>(fixed at bound)  |

**Table 4-2.** Parameters for best fit exponential to subjects' discrimination threshold with training on the Local Motion Task. Least squares estimates of subjects' pre-training threshold ( $\phi_{pre}$ ),  $b=1/\tau$ , and post-training thresholds ( $\phi_{post}$ ) are shown together with their 95% confidence interval (in brackets) for each subject. The negative time constant obtained with S11 indicates the subject was a nonlearner (highlighted in gray).

Table 4-1 and Table 4-2 show the results of the least-square exponential fits to subjects' discrimination threshold improvements with training for the Global and Local motion trained groups respectively.

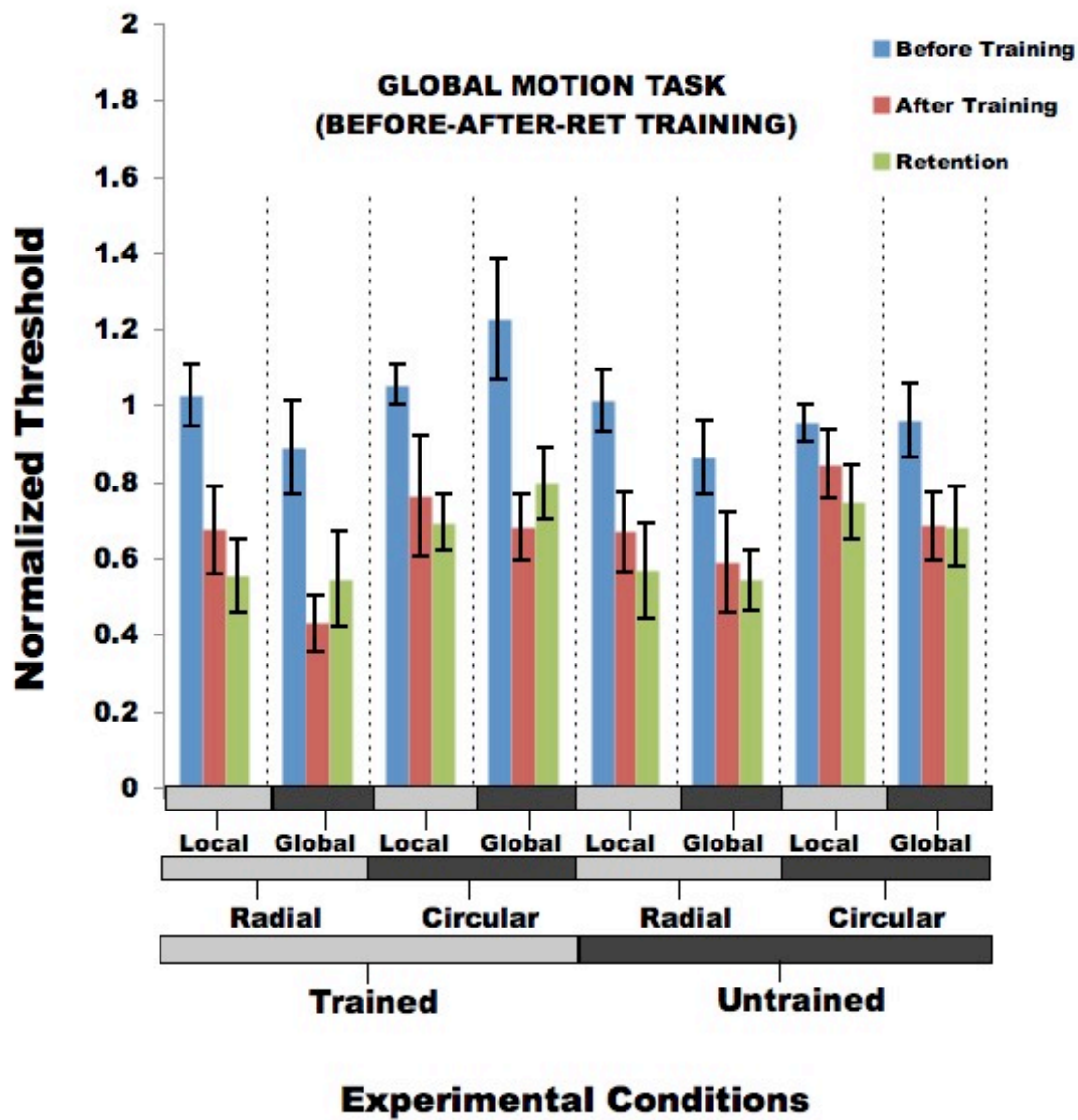


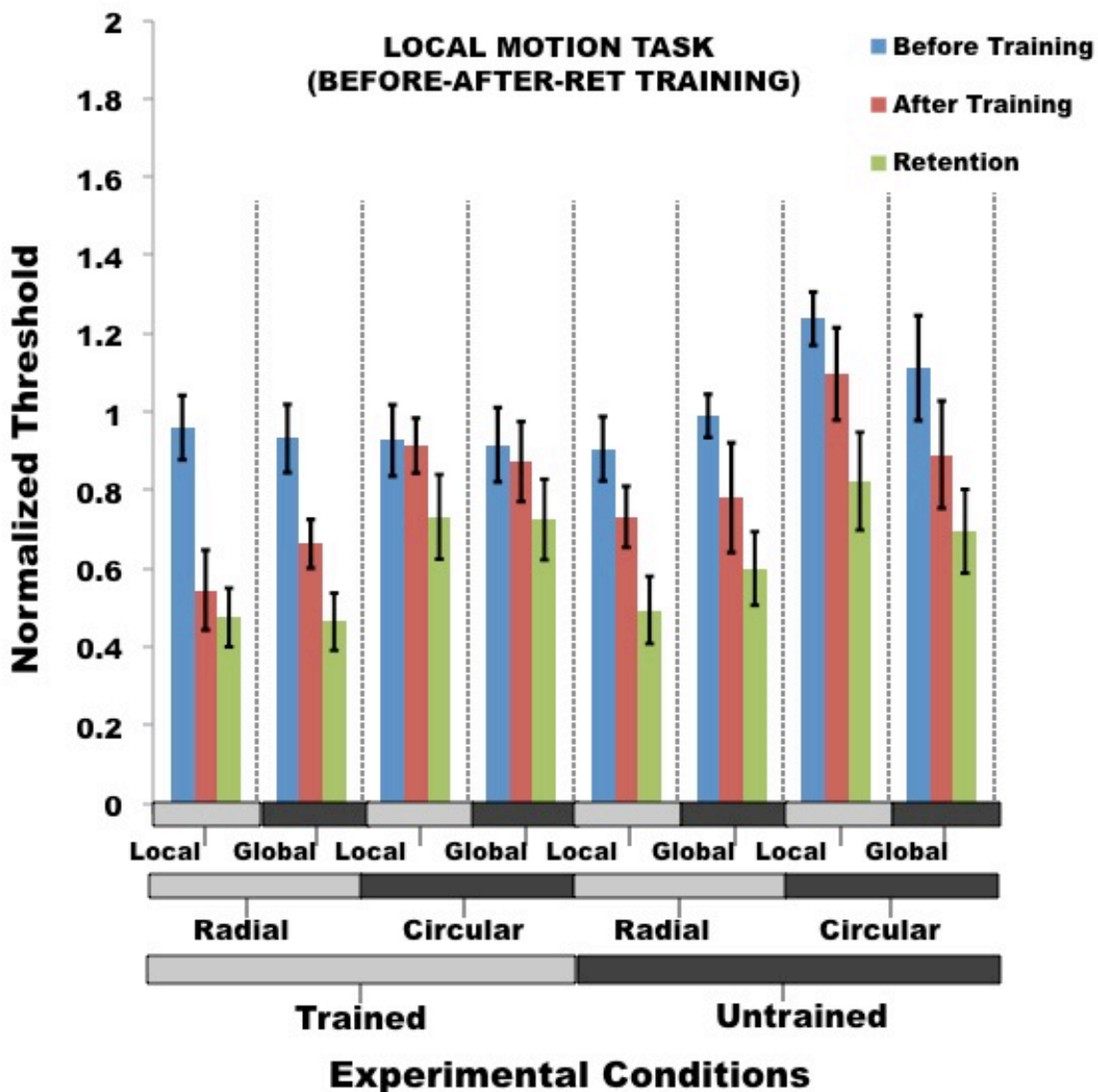


**Figure 4-2.** Average percent correct performance on the dot discrimination task (task-2) as a function of training block for subjects trained on the (A) Global Motion and (B) Local Motion tasks. Performance is reported within each group as the mean across subject's  $\pm 1$  SE.

