Delineating the "Task-Irrelevant" Perceptual Learning Paradigm

in the Context of Temporal Pairing, Auditory Pitch, and the Reading Disabled

by

Steven Robert Holloway

A Dissertation Presented in Partial Fulfillment of the Requirements for the Degree Doctor of Philosophy

Approved April 2016 by the Graduate Supervisory Committee:

Michael McBeath, Chair Stephen Macknik Donald Homa José E. Náñez, Sr.

ARIZONA STATE UNIVERSITY

May 2016

©2016 Steven Robert Holloway All Rights Reserved

ABSTRACT

Watanabe, Náñez, and Sasaki (2001) introduced a phenomenon they named "taskirrelevant perceptual learning" in which near-threshold stimuli that are not essential to a given task can be associatively learned when consistently and concurrently paired with the focal task. The present study employs a visual paired-shapes recognition task, using colored polygon targets as salient attended focal stimuli, with the goal of comparing the increases in perceptual sensitivity observed when near-threshold stimuli are temporally paired in varying manners with focal targets. Experiment 1 separated and compared the target-acquisition and target-recognition phases and revealed that sensitivity improved most when the near-threshold motion stimuli were paired with the focal target-acquisition phase. The parameters of sensitivity improvement were motion detection, critical flicker fusion threshold (CFFT), and letter-orientation decoding. Experiment 2 tested perceptual learning of near-threshold stimuli when they were offset from the focal stimuli presentation by ± 350 ms. Performance improvements in motion detection, CFFT, and decoding were significantly greater for the group in which near-threshold motion was presented after the focal target. Experiment 3 showed that participants with reading difficulties who were exposed to focal target-acquisition training improved in sensitivity in all visual measures. Experiment 4 tested whether near-threshold stimulus learning occurred cross-modally with auditory stimuli and served as an active control for the first, second, and third experiments. Here, a tone was paired with all focal stimuli, but the tone was 1 Hz higher or lower when paired with the targeted focal stimuli associated with recognition. In Experiment 4, there was no improvement in visual sensitivity, but there was significant improvement in tone discrimination. Thus, this study, as a whole,

i

confirms that pairing near-threshold stimuli with focal stimuli can improve performance in just tone discrimination, or in motion detection, CFFT, and letter decoding. Findings further support the thesis that the act of trying to remember a focal target also elicited greater associative learning of correlated near-threshold stimulus than the act of recognizing a target. Finally, these findings support that we have developed a visual learning paradigm that may potentially mitigate some of the visual deficits that are often experienced by the reading disabled. I would like to dedicate this dissertation to Kathryn L. Van Etten, whose patience, support, and editing skills have been essential to my success. She has been a beacon of encouragement and a stalwart critic who has always ensured that I will never suffer from a lack of opposition. Thank you for all that you do!

I would also like to dedicate this dissertation to my late father, Billy Dee Holloway. My pursuit of this degree has enabled me to realize a dream my father had, but one he was unable to fulfill due to his untimely death. Although my Dad died when I was only nine years old, he set my feet on the path to enlightenment. He also instilled in me the importance of setting goals and persevering in the pursuit of an education. It has been my father's principles that I have employed to accomplish my aspirations. I am forever grateful!

ACKNOWLEDGMENTS

I wish to thank my graduate advisor, Dr. Michael McBeath, for the guidance and support he has provided throughout my graduate school tenure.

I would also like to thank Dr. José Náñez for his exceptional mentorship, the use of his lab, and the financial assistance he generously provided in support of this study, without which I do not think I could have finished this project or my degree.

Additionally, I wish to express my appreciation to Dr. Donald Homa and Dr. Stephen Macknik who graciously donated their time and energy to serve on my dissertation committee and for the training and advice they have imparted to me over the past few years.

I also want to thank the undergraduate research assistants in the Cognitive Vision Science Lab and the numerous colleagues with whom I have worked these many years.

Finally, I would like to thank Joseph Gordon for his exceptional programming skills, his tolerance of my lack of programming skills, and his ever present sense of humor.

TABLE OF CONTENTS

LIST OF TABLES	vii
LIST OF FIGURES	viii
INTRODUCTION	1
Experiment 1: Target Acquisition versus Recognition	7
Experiment 2: Timing of Pairing with Motion Exposure	10
Experiment 3: Decoding, Flicker, and the Reading Disabled	
Experiment 4: Tone Discrimination and the Visual Learning Paradigm	15
Summary	16
METHOD	17
Participants	17
General Procedures	17
Testing Procedures	19
Motion Detection Test	19
Flicker Perception Test	20
Decoding Test	20
Tone Discrimination Test	22
Training Procedures	23
Motion Training	23
Tone Discrimination Training	26
Data Analysis	