Performance on the dot discrimination task (task-2) ranged from 88%-96% for all subjects (Figure 4-2), indicating that subjects attended simultaneously to both apertures throughout training. Figure 4-3 shows the training-induced changes in direction discrimination thresholds across conditions before and after training and one week following the completion of training. Results are reported across test conditions as the mean across subjects ( $\pm$ SE) of the (within-subject) performance thresholds.







**Figure 4-3.** Group averaged direction discrimination thresholds across experimental conditions. (A) Pre- and post-training performance and (C) post-training and learning retention (one week after training) for subjects trained on the Global motion task. (B) Pre- and post-training performance and (D) post-training and learning retention (one week after training) for subjects trained on the Local motion task. Performance is reported as the mean  $\pm$  SE. The single asterisk denotes conditions that were significantly different ( $p < 0.05$ ).

To account for the wide range of subject's initial discrimination thresholds, subjects' individual thresholds within each experimental condition were

normalized to the pre-training thresholds averaged across all conditions prior to the statistical analysis. A three-way (2x2x2) repeated measures ANOVA was performed on the results of each training group with task type (local/global), visual field (left/right), and motion direction (radial/circular) as factors. Both training groups (local and global motion training) showed significant effects of training across tasks ( $p < 0.05$ ), visual field ( $p < 0.05$ ), and motion direction ( $p < 0.05$ ). No interactions between conditions were observed ( $p > 0.05$ ).

Table 4-3 shows the results of paired t-test comparisons (two-tailed) of normalized pre- versus post-training thresholds<sup>1</sup>. Comparisons of pre-versus post-training thresholds revealed group-specific differences in the pattern and transfer of learning between experimental conditions. Subjects trained on global radial motions showed significant learning for the trained motion direction and visual field (denoted by (\*) in Figure 4-3A), transfer to the orthogonal (circular) motions presented in the trained visual field and to the global radial motion presented in the untrained visual field. Improvements in direction discrimination post-training, also transferred to the local radial motion stimuli in both trained and untrained visual fields (See Table 4-3A). When subjects trained on the equivalent local motion condition, the transfer in improved direction discrimination was restricted to the equivalent global (radial) motion presented in the trained visual field (Table 4-3B). Retention data collected one week following the end of training

---





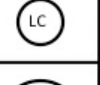
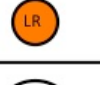






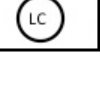
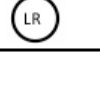

<sup>1</sup> All subjects' thresholds were included in the analyses with the exception of subject S5 whose threshold for the global radial motion task presented in the untrained visual field, was excluded as an outlier ( $>4\sigma$  from the group mean).

showed that no significant changes in direction discrimination between the post training session and retention session.

| <b>(A) GLOBAL TRAINED SUBJECTS: T-TEST RESULTS (D.F. =7)</b> |                 |         |         |              |
|--|-----------------|---------|---------|--------------|
| Experimental Conditions                                      |                 | T-value | P-value | Sig (p<0.05) |
| Trained Visual Field   | Local Radial    | 2.799   | 0.026   | Yes          |
|  | Global Radial   | 3.453   | 0.010   | Yes          |
|  | Local Circular  | 1.662   | 0.140   | No           |
|  | Global Circular | 2.552   | 0.037   | Yes          |
| Untrained Visual Field                                       | Local Radial    | 2.516   | 0.040   | Yes          |
|  | Global Radial   | 1.811   | 0.006   | Yes          |
|  | Local Circular  | 1.788   | 0.116   | No           |
|  | Global Circular | 1.387   | 0.208   | No           |

| <b>(B) LOCAL TRAINED SUBJECTS: T-TEST RESULTS (D.F. =7)</b> |                 |         |         |              |
|---|-----------------|---------|---------|--------------|
| Experimental Conditions                                     |                 | T-value | P-value | Sig (p<0.05) |
| Trained Visual Field  | Local Radial    | 3.429   | 0.011   | Yes          |
|   | Global Radial   | 2.777   | 0.027   | Yes          |
|   | Local Circular  | 0.093   | 0.928   | No           |
|   | Global Circular | 0.355   | 0.732   | No           |
| Untrained Visual Field                                      | Local Radial    | 1.912   | 0.097   | No           |
|   | Global Radial   | 1.418   | 0.198   | No           |
|   | Local Circular  | 2.187   | 0.064   | No           |
|   | Global Circular | 1.312   | 0.230   | No           |

**Table 4-3.** Group analyses of pre- versus post-training direction discrimination thresholds across experimental conditions as shown in table on left for subjects trained with **(A)** Global radial motions and **(B)** Local radial motions. Difference in pre versus post-training thresholds were evaluated across subjects using paired t-tests with seven degrees of freedom. Test conditions highlighted in grey showed statistically significant decreases in discrimination thresholds following training.

|                        |                       | Experimental Results  |   |  |   |
|------------------------|-----------------------|---|---|--|---|
|                        |                       | Trained   |   | Untrained  |   |
| Trained Task           | Visual field          |   |   |  |   |
|                        | Global motion pattern |   |  |   |   |
|                        |                       |  |  |  |  |
| Local motion direction |                       |  |  |  |  |
|                        |                       |  |  |  |  |

**Figure 4-4.** Diagrammatic comparison of statistically significant training-induced changes in direction discrimination thresholds across experimental conditions. Visual fields were classified as trained and untrained, based on the conditions the subjects were trained on. Color Representation: Blue denotes the trained task and condition. Orange indicates significant improvement in post (versus pre-) training thresholds ( $p < 0.05$ ). White indicates no significant change in thresholds before and after training. Condition Annotations: The task condition annotations correspond to the task and motion type presented during training (GR: Global-Radial, GC: Global-Circular, LR: Local-Radial, LC: Local-Circular).

Figure 4-4 shows a diagrammatic illustration of the training-induced changes in direction discrimination thresholds across tasks, motion directions, and visual field locations for the two training groups. For subjects trained on the Local Motion task, learning was restricted to the trained visual field but transferred to the global motion task for stimuli (i.e. radial motions) that contained the directions of local motion presented within apertures during training. For subjects trained on the Global Motion task, improvements in direction discrimination thresholds occurred in the untrained visual field, for orthogonal

motions presented in the trained visual field and for the Local motion task in the trained visual field whose within-aperture directions of motion matched those of the trained (radial) global motion.

## 5 DISCUSSION

The transfer of perceptual performance to modified forms of the same task or to different related tasks has been the primary tool for discovering what is learned and inferring the physiological basis of that learning [Fahle and Poggio, 2002]. In the approach developed here, we used the known functional hierarchy of visual motion processing together with carefully controlled tests of visual motion discrimination to determine the processing stage at which learning occurs for wide field motion patterns associated with self-movement through the environment. By tracking threshold performance during training, the experimental approach applied here has the benefit of equating task difficulty across observers, facilitating a comparable engagement of the underlying visual motion and learning mechanisms.

The results indicate that when subjects trained on radial motion patterns (Global Motion task), learning transferred to radial motions presented in the untrained visual field, orthogonal (circular) motion patterns presented in the trained visual field, and to equivalent local motions (oriented radially with respect to fixation) presented in both visual fields. By comparison, when subjects were trained on the equivalent local motions (Local Motion task), learning was restricted to the same visual field and directions of motion. Improvements in direction discrimination did transfer to the equivalent global motion in the trained visual field. The results suggest that training with global, and to a lesser extent local, motions leads to training-induced changes in performance across multiple

stages of visual processing. A key question, is how these results relate to current theories of task-dependent or task-relevant learning.

### **5.1 Reverse Hierarchy Theory**

Reverse Hierarchy Theory (RHT) suggests that task-dependent learning is a top-down guided process, which begins at later stages of sensory processing, and when those stages do not suffice in showing learning even after training, then the learning progresses backwards to earlier stages of processing, which have a better signal-to-noise ratio. Within this framework, RHT makes two important predictions that can be tested experimentally (Ahissar, M. and Hochstein, S. 1997a, 1997b, 1999, 2004):

Case (A): Perceptual learning will be contingent on attention on the entire task (global level) to guide the backward (top-down) search for the highest level of processing sufficient to perform the task. This follows directly from the assumption that high-level representations are more immediately accessible to conscious perception, whereas the more focal representations of sensory attributes that occur at earlier stages of processing can result in a higher signal-to-noise ratio. As such, RHT proposes that learning will occur at the stage of visual motion processing whose output is sufficiently discriminative with respect to the task. Thus, when spatial attention is broad, perceptual learning will occur at higher levels of visual processing whose receptive fields span the attended region.



In the context of the current experiments, an attention-driven interpretation of RHT predicts that learning in subjects trained on the Global Motion task, will be restricted primarily to higher-levels of visual processing that represent complex patterns of motion across stimulus apertures. Little if any transfer of learning to the Local Motion tasks associated with earlier stages of visual processing (Figure 5-1, top-right) would be predicted. Even when subjects were trained on the Local Motion task, the dual-task paradigm required that they allocate their attention “globally” across stimulus apertures resulting in similar predictions for the transfer of learning following training on the Global and Local Motion tasks (Figure 5-1, bottom-right).



























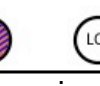



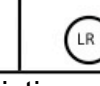

|                             |                       | Experimental Results |           | RHT- Case A (Attention) |           |
|-----------------------------|-----------------------|----------------------|-----------|-------------------------|-----------|
| Trained Task \ Visual field |                       | Trained              | Untrained | Trained                 | Untrained |
|                             | Global motion pattern | Global               |           |                         |           |
| Local                       |                       |                      |           |                         |           |
| Local motion direction      | Global                |                      |           |                         |           |
|                             | Local                 |                      |           |                         |           |

**Figure 5-1.** Comparison of experimental results with predictions from a task-specific attention driven interpretation of Reverse Hierarchy Theory (RHT). The color representation and designation of experimental conditions follows the convention detailed in Figure 4-4.

Case (B): Previous studies have shown that as a task becomes more difficult, the window of attention shrinks and learning becomes more localized

(Ahissar, M. and Hochstein, S. 2000). When fine discrimination is required, learning shifts to earlier stages of visual processing to increase the signal-to-noise ratio of the visual attribute being compared. This induces more spatially restricted learning. Within a hierarchical processing architecture, training with coarse changes in a visual attribute leads to generalized learning, while training with fine changes in a visual attribute leads to more specific learning. Hence, when greater spatial refinement is needed, learning occurs at earlier stages of visual processing resulting in more focal training effects.

For the threshold tracking paradigm used in the current experiments, a task-difficulty driven interpretation of RHT predicts that learning in subjects trained on the Global Motion task should shift to earlier stages of processing as the direction discrimination becomes progressively more refined, resulting in less transfer across visual field locations and motion directions. For subjects trained on the Local Motion task, learning should remain focal, with little if any transfer across visual field locations or directions of motion.

|                        | Experimental Results  |   |   |   | RHT- Case B (Task Difficulty)  |   |   |   |
|------------------------|---|---|---|---|--|---|---|---|
| Visual field           | Trained   |   | Untrained   |   | Trained  |   | Untrained   |   |
| Trained Task           |   |   |   |   |  |   |   |   |
| Global motion pattern  |  |  |  |  |  |  |  |  |
|                        |  |  |  |  |  |  |  |  |
| Local motion direction |  |  |  |  |  |  |  |  |
|                        |  |  |  |  |  |  |  |  |

**Figure 5-2.** Comparison of experimental results with predictions from a task-difficulty driven interpretation of Reverse Hierarchy Theory (RHT). The color representation and designation of experimental conditions follows the convention detailed in Figure 4-4.































In both cases, the pattern of transfer of learning predicted by a RHT model of perceptual learning are inconsistent with the experimental results. This suggests that learning was not driven solely by a top-down attention driven mechanism that focused on learning at the highest level of visual motion processing sufficient to perform the task.

## 5.2 Bottom-Up theory of perceptual learning

Seitz and Watanabe (2005) have shown that the required condition for task irrelevant learning is for the task irrelevant feature to coincide with the stimulus features required to perform the task (Seitz and Watanabe, 2005). In the case of task-irrelevant learning for coarse motion direction, Watanabe and colleagues showed that task irrelevant learning occurs at the level of local motion

mechanisms and does not transfer to global level mechanisms (Watanabe et. al., 2002). Most recently, Nishina and Watanabe (2009) showed that this “bottom-up” effect of learning occurs for even when the discrimination of coarse changes in the direction of global (radial) motions is task-relevant. As a result they have proposed that perceptual learning of visual motion is based on changes at the level of local rather than global motion mechanisms.

If learning to discriminate fine changes in the direction of global (radial) motions is mediated primarily by bottom-up mechanisms then training-based improvements in performance on the Global Motion task should occur primarily at the level of the local motion mechanisms that operate within apertures. Although Nishina and Watanabe (2009) did not explicitly test the effects of local motion training, a bottom-up theory of learning would predict that for subjects trained on the Local Motion task, task-specific improvements in performance should be restricted primarily to the trained task and visual field. Within this framework, improvements in direction discrimination for radial motions (Global Motion task) could occur due to the increased sensitivity of the local motion mechanisms that provide the inputs to the global motion mechanisms associated with the task. A visual representation of the predicted patterns of task and visual field specific transfer associated with a bottom-up theory is shown in Figure 5-3.

|                             |                       | Experimental Results  |   | Bottom – Up Theory   |   |
|-----------------------------|-----------------------|---|---|--|---|
| Trained Task \ Visual field |                       | Trained   | Untrained   | Trained  | Untrained   |
|                             | Global motion pattern |   |   |      |    |
|                             |                       |   |   |   |   |
| Local motion direction      |                       |   |   |   |   |
|                             |                       |   |   |   |   |

**Figure 5-3.** Comparison of experimental results with predictions from a bottom-up theory of perceptual learning. The color representation and designation of experimental conditions follows the convention detailed in Figure 4-4.

The pattern of learning observed in the current tasks indicates that perceptual learning in the Global Motion task transfers to the untrained visual field. Such transfer is generally inconsistent with a purely bottom-up learning mechanism, wherein improvements in radial motion discrimination would be expected to reflect changes among local motion mechanisms that are largely restricted to the trained visual field (Nishina and Watanabe, 2009) as opposed to global motion mechanisms that span visual fields.