	Page
RESULTS	
Experiment 1	29
Target-Acquisition Condition	29
Target-Recognition Condition	
Comparison of the Acquisition and Recognition Conditions	37
Experiment 2	
Motion Presented 350 ms before Target-Recognition Condition	
Motion Presented 350 ms after Target-Recognition Condition	42
Comparison of the 350 ms Before and 350 ms After Conditions	46
Experiment 3	47
Reading Disabled Target-Acquisition Condition	47
Reading Disabled Tone-Recognition Condition	51
Experiment 4	55
Tone-Discrimination Condition (Control)	55
Overall Relation across Effects	59
DISCUSSION	60
Experiment 1	61
Experiment 2	62
Experiment 3	62
Experiment 4	65
Take Home Message	65
REFERENCES	67

LIST OF TABLES

Table	Ι	Page
1.	Overall Relation across P-values and Effect Size	59

LIST OF FIGURES

Figure	Page
1.	Schematic of Experimental Procedure for All Conditions
2.	Schematic of Target-Recognition Training Procedure
3.	Schematic of Testing Procedure for Motion Detection
4.	Schematic of Testing Procedure for Decoding
5.	Schematic of Training Procedure for Motion
6.	Schematic of Timing Where Motion is Paired with Recognition
7.	Schematic of Timing Where Motion is 350 ms before Recognition
8.	Schematic of Timing Where Motion is 350 ms after Recognition
9.	Schematic of Timing Where Tone is Paired with Recognition
10.	Schematic of Training Procedure for Tone
11.	Motion Detection Accuracy for Target-Acquisition Condition
12.	Flicker Perception Thresholds for Target-Acquisition Condition
13.	Decoding Accuracy for Target-Acquisition Condition
14.	Tone Discrimination Accuracy for Target-Acquisition Condition
15.	Motion Detection Accuracy for Target-Recognition Condition
16.	Flicker Perception Thresholds for Target-Recognition Condition
17.	Decoding Accuracy for Target-Recognition Condition
18.	Tone Discrimination Accuracy for Target-Recognition Condition
19.	Comparison of the Acquisition and Recognition Conditions
20.	Motion Detection Accuracy for 350 ms Before Recognition Condition
21.	Flicker Perception Thresholds for 350 ms Before Recognition Condition 39

22.	Decoding Accuracy for 350 ms Before Recognition Condition
23.	Tone Discrimination Accuracy for 350 ms Before Recognition Condition 41
24.	Motion Detection Accuracy for 350 ms After Recognition Condition
25.	Flicker Perception Thresholds for 350 ms After Recognition Condition 43
26.	Decoding Accuracy for 350 ms After Recognition Condition 44
27.	Tone Discrimination Accuracy for 350 ms After Recognition Condition 45
28.	Comparison of the 350 ms Before and 350 ms After Conditions 46
29.	Reading Disabled Motion Detection Accuracy for Acquisition Condition 47
30.	Reading Disabled Flicker Perception Thresholds for Acquisition Condition 48
31.	Reading Disabled Decoding Accuracy for Acquisition Condition 49
32.	Reading Disabled Tone Discrimination Accuracy for Acquisition Condition 50
33.	Reading Disabled Motion Detection Accuracy for Tone Condition
34.	Reading Disabled Flicker Perception Thresholds for Tone Condition
35.	Reading Disabled Decoding Accuracy for Tone Condition
36.	Reading Disabled Tone Discrimination Accuracy for Tone Condition
37.	Motion Detection Accuracy for Tone Condition
38.	Flicker Perception Thresholds for Tone Condition
39.	Decoding Accuracy for Tone Condition 57
40.	Tone Discrimination Accuracy for Tone Condition

Introduction

A fundamental concern in neuroscience is how the adult brain adapts to salient environmental changes without over-responding to the relentless stream of trivial information to which observers are exposed. In 1980, Stephan Grossberg argued that any neurally-based learning system would need to mediate what he termed the *noisesaturation dilemma*. The current study explores the possibility that this dilemma would be mitigated if a neuro-modulator system exists that requires concentration to elicit plasticity. If this notion is true, we should be able to observe the effects of the neuromodulator system by using particular behavioral measures incorporated into a precisely designed experiment.

High-level perceptual processing has been shown to exhibit extensive plasticity, especially for implicit learning (Jiménez & Méndez, 2001), such as priming (Tipper & Cranston, 1985; Wiggs & Martin, 1998) and contextual learning (Adini, Sagi, & Tsodyks, 2002; Olson & Chun, 2001). In contrast, the early sensory systems traditionally have been thought to exhibit plasticity primarily during early development and to a much lesser extent in adults (Marr, 1982). This view has been supported by studies of critical period development which have shown that the occurrence of gross plasticity in early sensory areas is restricted to brief periods occurring shortly after birth (Wiesel & Hubel, 1965). These findings support the thesis that the low-level sensory systems principally process primitive sensory features such as visual orientation, spatial frequency, and local motion. One proposed solution to the noise-saturation dilemma in adults is that a given organism has a rigid, low-level, neural architecture with significant plasticity occurring only at the higher-level processing systems.