### 5.3 Sensitivity-Specificity Theory (SST)

The inconsistencies between the patterns of learning observed here and the predictions of top-down (Reverse Hierarchy) or bottom-up learning mechanisms, suggest that learning in the task may be mediated by an

alternative mechanism. For example, learning could be mediated by a mechanism wherein learning occurs at the processing stage that is most discriminative with respect to the task (i.e. learning occurs at the stage which is sensitive to that particular task and which can induce learning due to training). We refer to this as “Sensitivity-Specificity Theory” (SST).

Within this framework the increase in sensitivity (i.e. increase in the level of performance of task) at successive stages of processing due to spatial summation predicts that learning should occur at the level of visual field spanning global motion mechanisms for subjects trained on the Global Motion task. Thus we would expect that training should transfer to the untrained visual field and could transfer to the untrained (orthogonal) directions of motion due to the broader representation of motion directions within global motion mechanisms (Meese and Anderson, 2002; Meese and Harris, 2001; Freeman and Harris, 1992; Snowden and Milne, 1996), (Figure 5-4). Conversely, following training on the Local Motion task we would expect learning to occur at the level of the local motion mechanisms due to the lack of a discriminative motion pattern across apertures. Thus, we would expect that training should not transfer to either the untrained (orthogonal) motions or the untrained visual field due to the narrower representation of motion directions within local motion mechanisms and the corresponding restriction of local motion mechanisms to the contra-lateral visual field.

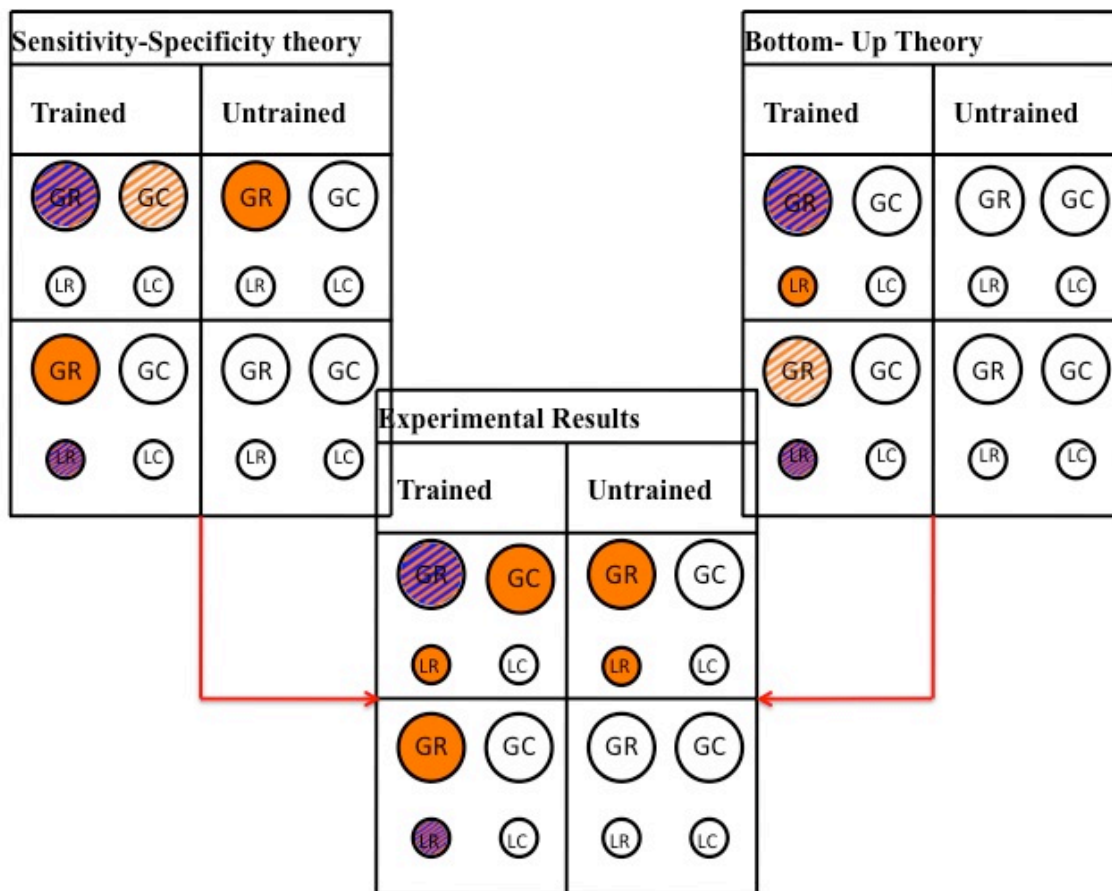
|                             |                       | Experimental Results                   |   | Sensitivity - Specificity theory (SST) |  |
|-----------------------------|-----------------------|--|---|--|--|
| Trained Task \ Visual field |                       | Trained                                | Untrained                               | Trained                                | Untrained  |
|                             | Global motion pattern | Global                                 | GR (blue diagonal stripes), GC (orange) | GR (orange), GC (white)                | GR (blue diagonal stripes), GC (orange diagonal stripes) |
| Local                       |                       | LR (orange), LC (white)                | LR (orange), LC (white)                 | LR (white), LC (white)                 | LR (white), LC (white)                                   |
| Local motion direction      | Global                | GR (orange), GC (white)                | GR (white), GC (white)                  | GR (orange), GC (white)                | GR (white), GC (white)                                   |
|                             | Local                 | LR (blue diagonal stripes), LC (white) | LR (white), LC (white)                  | LR (blue diagonal stripes), LC (white) | LR (white), LC (white)                                   |

**Figure 5-4.** Comparison of experimental results with predictions from a sensitivity-specificity theory of perceptual learning. The color representation and designation of experimental conditions follows the convention detailed in Figure 4-4.

While SST appears to account for a wider range of trained performance across task and conditions, closer inspection shows that it fails to account for the transfer to local motions following training on global motions. In case of SST as seen it doesn't account for local motions and so if it is applied in combination with the bottom up theory, which seems to be a good fit to the experimental results. As the bottom-up accounts for the local motion learning during both globally and locally trained tasks. The Reverse hierarchy theory shows learning in global trained and untrained motion, which is not seen when subject is trained on local motion task. Hence the transfer of learning to the untrained tasks during local motion training makes it a disagreeable fit if it is combined with the bottom-up approach.

But if we consider the feedback mechanism in learning during the SST when we see learning in the global motion when trained in Global radial task, then we

shall see learning in the local radial of both trained and untrained visual field. Thus making SST and experimental results the same.



**Figure 5-5.** Comparison of experimental results with predictions from a combination of sensitivity-specificity theory and bottom-up theory of perceptual learning. The color representation and designation of experimental conditions follows the convention detailed in Figure 4-4.

#### 5.4 Alternative theories of Perceptual Learning

In a separate series of studies Doshier and Lu (Doshier and Lu, 1998) investigated plasticity of visual system by characterizing perceptual learning in the context of external noise applied to an orientation discrimination task. The orientation discrimination performance for both criterion of external noise



exclusion and stimulus enhancement showed improved performance with practice at all levels of external noise (Doshier and Lu, 1998). According to their theory, coupled changes in external noise exclusion and stimulus enhancement could reflect plasticity in the feed-forward weighting of task-relevant spatial frequency. In the current study external noise was not included as a confounding input in task performance and hence an external noise exclusion learning mechanism it is not directly applicable to our study.