The notion that low-level sensory systems are stable and not subject to change has been challenged by studies of perceptual learning (Ahissar & Hochstein, 1997; Dosher & Lu, 1998; Glenberg et al., 2010; Morikawa & McBeath, 1992) which show that with repeated exposure or training, even adult sensory systems can exhibit improvement in perceptual abilities. Moreover, psychophysical studies of visual plasticity have demonstrated that perceptual thresholds can be improved with a very high degree of specificity with respect to the visual sensory features orientation (Fiorentini & Berardi, 1980; Li, Thier, & Wehrhahn, 2000), ocularity (Fahle, Edelman, & Poggio, 1995), motion direction (Ball & Sekuler, 1981; Watanabe et al., 2001), and retinotopic location (Fiorentini & Berardi, 1980). The extreme task specificity provides evidence that the plasticity in these sensory cortical areas must include very low-level stages of processing (Crist, Kapadia, Westheimer, & Gilbert, 1997), although this does not exclude the possible contributions from higher-level neural systems (Ahissar & Hochstein, 1997; Dosher & Lu, 1998).

Sensory plasticity of basic, low-level, sensory features has been confirmed by studies of electrophysiology in animals and functional imaging in humans. Specifically, vision research using single-cell recordings has confirmed activity of cells changes in the early visual cortex of monkeys (Gilbert, Sigman, & Crist, 2001; Schoups, Vogels, Qian, & Orban, 2001; Yang & Maunsell, 2004; Zohary, Shadlen, & Newsome, 1994). In addition, magnetic resonance studies documented neural change in the V1 area of humans (Furmanski, Schluppeck, & Engel, 2004; Schwartz, Maquet, & Frith, 2002) and in the primate homologue to the MT/V5 (Vaina, Soloviev, Bienfang, & Cowey, 2000), while at the same time confirming a correlation of neural change with perceptual

learning. Plasticity of early processing areas has also been observed with other modalities such as audition (Bao, Chan, & Merzenich, 2001; Kilgard & Merzenich, 1998), somato-sensation (Dinse, Ragert, Pleger, Schwenkreis, & Tegenthoff, 2003; Kaas, Merzenich, & Killackey, 1983), and with motor functions (Li, Padoa-Schioppa, & Bizzi, 2001; Pascual-Leone, Bartres-Faz, & Keenan, 1999). These findings are consistent with neural plasticity in the primary cortical areas for these modalities.

In 2001, Watanabe, Náñez, and Sasaki demonstrated that associative perceptual learning can occur as a result of a participant's exposure to the pairing of a salient focal visual target with a near-threshold stimulus, designed to be unattended (i.e., awareness of the stimulus is not essential in order to accurately perform the focal task). This work supports the theory that sensory plasticity to the near-threshold signal occurs as a result of associative reinforcement that is a byproduct of the intended reinforced learning of the focal task. The neural activity associated with the non-essential task is inadvertently reinforced along with the neural activity associated with the paired focal stimulus on which the participant is concentrating (Watanabe et al., 2002). This reinforcement system is likely mediated by neuro-modulators such as acetylcholine, noradrenalin, and dopamine, that are widely released throughout the whole brain during task-specific concentration and have been implicated in neural plasticity (Arnsten, 1997; Dalley et al., 2001; Schultz, 2000). When a participant concentrates on a focal task-target, the increased neuro-modulators support and strengthen all neurons that are active, including those that are responding to the near-threshold stimuli, resulting in plasticity in neurons associated with both focal and dim, non-essential stimuli that are active at the moment of concentration. Thus, visual neurons that are responsive to dim, or very weak, but

associated stimuli show improved sensitivity simply because they were reinforced concurrently with the occurrence of a salient focal perceptual task that required concentration.

Interestingly, Tsushima, Seitz, and Watanabe (2008) found that plasticity to associated, non-essential, near-threshold stimuli only occurs when such stimuli are dim. Their results indicate that features not related to the focal task are learned only when they are presented near-threshold, not when they are presented supra-threshold. Tsushima argues that when a feature in the environment is noticeable and not essential to the task at-hand, an active suppression system inhibits the neural network's response to the nonsalient feature. The neural network can be reinforced and induce plasticity only when a stimulus that is non-essential to the task is near-threshold. This notion is supported by recent research that found that the human pre-frontal cortex has a higher threshold for responding to supraliminal motion signals that are presented as distractors compared to the central dorsal visual system responding to dim, distracting, perceptual stimuli. In essence, Tsushima contends that when motion is presented supraliminally and is not essential to the task, the area in the pre-frontal cortex which is involved in the inhibitory control of attention is likely impeding the area of the visual system known to be specialized in motion-direction processing (Knight, Staines, Swick, & Chao, 1999; Tsushima, Sasaki, & Watanabe, 2006).

Seitz and Watanabe (2003) suggested that, similar to classical conditioning, these reinforcement signals occur as a result of a participant's successful recognition of the serially presented task-targets and the awareness of performance levels. By pairing a challenging, salient focal task with a perceptually dim, non-essential, near-threshold

stimulus during large numbers of trials, the near-threshold stimulus is inadvertently learned. By having some long-term plasticity expressed in all neural systems, the learning of low-level perceptual features could occur but be limited to cases when it is reliably paired with performance of salient, focal, higher-level tasks.

The current study seeks to expand our understanding of the relationship between a person's concentration on a strong, focal stimuli and the associated learning of a weak, non-essential, near-threshold stimuli. In a series of experiments, we examine the differences that occur in learning by varying the placement of near-threshold stimuli, comprised of dim motion gradients, in relation to the presentation of focal target stimuli. Experiment 1 tests associative learning when the non-essential, near-threshold stimuli is presented at the moment an associated focal target is initially observed and remembered (a condition that we labeled "target-acquisition") versus at the moment when the focal target is later recognized in a serial string of distractors (a condition that is labeled "target-recognition"). Experiment 2 tests the strength of learning the non-essential, nearthreshold motion when it is paired with the recognition of the focal target, but with a temporal offset either 350 ms before or 350 ms after the focal target. Experiment 3 tests the effects of this learning paradigm on participants with reading difficulties, particularly with regard to their ability to decode letters following learning the near-threshold motion gradient stimuli. Experiment 4 serves as an active control, with the same focal stimuli, but with nonessential, near-threshold stimuli of a different modality. Instead of dim visual motion-gradients, the near-threshold stimuli consist of acoustic tones that are paired with the focal target stimuli at the time of target-recognition.

Four measures were used to assess learned changes in perceptual sensitivity as an effect of the associative perceptual learning paradigm. First, motion-gradient sensitivity was included because most of the previous research in associated, near-threshold stimulus learning (or "task-irrelevant" learning) used motion-detection changes to assess the effectiveness of the paradigm; we, too, paired peripheral motion-gradients with the focal targets. Second, critical flicker fusion threshold (CFFT) was used because it is wellestablished as a measure of central dorsal stream visual processing (Holloway & McBeath, 2013; Leonards & Singer, 1997) and because low flicker threshold rates have been observed in reading disabled populations (Felmingham & Jakobson, 1995; Martin & Lovegrove, 1987). Moreover, research has shown that flicker perception improves when participants are trained to better see motion (Seitz, Náñez, Holloway, & Watanabe, 2005; Seitz, Náñez, Holloway, & Watanabe, 2006). Third, a psychophysical, non-linguistic measure of letter or shape decoding was used because this particular test has been shown to be highly correlated with real word and non-word decoding (Holloway, Náñez, & Seitz, 2013). Finally, in Experiment 4, tone discrimination was used to assess whether an auditory signal could be used as the non-essential, near-threshold stimuli that is paired with a visual focal target, using the current perceptual learning paradigm. Peripherally learned tone-discrimination thus served as an active different-modality control test compared to the peripherally learned motion-gradient conditions in the prior three experiments.

Experiment 1: Target Acquisition versus Recognition

An important question in perceptual learning research is: How do our sensory systems know *what* to learn? In other words, how does a sensory learning system process the relevance of information in a busy "real world" environment? Given that plasticity can occur in early sensory systems, there must be some mechanism, or gate, that solves the noise-saturation dilemma other than a rigid, low-level architecture. In particular, the early sensory system must have some means to control what aspects of the sensory environment are learned and what aspects are not.

Although focused attention has been proposed to provide a type of gate that allows perceptual learning to occur (Ahissar & Hochstein, 1993), more recent research supports that perceptual learning also can occur without focal attention (Dinse et al., 2003; Watanabe et al., 2001). Attentional learning theories suggest that an active selection mechanism is typically necessary for learning (Nissen & Bullemer, 1987). The theory states that what is "attended to" will be learned. Accordingly, when nearthreshold stimuli are non-essential and do not appear to merit attention, they should not be learned. While attention is clearly important for some types of learning, universally requiring it for all learning is incorrect since non-essential, unattended features can be learned in cases where they are paired with important, attended to focal targets.

In 2003, Seitz and Watanabe suggested that the solution to this problem might be found in the conditioning mechanisms described by Pavlov (1927). Their idea was that non-essential elements in the sensory environment will be learned if they are repeatedly reinforced due to being paired with the moment that a focal target is recognized and remembered. In this way, an organism can efficiently adapt to the environment while

protecting itself from the instability that would occur if all environmental stimuli were learned. Consequently, they argue that a form of conditioning at the neuronal level and focused attention at a higher level work together to facilitate a type of adaptive low-level plasticity. Thus, it is through repeated reinforcement that the visual system, directed by prior knowledge that focuses attention, parses out what is important in the environment, thereby leading to learning only the information that is consistently available and correlated with salient information. In short, Seitz and Watanabe suggest that the mechanisms that are utilized in attention are actually the same as those that drive conditioning. They argue that the term "attention" is not consistently defined and is inconsistently applied between studies. Rather, they propose a more perfunctory view of attention in which the learning systems that support attention are more closely related to conditioning, and they suggest that researchers could employ their associative learning framework to better understand low-level perceptual learning.