Fink et. al. (1997) used functional imaging to explore the functional anatomy involved in sustaining or switching visual attention between local and global perceptual levels. Subjects attended either the global or local level of the stimuli throughout trials in the directed attention task; which resulted in significant activation in right lingual gyrus due to attention in global task and attention to local task activated left inferior occipital cortex. This study mainly concentrates on attentional specificity and shows that the temporal parietal areas control the attentional processes, which in turn modulates neural responses during global and local processing. This study looks at the function anatomy of the cortex related to visual attention while performing attentional tasks which is not entirely related to our study as our study looks at the hierarchy of perceptual learning in visual complex motions. Some of these other studies concentrate on other aspects of perceptual learning and visual motion processing like changes in the human brain activity while training (Schiltz et. al., 1998) and sleep dependent learning (Mednick et. al. 2003), which are not directly related to our study but investigate the effects of different tasks and stimuli on learning.

## 6 CONCLUSION

The results of this study have provided new insight into the stages of visual motion processing where learning for complex motions occurs and perhaps more importantly into the mechanisms that mediate task-dependent learning. The dissociation in the directionality of learning across stages of visual processing is not fully consistent with a reverse hierarchy model or Nishina and Watanabe's finding that global motion occurs on the basis of local motion. Instead the experimental results seem to suggest a combination of learning mechanisms, in this case Sensitivity-Specificity Theory in conjunction with bottom-up learning to account for the transfer of learning to local motion which is accounted by the bottom up theory as seen in experimental results. The results suggest a mechanism wherein perceptual learning occurs simultaneously across multiple stages of visual processing whose activities are interconnected with the task.

## 7 FUTURE DIRECTIONS

In the current study we put forward a mechanism wherein perceptual learning occurs simultaneously across multiple stages of visual processing whose activities are interrelated with the task. Future studies could directly test the applicability of RHT to learning in the visual motion pathway by examining the stage at which learning occurs for motions (e.g. planar motions) that are processed by both local and global motion mechanisms. Alternatively the contribution of bottom-up learning could be directly tested by characterizing the motion mechanisms modulated by task irrelevant learning of complex motion patterns, as opposed to the local motions examined by Watanabe and colleagues.

The statistical power of future studies that utilize the threshold-tracking paradigm could be improved by controlling for confounding effects associated with perceptual learning during testing on the control conditions. One approach that could be used to control for the effects of learning in the control conditions would be to incorporate a test condition whose stimuli have the same image statistics but whose task is not related to direction discrimination, e.g., speed discrimination. By including this condition as part of the pre and post-training sessions, we could quantify the effects of learning due to the measurement of thresholds in the pre and post-training sessions. The differences in pre- versus post-training thresholds for the unrelated task could then be included as a covariate in the statistical analyses to control for the effects of learning during testing on the control tasks.

## 8 BIBLIOGRAPHY

- Ahissar, M. (2000) **The spread of attention and learning in feature search: effects of target distribution and task difficulty.** *Vision Res.* 40, 1349-1364
- Ahissar, M.; Hochstein, S. (2004) **The reverse hierarchy theory of visual perceptual learning.** *Trends Cogn. Sci.* 8, 457-464
- Ahissar, M.; Hochstein, S. (1997) **Task difficulty and the specificity of perceptual learning.** *Nature* 387, 401-406
- Ahissar, M.; Laiwand, R.; Kozminsky, G.; Hochstein, S. (1998) **Learning pop-out detection: building representations for conflicting target-distractor relationships.** *Vision Res.* 38, 3095-3107
- Ahissar, M.; Nahum, M.; Nelken, I.; Hochstein, S. (2009) **Reverse hierarchies and sensory learning.** *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* 364, 285-299
- Albright, T. D. (1993) **Cortical processing of visual motion.** *Rev. Oculomot. Res.* 5, 177-201
- Andersen, R. A. (1997) **Neural mechanisms of visual motion perception in primates.** *Neuron* 18, 865-872
- Angelucci, A.; Levitt, J. B.; Walton, E. J.; Hupe, J. M.; Bullier, J.; Lund, J. S. (2002) **Circuits for local and global signal integration in primary visual cortex.** *J. Neurosci.* 22, 8633-8646
- Babkoff, H.; Zukerman, G.; Fostick, L.; Ben-Artzi, E. (2005) **Effect of the diurnal rhythm and 24 h of sleep deprivation on dichotic temporal order judgment.** *J. Sleep Res.* 14, 7-15
- Ball, K.; Sekuler, R. (1987) **Direction-specific improvement in motion discrimination.** *Vision Res.* 27, 953-965
- Ball, K.; Sekuler, R. (1982) **A specific and enduring improvement in visual motion discrimination.** *Science* 218, 697-698
- Beardsley, S. A.; Vaina, L. M. (2006) **Global motion mechanisms compensate local motion deficits in a patient with a bilateral occipital lobe lesion.** *Exp. Brain Res.* 173, 724-732
- Beardsley, S. A.; Vaina, L. M. (2005) **Psychophysical evidence for a radial motion bias in complex motion discrimination.** *Vision Res.* 45, 1569-1586

- Beardsley, S. A.; Vaina, L. M. (2001) **A laterally interconnected neural architecture in MST accounts for psychophysical discrimination of complex motion patterns.** *J. Comput. Neurosci.* 10, 255-280
- Bertone, A.; Mottron, L.; Jelenic, P.; Faubert, J. (2003) **Motion perception in autism: a "complex" issue.** *J. Cogn. Neurosci.* 15, 218-225
- Bex, P. J.; Metha, A. B.; Walter, M. (1998) **Psychophysical evidence for a functional hierarchy of motion processing mechanisms.** *J. Opt. Soc. Am. A* 15, 769-776
- Bex, P. J.; Walter, M. (1997) **Radial motion looks faster.** *Vision Res.* 37, 3399-3405
- Bruce, V.; Green, P. R.; Georgeson, M. A. (2003) **Visual perception : physiology, psychology and ecology.** 496
- Burr, D. (2001) **Temporal integration of optic flow, measured by contrast and coherence threshold.** *Vision Res.* 41, 1891-1899
- Burr, D. (1998) **Large receptive fields for optic flow detection in humans.** *Vision Res.* 38, 1731-1743
- Carmel, D.; Carrasco, M. (2008) **Perceptual learning and dynamic changes in primary visual cortex.** *Neuron* 57, 799-801
- Chey, J. (1998) **Neural dynamics of motion processing and speed discrimination.** *Vision Res.* 38, 2769-2786
- Clifford, C. W.; Beardsley, S. A.; Vaina, L. M. (1999) **The perception and discrimination of speed in complex motion.** *Vision Res.* 39, 2213-2227
- Cropper, S. J. **Local and global motion signals and their interaction in space and time.**
- Dawson, D.; Reid, K. (1997) **Fatigue, alcohol and performance impairment.** *Nature* 388, 235
- Derrington, A. M.; Allen, H. A.; Delicato, L. S. (2004) **Visual mechanisms of motion analysis and motion perception.** *Annu. Rev. Psychol.* 55, 181-205
- DeYoe, E. A.; Van Essen, D. C. (1988) **Concurrent processing streams in monkey visual cortex.** *Trends Neurosci.* 11, 219-226