Research by Watanabe et al. (2001) has shown that the act of identifying a target among a serial string of distractors creates a moment of recognition that is concurrent with the acquisition of the target (Watanabe et al., 2001). In their original learning paradigm, two off-color (slightly lighter or darker shades of grey) letters are nested among distractors in a string of eight letters. The participants were required to remember and report the off-color letters and ignore the distractors. However, within this structure, two active gateways are functioning at once: The recognition that the off-color letter is the target; and the concentration exerted to remember the letter, so it can be correctly reported after the series has been completed.

More specifically, when participants see an off-color letter in a string of distractors, they recognize that the letter is off-color - this is target recognition. Then, they must remember the specific letter in order to report that letter when the string ends - this is target acquisition. The temporal occurrence of the acquisition-recognition event paired with the non-essential, near-threshold stimulus increases perceptual sensitivity to the latter. The present study tests the effect of pairing non-essential, near-threshold stimuli with either the acquisition of a focal target or the recognition of the focal target in a serial string of distractors.

In order to do this, we modified the structure of the learning paradigm to separate the acquisition of the focal target from the recognition of it. We predict that associative, "task-irrelevant" learning will occur in a visual paired-shapes recognition task, using colored polygon targets as salient, attended, focal stimuli. We predict that, because of the focal concentration required, there will be associative learning of the non-essential, nearthreshold stimuli which consists of dim, background motion gradients with one offcardinal direction paired with the occurrence of the focal target shapes. In addition, we predict that associative learning of the non-essential, near-threshold stimuli and performance on related psychophysical tests will be superior when the near-threshold stimuli are presented with the focal target stimulus as it is initially introduced (i.e., the target-acquisition condition) versus when it is presented later as a focally-targeted recognition stimulus (i.e., the target-recognition condition). If true, this finding would support the contention that a neuro-modulation system requiring concentration to elicit plasticity could mitigate the noise-saturation dilemma.

Experiment 2: Timing of Pairing with Motion Exposure

Another unanswered question regarding "task-irrelevant" learning is the temporal relation of concentration and dim stimuli exposure. Thus far, research in "task-irrelevant" learning predominantly has used methodology that simultaneously pairs near-threshold motion gradients with a target that is recognized and must be remembered (Seitz & Watanabe, 2003; Watanabe et al., 2001). How the timing of this pairing affects plasticity has been largely unexplored. More precisely, does the non-essential, near-threshold stimulus need to be presented at exactly the moment of focal concentration, or does some level of neural flexibility exist that would allow for pairing to be temporally close, but not simultaneous to the concentration? The limited research that has addressed this question expresses contradictory findings regarding the timing of reinforcement or stimulus exposure and plasticity.

Killeen and Fetterman (1988) developed a behavior model of timing based on the concept that there are pulses from an internal pacemaker that prompt a neural transition from one behavioral state to another. Their model suggests that each pulse from a pacemaker instigates a move from a current neural state to that of a new neural state, and that, in turn, affects behavior. A few years later, the researchers confirmed their theory using pigeons (Fetterman & Killeen, 1995). Essentially, Fetterman and Killeen's experiment found that certain neural states were tied to behavioral states, and that experimentally-derived pacemaker activity in pigeons demonstrated that learning improved only if the pulses were paired between 300 ms and approximately four minutes after the behavior. In the 1995 experiment, no pacemaker activity was paired less than 300 ms after a behavior. Similarly, Grondin (2001) showed that a reinforcement paired

with targeted behavior in humans was most effective when the reinforcement followed the desired behavior by 300 ms to 600 ms; no reinforcement was presented less than 150 ms after the behavior. It should be mentioned that neither of these studies reported pairing any type of reinforcement before a desired behavior.

Conversely, research in Spike-Timing-Dependent Plasticity (STDP), a form of Hebbian synaptic plasticity considered to be very temporally precise, has demonstrated that plasticity can be induced by creating isolated pre- and post-synaptic spikes in neurons (Bi & Poo, 1998; Gerstner, Kempter, van Hemmen, & Wagner, 1996; Markram, Lubke, Frotscher, & Sakmann, 1997; Sjöström, Turrigiano, & Nelson, 2001). In most cases, plasticity occurred when repeated activation of synaptic spikes were activated within 10 ms before or 10 ms after synaptic potentiation (Abbott & Nelson, 2000). Indeed, Abbott and Nelson found that no plasticity occurred outside of this window of 10 ms before to 10 ms after synaptic potentiation.

Contrasting these findings generates a number of questions regarding the current study. It appears that Fetterman and Killeen (1995) and Grondin (2001) are measuring something very different than the researchers investigating STDP. The obvious difference is that the pacemaker experiments and human behavior studies are affecting neural networks, while the STDP studies are affecting single cells. Although "taskirrelevant" perceptual learning must affect neural networks, not single cells, and thus, it is unlike the STDP studies, it is also unlike behavioral research which uses overt reinforcement to affect behavior.