- Dosher, B. A. (1998) **Perceptual learning reflects external noise filtering and internal noise reduction through channel reweighting.** *Proc Natl Acad Sci* 95, 13988-13993
- Dosher, B. A.; Lu, Z. L. (1999) **Mechanisms of perceptual learning.** *Vision Res.* 39, 3197-3221
- Duffy, C. J.; Wurtz, R. H. (1991) **Sensitivity of MST neurons to optic flow stimuli. II. Mechanisms of response selectivity revealed by small-field stimuli.** *J. Neurophysiol.* 65, 1346-1359
- Fahle, M. (2005) **Perceptual learning: specificity versus generalization.** *Curr. Opin. Neurobiol.* 15, 154-160
- Fahle, M.; Edelman, S.; Poggio, T. (1995) **Fast perceptual learning in hyperacuity.** *Vision Res.* 35, 3003-3013
- Fahle, M.; Poggio, T. (2002) **Perceptual Learning.** *MIT Press. Cambridge*
- Fahle, M.; Morgan, M. (1996) **No transfer of perceptual learning between similar stimuli in the same retinal position.** *Curr. Biol.* 6, 292-297
- Felleman, D. J.; Van Essen, D. C. (1991) **Distributed hierarchical processing in the primate cerebral cortex.** *Cereb. Cortex* 1, 1-47
- Fine, I.; Jacobs, R. A. (2002) **Comparing perceptual learning across tasks: A review.** *Journal of Vision* 2, 5-5
- Fink, G. (1997) **Neural mechanisms involved in the processing of global and local aspects of hierarchically organized visual stimuli.** *Brain* 120, 1779-1791
- Freeman, T.; Harris, M. (1992) **Human sensitivity to expanding and rotating motion: effects of complementary masking and directional structure.** *Vision Res.* 32, 81-87
- Geesaman, B. (1998) **The effect of complex motion pattern on speed perception.** *Vision Res.* 38, 1223-1231
- Gescheider, G. A. (1997) **Psychophysics: The Fundamentals.** 448
- Ghose, G. M. (2004) **Learning in mammalian sensory cortex.** *Curr. Opin. Neurobiol.* 14, 513-518
- Ghose, G. M.; Yang, T.; Maunsell, J. H. (2002) **Physiological correlates of perceptual learning in monkey V1 and V2.** *J. Neurophysiol.* 87, 1867-1888

- Gibson, J. J. (1950) **The Perception of the Visual World.**
- Gilbert, C. D.; Sigman, M.; Crist, R. E. (2001) **The neural basis of perceptual learning.** *Neuron* 31, 681-697
- Goldberg, H. J.; Wichansky, A. M. (2003) **Eye Tracking in Human-Computer Interaction and Usability Research: Current Status and Future Prospects.** *Amsterdam: Elsevier.* 493-516
- Goldstone, R. L. (1998) **Perceptual learning.**
- Graziano, M. S.; Andersen, R. A.; Snowden, R. J. (1994) **Tuning of MST neurons to spiral motions.** *J. Neurosci.* 14, 54-67
- Grossman, E.; Donnelly, M.; Price, R., et al (2000) **Brain areas involved in perception of biological motion.** *J. Cogn. Neurosci.* 12, 5, 711-720
- Harris, J.; Watamaniuk, S. (1995) **Speed discrimination of motion-in-depth using binocular cues.** *Vision Res.* 35, 885-896
- Harris, J. A.; Petersen, R. S.; Diamond, M. E. (2001) **The cortical distribution of sensory memories.** *Neuron* 30, 315-318
- Hochstein, S.; Ahissar, M. (2002) **View from the Top.** *Neuron* 36, 791-804
- Julesz, B. (2007) **Foundations of Cyclopean Perception.** *Optometry and Vision Science* 84, 9, 827-828
- Kaernbach, C. (2001) **Adaptive threshold estimation with unforced-choice tasks.** *Percept. Psychophys.* 63, 1377-1388
- Kapadia, M. K.; Gilbert, C. D.; Westheimer, G. (1994) **A quantitative measure for short-term cortical plasticity in human vision.** *J. Neurosci.* 14, 451-457
- Karni, A.; Sagi, D. (1991) **Where practice makes perfect in texture discrimination: evidence for primary visual cortex plasticity.** *Proc. Natl. Acad. Sci. U.S.A.* 88, 4966-4970
- Karni, A.; Sagi, D. (1993) **The time course of learning a visual skill.** *Nature* 365, 250-252
- Kastner, S.; Ungerleider, L. G. (2000) **Mechanisms of visual attention in the human cortex.** *Annu. Rev. Neurosci.* 23, 315-341
- Leek, M. R. (2001) **Adaptive procedures in psychophysical research.** *Percept. Psychophys.* 63, 1279-1292

Liu,Z.; Weinshall,D.(2000)**Mechanisms of generalization in perceptual learning.***Vision Res.*40,97-109

Logothetis,N. K. (2002)**The neural basis of the blood-oxygen-level-dependent functional magnetic resonance imaging signal.***Philos. Trans.R. Soc.Lond.B.Biol.Sci.*357,1003-1037

Logothetis,N. K.; Pauls,J.; Augath,M.; Trinath,T.;Oeltermann,A.(2001)**Neurophysiological investigation of the basis of the fMRI signal.***Nature*412,150-157

Lopez-Moliner,J.; Smeets,J. B.;Brenner,E.(2004) **Components of motion perception revealed: two different after-effects from a single moving object.***Vision Res.*44,2545-2549

Lu,Z. L.; Hua,T.; Huang,C. B.; Zhou,Y.;Doshier,B. A.(2011) **Visual perceptual learning.***Neurobiol.Learn.Mem.*95,145-151

Mackay,T. L.; Jakobson,L. S.; Ellemberg,D.; Lewis,T. L.; Maurer,D.;Casiro,O.(2005) **Deficits in the processing of local and global motion in very low birthweight children.***Neuropsychologia*43,1738-1748

Maunsell,J. H.; Van Essen,D. C.(1983) **Functional properties of neurons in middle temporal visual area of the macaque monkey. I. Selectivity for stimulus direction, speed, and orientation.***J.Neurophysiol.*49,1127-1147

Maunsell,J. H.; Van Essen,D. C.(1983) **The connections of the middle temporal visual area (MT) and their relationship to a cortical hierarchy in the macaque monkey.***J.Neurosci.*3,2563-2586

Mednick,S.; Nakayama...,K.(2003)**Sleep-dependent learning: a nap is as good as a night.**

Meese,T. (2002) **Spiral mechanisms are required to account for summation of complex motion components.***Vision Res.*42,1073-1080

Meese,T. S.; Harris,M. G.(2001) **Independent detectors for expansion and rotation, and for orthogonal components of deformation.***Perception*30,1189-1202

Meese,T. S.; Harris,M. G.(2001) **Broad direction bandwidths for complex motion mechanisms.***Vision Res.*41,1901-1914

Merians,A. S.; Poizner,H.; Boian,R.; Burdea,G.;Adamovich,S.(2006)**Sensorimotor training in a virtual reality**



**environment: does it improve functional recovery poststroke?**

*Neurorehabil. Neural Repair*20,252-267

Morrone, M. C.; Burr, D.; Vaina, L. M. (1995) **Two stages of visual processing for radial and circular motion.***Nature*376,507-509

Morrone, M. C.; Tosetti, M.; Montanaro, D.; Fiorentini, A.; Cioni, G.; Burr, D. C. (2000) **A cortical area that responds specifically to optic flow, revealed by fMRI.***Nat. Neurosci.*3,1322-1328

Movshon, J. A., Adelson, E. H., Gizzi, M. S. & Newsome, W. T. (1985) **The Analysis Of Moving Visual Patterns.***In C. Chagas, R. Gattass & C. Gross (Eds.), Pattern recognition mechanisms*,117-151

Movshon, J. A.; Newsome, W. T. (1996) **Visual Response Properties of Striate Cortical Neurons Projecting to Area MT in Macaque Monkeys.***Visual Neuroscience*16,7733-7741

Nawrot, M.; Rizzo, M. (1995) **Motion perception deficits from midline cerebellar lesions in human.***Vision Res.*35,723-731

Newsome, W. T.; Pare, E. B. (1988) **A selective impairment of motion perception following lesions of the middle temporal visual area (MT).***J. Neurosci.*8,2201-2211

Nishina, S.; Kawato, M.; Watanabe, T. (2009) **Perceptual learning of global pattern motion occurs on the basis of local motion.***J. Vis.*9,15.1-15.6

Paz, R.; Wise, S. P.; Vaadia, E. (2004) **Viewing and doing: similar cortical mechanisms for perceptual and motor learning.***Trends Neurosci.*27,496-503

Piedade, M.; Gerald, J.; Sousa, L. A.; Tavares, G.; Tomas, P. (2005) **Visual neuroprosthesis: a non invasive system for stimulating the cortex.***IEEE Transactions on Circuits and Systems I: Regular Papers*52,2648-2662

Pleger, B.; Foerster, A. F.; Ragert, P., et al (2003) **Functional imaging of perceptual learning in human primary and secondary somatosensory cortex.***Neuron*40,643-653

Poole, A.; Ball, L. J. (2005) **Eye Tracking in Human-Computer Interaction and Usability Research: Current Status and Future.***Prospects", Chapter in C. Ghaoui (Ed.): Encyclopedia of Human-Computer Interaction. Pennsylvania: Idea Group, Inc.*780,

Recanzone, G. H.; Merzenich, M. M.; Jenkins, W. M.; Grajski, K. A.; Dinse, H. R. (1992) **Topographic reorganization of the hand representation in cortical**

**area 3b owl monkeys trained in a frequency-discrimination task.***J.Neurophysiol.*67,1031-1056

Recanzone,G. H.; Schreiner,C. E.;Merzenich,M. M.(1993) **Plasticity in the frequency representation of primary auditory cortex following discrimination training in adult owl monkeys.***J.Neurosci.*13,87-103

Rodman,H. R.; Albright,T. D.(1989) **Single-unit analysis of pattern-motion selective properties in the middle temporal visual area (MT).***Exp.Brain Res.*75,53-64

Rouger,J.; Lagleyre,S.; Fraysse,B.; Deneve,S.; Deguine,O.;Barone,P.(2007) **Evidence that cochlear-implanted deaf patients are better multisensory integrators.***Proc.Natl.Acad.Sci.U.S.A.*104,7295-7300

Saito,H.; Yukie,M.; Tanaka,K.; Hikosaka,K.; Fukada,Y.;Iwai,E.(1986) **Integration of direction signals of image motion in the superior temporal sulcus of the macaque monkey.***J.Neurosci.*6,145-157

Schiltz,C.; Bodart,J. M.; Dubois,S., et al(1999) **Neuronal mechanisms of perceptual learning: changes in human brain activity with training in orientation discrimination.***Neuroimage*9,46-62

Schnupp,J. W.; Kacelnik,O.(2002) **Cortical plasticity: learning from cortical reorganization.***Curr.Biol.*12,R144-6

Schwartz,S.; Maquet,P.;Frith,C.(2002) **Neural correlates of perceptual learning: a functional MRI study of visual texture discrimination.***Proc.Natl.Acad.Sci.U.S.A.*99,17137-17142

Seitz,A.; Watanabe,T.(2005) **A unified model for perceptual learning.***Trends Cogn.Sci.*9,329-334

Seitz,A. R.; Watanabe,T.(2003) **Psychophysics: Is subliminal learning really passive?***Nature*422,36

Shepherd,A. J. (2006) **Local and global motion after-effects are both enhanced in migraine, and the underlying mechanisms differ across cortical areas.***Brain*129,1833-1843

Shiu,L. P.; Pashler,H.(1992) **Improvement in line orientation discrimination is retinally local but dependent on cognitive set.***Percept.Psychophys.*52,582-588

Smith,L. B. (1989) **A model of perceptual classification in children and adults.***Psychol.Rev.*96,125-144

- Snowden, R. J.; Milne, A. B. (1996) **The Effects of Adapting to Complex Motions: Position Invariance and Tuning to Spiral Motions.** *J. Cogn. Neurosci.* 8, 435 - 452
- Snowden, R. J.; Kavanagh, E. (2006) **Motion perception in the ageing visual system: minimum motion, motion coherence, and speed discrimination thresholds.** *Perception* 35, 9-24
- Stone, L.; Thompson, P. (1992) **Human speed perception is contrast dependent.** *Vision Res.* 32, 1535-1549
- Sundareswaran, V.; Vaina, L. M. (1995) **Learning direction in global motion: two classes of psychophysically-motivated models.**
- Treisman, A. (1977) **Focused attention in the perception and retrieval of multidimensional stimuli.** *Percept. Psychophys.* 22, 1-11
- Tsotsos, J. K.; Liu, Y.; Martinez-trujillo, J. C.; Pomplun, M.; Simine, E.; Zhou, K. (2004) **Attending to Visual Motion.** *CVIU* 100, 3-40
- Turpin, A.; McKendrick, A. M.; Johnson, C. A.; Vingrys, A. J. (2003) **Properties of perimetric threshold estimates from full threshold, ZEST, and SITA-like strategies, as determined by computer simulation.** *Invest. Ophthalmol. Vis. Sci.* 44, 4787-4795
- Ungerleider, L. G.; Desimone, R. (1986) **Cortical connections of visual area MT in the macaque.** *J. Comp. Neurol.* 248, 190-222
- Vaina, L. M. (1998) **Complex motion perception and its deficits.** *Curr. Opin. Neurobiol.* 8, 494-502
- Van Essen, D.; Anderson, C.; Felleman, D. (1992) **Information processing in the primate visual system: an integrated systems perspective.** *Science* 255, 419-423
- Van Essen, D. C.; Gallant, J. L. (1994) **Neural mechanisms of form and motion processing in the primate visual system.** *Neuron* 13, 1, 1-10
- Van Essen, D. C.; Maunsell, J. H. R. (1983) **Hierarchical organization and functional streams in the visual cortex.** *Trends Neurosci.* 6, 370-375
- Vanduffel, W.; Denis, F.; Mandeville, J. B., et al (2001) **Visual Motion Processing Investigated Using Contrast Agent-Enhanced fMRI in Awake Behaving Monkeys.** *Neuron* 32, 565 -577

Vidyasagar, T. R.; Stuart, G. W. (1993) **Perceptual learning in seeing form from motion.** *Proc. Biol. Sci.* 254, 241-244

Vogels, R. (2010) **Mechanisms of Visual Perceptual Learning in Macaque Visual Cortex.** *Topics in Cognitive Science* 2, 239-250

Volpe, B. T.; Krebs, H. I. (2001) **Is robot-aided sensorimotor training in stroke rehabilitation a realistic option?**

Wakde S., Beardsley S. (2009) **Task dependent learning of complex motion across visual motion areas.**

Wall, M. B.; Smith, A. T. (2008) **The representation of Egomotion in the human brain.** *Journal of Current Biology* 18, 3, 191-194

Watanabe, T.; Nanez JE, S.; Koyama, S.; Mukai, I.; Liederman, J.; Sasaki, Y. (2002) **Greater plasticity in lower-level than higher-level visual motion processing in a passive perceptual learning task.** *Nat. Neurosci.* 5, 1003-1009

Yang, T.; Maunsell, J. H. (2004) **The effect of perceptual learning on neuronal responses in monkey visual area V4.** *J. Neurosci.* 24, 1617-1626

Zeithamova, D.; Maddox, W. T. (2006) **Dual-task interference in perceptual category learning.** *Memory Cognition* 34, 3, 387-398; -398