The current study explores the question of how the timing of pairings may affect plasticity by pairing dim motion gradients 350 ms before target recognition and 350 ms

after target recognition. If mechanisms involved with "task-irrelevant" learning are precise and similar to the STDP paradigm, motion training should have no effect because the dim motion gradients are presented well outside the 10 ms before to 10 ms after window. Accordingly, no improvement in motion recognition should occur. However, if the mechanisms involved with this kind of learning are flexible and are similar to the behavioral studies, then learning should occur. Anticipating this will be the case, we predict that a pairing presented 350 ms after the recognition condition will show a more robust change in motion detection than a pairing presented 350 ms before the recognition condition.

Experiment 3: Decoding, Flicker, and the Reading Disabled

In 2005, Seitz et al. showed that "task-irrelevant" learning of near-threshold motion led to increased perception of flicker. Critical flicker fusion thresholds (CFFT) or flicker perception have been shown to be significantly lower in people who have a reading disability (Livingstone, Rosen, Drislane, & Galaburda, 1991). Research has implicated that the central dorsal stream, specifically the V3a to the MT, is at least partially responsible for one aspect of reading, namely word decoding (Holloway et al., 2013; Merzenich et al., 1996). Interestingly, this is the same region of the brain that is responsible for processing motion, contrast, and flicker (Maunsell, Nealey, & DePriest, 1990).

Cornelissen, Richardson, Mason, Fowler, and Stein (1995) demonstrated another magnocellular deficit that is present in dyslexics. Specifically, they showed that dyslexics have impaired motion sensitivity even at high contrast and illumination levels. This result has been confirmed by research exploring elicited potentials (Livingstone et al., 1991) and functional magnetic resonance imaging (fMRI) (Eden et al., 1996). The most convincing evidence however, is research showing that the post-mortem examination of the magnocellular layers of the lateral geniculate nucleus (LGN) in five dyslexic brains were disordered, and that the neurons themselves were over 20% smaller than in control brains (Livingstone et al.). This evidence suggests that many dyslexics may have a fundamental impairment in their low-level visual processing.

Recently, Gori, Seitz, Ronconi, Franceschini, and Facoetti (2015) demonstrated that motion training related to "task-irrelevant" perceptual learning radically improves the reading ability of Italian-speaking adults with dyslexia. They concluded that motion training not only elicited improvements in the magnocellular/dorsal (MD) pathway, but that it directly translated to better reading skills in Italian-speaking adults. Interestingly, their training paradigm also increased both peripheral visual perception and a temporal aspect of visual attention in the dyslexics who participated. However, the fact that Gori's study was done within the context of the Italian language leaves certain questions unanswered. Italian is a phonologically shallow language as compared to other languages, such as English. Accordingly, it is possible that Gori's results cannot be generalized to other languages.

To test whether our version of this learning paradigm would improve decoding in English speakers with reading difficulties, we recruited eight participants who selfidentified as having difficulty reading. Then, we exposed half of the subjects to the target-acquisition condition and half of them to the tone-training control condition. In participants with reading disabilities, we predict that not only will training increase their motion sensitivity, but also that it will improve flicker perception (CFFT) and decoding. In the present study, we used a non-linguistic, psychophysical decoding measure because it is highly correlated to real word decoding, and because it is highly relevant to studying reading disabilities (Holloway et al., 2013).

Experiment 4: Tone Discrimination and the Visual Learning Paradigm

In order to be confident that no extraneous variables were affecting the results of this study, we needed to establish a control group who were exposed to the training paradigm without motion. Moreover, it was decided that it would be preferable if the group was exposed to an active control that could train a different perceptual system.

Pitch discrimination is the ability to recognize that one tone is different from another by mentally establishing a relationship between a pitch and that of a recently heard tone. Most experienced musicians are very adept at pitch discrimination, and it is considered to be a trainable aptitude (Pantev et al., 1998). Moreover, Seitz et al. (2010) showed that auditory detection thresholds can be improved by pairing specific sounds with the task targets in a learning paradigm that presented near-threshold phonemes with an auditory perceptual task.

Therefore, as an active control for these studies, we chose to train participants to better discriminate between tones with a learning paradigm that paired non-essential, near-threshold tonal differences with the paired-shapes recognition paradigm. We predict that pairing a perceptually dim tone stimulus with target-recognition tasks will result in improvement of relative pitch perception but not motion detection, flicker perception, or decoding.

Summary

In this study, we predict that associative learning of near-threshold stimuli will occur in a visual paired-shapes recognition task, using colored polygon targets as salient attended focal stimuli.

In the first experiment, we pair near-threshold background motion gradients with salient, focal target shapes that the participant is asked to remember (i.e., the target-acquisition condition). We predict this pairing will elicit greater learning than pairing the near-threshold motion with the target as it repeats in a string of focal distractors (i.e., the target-recognition condition).

In the second experiment, we predict that the target-recognition group will perform better than a group who experiences motion presented 350 ms before the target in a string of distractors. We also predict that the group who experiences motion presented 350 ms after the target in the recognition paradigm will perform nearly as well as those in the target-recognition group.

In the third experiment, we predict that participants with reading disabilities who are exposed to target-acquisition training will improve in motion perception, flicker processing, and letter decoding, and those reading disabled who are engaged in tonetraining will improve in tone discrimination but not motion processing, flicker perception, or decoding.

The fourth experiment is an active control for the first three experiments where we paired a 400 Hz tone with the distractors and paired a 401 Hz tone with the target. Here, we predict that participants will improve in tone discrimination but not in motion perception, flicker processing, or letter decoding.

Method

Participants

Thirty participants were recruited from Arizona State University for this study, six in each of the five experimental conditions that comprised Experiments 1, 2, and 4. An additional eight participants with self-reported reading difficulties were recruited and paid \$75.00 each for their participation, resulting in a total of 38 participants for the entire project. Subjects participated in ten 60 - 90 minute sessions over three weeks, no more than one session per day, with no testing or training occurring during the weekends. The 10 "session days" consisted of a 1-day pre-test phase in which a total of four tests were administered, followed by an 8-day exposure/training stage, and ultimately, a 1-day post-test phase in which the initial four tests were re-administered. All participants reported good ocular health and had a best-corrected visual acuity (tested on-site) of 20/40 or better (Snellen). All experiments were run using custom software. Participants viewed displays at a distance of approximately three feet. Data collection and participant training occurred in a dim room wherein the ambient light level was maintained at approximately 4.7 cd/m^2 . Additionally, all participants were naive as to the purpose of the study. Informed consent was obtained from all participants, and this study conformed to the tenants of the Declaration of Helsinki (WMA General Assembly, 2008).

General Procedure

The perceptual learning paradigm, as described by Seitz and Watanabe (2003), served as the foundation for this study. The experiment consisted of three phases: Pretest; training; and post-test. First, in the pre-test phase, each participant's performance was evaluated for low-luminance motion perception, flicker perception, decoding ability, and tone discrimination. The order of tests within each testing phase was randomized across subjects. Second, in the training phase, participants completed eight sessions of a paired-shapes identification task. Third, in the post-test phase, each participant's performance was re-evaluated using the same four tests as those administered in the pretest phase.



Figure 1. Schematic of experimental procedure for all conditions.

During each of the 8 days of training, all subjects conducted a rapid serial visual presentation (RSVP) paired-shapes identification task. A pair of target shapes appeared in a central circle for 2000 ms, followed by a sequence of eight paired shapes in which the target shapes recurred in 70% of trials, after which the participant reported whether the target shapes were among the sequence of pairs. The paired-shapes presentation was 500 ms temporally centered in a 1000 ms frame. Percentage correct was assessed over 5 blocks of 108 trials each for a total of 540 trials.



Figure 2. Schematic of training procedure for all conditions that presented dim stimulus with target-recognition.

Testing Procedures

Motion detection test.

For motion testing, a subject's performance was evaluated for four directions of motion (45°, 135°, 225°, 315°). In the motion-perception test, a fixation point appeared for 300 ms, and then, a motion stimulus was presented for 500 ms. Subjects were presented with 100% coherence motion at 10 randomly interleaved contrasts (0.12, 0.23, 0.38, 0.49, 0.58, 0.69, 0.8, 0.94, 1.2, 1.8 cd/m²) and asked to use a mouse-click to choose

one of four arrows that corresponded to the direction of the motion stimulus. Each direction was presented 20 times at each of the contrast levels, and thus, subjects completed 800 trials during each session.



Figure 3. Schematic of testing procedure for motion detection.

Flicker perception test.

Flicker fusion thresholds were assessed in Hertz with a Macular Pigment Densitometer, using the method of limits (the mean of three descending measures from a high speed of flicker to a low speed in which the participants reported when the stimulus begins to flicker and three ascending measures from a slow speed to a fast speed in which the participant reported when the flicker stops) with a 1-deg diameter green (543 nm) test field.

Decoding test.

The psychophysical test used in this experiment was non-linguistic and was more akin to novel shape-recognition than it was to reading. However, it still required the visual system to assess the direction of the opening of a letter in a manner similar to word decoding, and it has been shown to strongly correlate with word and non-word decoding measures (Holloway et al., 2013). This psychophysical, non-linguistic decoding measure was obtained using a custom computer program that provided for Landolt C targets to be randomly presented in four cardinal orientations at 3-radial distances from a focus point (2.39, 4.77, and 7.95 degrees of visual angle), for eight cardinal and inter-cardinal compass points in a circular pattern. It is important to note that although any given target was at one of the 3-radial distances from the focus point, the targets could be placed anywhere within 360°. Therefore, this task required a participant's attention to be placed in the entire space subtended by 4.77, 9.53, and 15.81 degrees of visual angle respectively. A focus point was presented for 900 ms followed by a 100 ms Landolt C target. Subjects responded by pressing the arrow key on the keyboard that matched the direction the target was facing. Percentage correct was assessed over 5 blocks of 96 trials per block for a total of 480 trials per session.