## 9 APPENDIX

### 9.1 APPENDIX A1

#### Monitor properties during testing

| Monitor Properties                      |            |          |       |       |
|---|------------|----------|-------|-------|
| Nominal Refresh Rate (Hz):              | 60         |          |       |       |
| Actual Refresh Rate (Hz):               | 59.94      |          |       |       |
| StD of Refresh Rate (Hz):               | 0.63       |          |       |       |
| Pixel Color Depth (bits):               | 32         |          |       |       |
| Width (pixels):                         | 1920       |          |       |       |
| Height (pixels):                        | 1440       |          |       |       |
| Viewing Distance (cm):                  | 60         |          |       |       |
| Pixels per Degree:                      | 52.08      |          |       |       |
| Pixels per Minute:                      | 0.87       |          |       |       |
|   | Horizontal | Vertical |       |       |
| Dimensions (cm):                        | 40         | 30       |       |       |
| Center (pixels):                        | 960        | 720      |       |       |
|   | Gray       | Red      | Green | Blue  |
| Maximum Luminance (Cd/m <sup>2</sup> ): | 98.55      | 98.55    | 98.55 | 98.55 |

## 9.2 APPENDIX A2

**Stimulus aperture properties during testing**

| Aperture Properties                       |             |             |
|---|-------------|-------------|
| Polar angle (deg): Left visual field      | 145         | 215         |
| Polar angle (deg): Right visual field     | 35          | 325         |
| Outer diameter (deg of visual angle):     | 8           | 8           |
| Inner diameter (deg of visual angle):     | 0           | 0           |
|   | Aperture 1  | Aperture 2  |
| Aperture Shape:                           | Circle      | Circle      |
| Eccentricity (deg of visual angle):       | 17.17       | 17.17       |
| Type of Motion:                           | Planar      | Planar      |
| Type of Noise:                            | Random Walk | Random Walk |
| Height (deg of visual angle):             | 8           | 8           |
| Width (deg of visual angle):              | 8           | 8           |
| Background Luminance (Cd/m <sup>2</sup> ) | Gray:       | 20.03       |

**9.3 APPENDIX A3****Stimulus properties during testing**

| Stimulus properties                              |                   |
|--|-------------------|
| Reference frame for aperture Eccentricity/Angle: | Fixation-Centered |
| Stimulus duration (sec):                         | 0.5               |
| Exit stimulus on key press (1=yes, 0=no):        | 0                 |
| Number of stimulus apertures:                    | 2                 |
| Delay between stimuli in 2-TAFC paradigm (sec) : | 0.5               |
| Max. Change in Direction (deg.):                 | 40                |
| Max. Change in Speed (deg/s):                    | 0                 |

## 9.4 APPENDIX A4

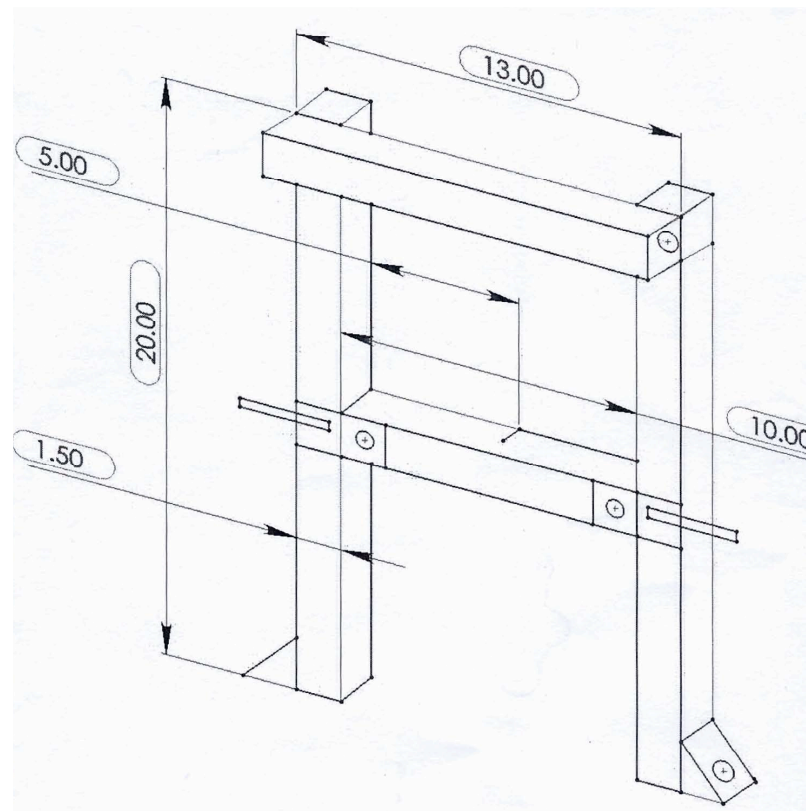
Key press responses accepted by the subject during testing.

| Action Required | Key Press   |
|-----------------|---|
| Quit            | 'q', 'ESCAPE'   |
| Repeat          | 'r'   |
| Help            | 'h'   |
| Answer          | ('1', '2') – Numeric keypad,<br>( '1!', '2@' ) -- Alphanumeric keypad |
| Abort Trial     | '*'   |
| fMRI Trigger    | '=', '=+'   |



## 9.5 APPENDIX A5

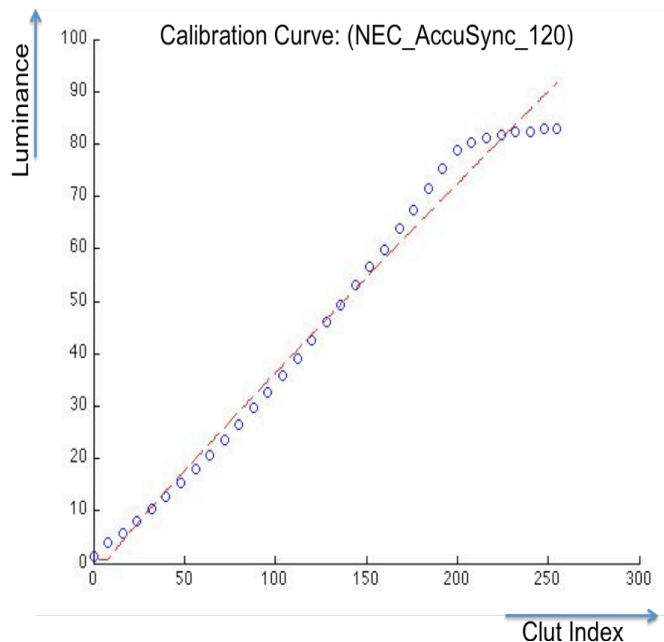
The chin-rest system has been designed for vision scientists and experimental psychologists, and includes facilities, which they require. The headrest designed is an adjustable piece with the height and size of the subject's head. The dimensional view of headrest is as shown in Figure 3.6. The material used is of high-tensile aluminum profiles and assembled cleanly without further surface processing. The headrest is designed with the help of software Solid Works and developed at the Discovery Learning center at Marquette University.



The head and chin rest dimensional view

## 9.6 APPENDIX A6

The monitor calibration with a luminance meter is one of the important steps conducted before experimentation. Luminance is used in visual experiments to characterize the brightness of displays. The luminance meter is used to get RGB luminance curves of the CRT monitor. Several stepwise luminance measurements are taken through all the combinations of 256 levels in color clut (color look-up table). The clut is a mechanism used to transform a range of input colors into another range of colors ( e.g. From hardware clut to logical clut(physical color) ). Plotting a luminance graph (shown below) with the help of the Luminance meter tests the luminance's of CRT monitor at different clut index and thus can be used for calibration of the monitor.



The calibration curve of the CRT monitor (NEC\_AccuSync\_120)