Figure 4. Schematic of testing procedure for decoding. A single Landolt C was presented at one of 24 locations, at 3-radial distances from a focus point, for eight cardinal and inter-cardinal compass points in a circular pattern.

Tone discrimination test.

Tone discrimination testing consisted of the presentation of a baseline note that was then followed by a comparison note that was either the same note or one ranging from 4.32 to 21.51 cents higher or lower than the baseline note. Participants were given a forced-choice option as to whether the second note was higher or lower than the first. Pitch discrimination trials were presented with the method of constant stimuli through a custom computer program. Percentage correct was assessed over 5 blocks of 60 trials each for a total of 300 trials per session.

Training Procedures

Motion training.

While the subject performed the shapes-identification tasks, 100% coherent motion stimuli were presented in a peripheral annulus. Motion stimuli consisted of a dynamic array of 200 light grey dots (0.2 degree radius) on a grey background with each dot having a 3-frame lifetime for both the testing phase and the training phase. Motion during the shapes-identification task was presented at 100% coherence with 0.23 cd/m² contrast, with each direction being presented for 300 ms. The 0.23 cd/m² contrast level was chosen because pilot studies indicated that this was the level at which subjects performed, on average, at chance in the contrast test and reported motion on less than 30% of trials on the detection task.



Figure 5. Schematic of training procedure for motion. A pair of target shapes appeared in a central circle for 2000 ms, followed by a sequence of eight paired shapes in which the target shapes recurred in 70% of trials, after which the participant reported whether the target shapes were among the sequence of pairs. Motion was presented either concurrently with the initial target shapes or in one of three presentation timings when the target shapes recurred.

In the target-acquisition condition, one direction of motion was presented concurrently with each of the first shape-pairs that the participant needed to remember. The other three directions of motion were presented concurrently with the distractor shape-pairs. In this condition, no motion was presented with the target shape-pair.

In the target-recognition condition, one motion direction temporally overlapped each paired-shapes target as it repeated among the distractors, and the other three directions temporally overlapped the distractor shape-pairs. In this condition, no motion was presented with the first paired shapes that the participant needed to remember.



Figure 6. Schematic of motion-presentation timing for the training procedure where motion was paired concurrently with target recognition.

In the 350 ms before target recognition condition, one motion direction was

presented 350 ms before each of the paired-shapes target.



Figure 7. Schematic of motion-presentation timing for the training procedure where motion was presented 350 ms before target recognition.
In the 350 ms after target recognition condition, one motion direction was presented 350 ms after the paired-shapes target disappeared.



Figure 8. Schematic of motion-presentation timing for the training procedure where motion was presented 350 ms after target recognition.

The paired direction for each condition was randomly chosen from the testing set

for each subject.

Tone discrimination training.

Similar to the motion-recognition training paradigm, but with no motion presented at anytime, the tone-discrimination training task exposed participants to 401 Hz tones played concurrently with the paired-shapes targets in the recognition paradigm and 400 Hz tones played concurrently with distractor shape-pairs.



Figure 9. Schematic of tone presentation timing for the training procedure where tone was presented concurrently with target recognition.



Figure 10. Schematic of training procedure for tone. A pair of target shapes appeared in a central circle for 2000 ms followed by a sequence of eight paired shapes in which the target shapes recurred in 70% of trials, after which the participant reported whether the target shapes were among the sequence of pairs. The trained tone was presented concurrently with the target shapes when they repeated among distractors.

Data Analysis

In light of the fact that three of the four measures used in this experiment had linear levels of difficulty built into their design, a simple analysis of the data would be insufficient. The motion tests had 10 levels of contrast ranging from chance performance at the dimmest level to near ceiling at the brightest level. The decoding measure displayed targets at three distances from a focus point with those presented furthest from the focus point being very difficult to see, and those presented near the focus point being much easier to see. The tone discrimination test had five levels of difficulty ranging from tone presented only 1 Hz apart where performance is near chance to 5 Hz apart where performance is much better. Given the linear nature of the testing protocols, a multivariate linear contrast analysis of variance was calculated for the motion, decoding, and tone measures, and they were Bonferroni corrected due to multiple comparisons. Independent t-tests were calculated to compare pre-test thresholds to post-test thresholds. Effect size was also reported.

Results

Experiment 1

Target-acquisition condition.

Participants in the target-acquisition group who trained with near-threshold, nonessential motion stimuli paired with the focal target that the participant was asked to remember demonstrated a significant and robust improvement in motion detection, F(1, 5) = 264.93, p < 0.001, $\eta^2 = 0.981$. After 8 days of training, participants in this group experienced an improvement in motion detection from an overall mean of 50% correct in the pre-test to an overall mean of 77% correct in the post-test, showing, on average, a $54\% (=\frac{77-50}{50})$ improvement in motion perception.



Figure 11. Motion detection accuracy for pre-tests and post-tests across 10 levels of contrast brightness in the target-acquisition condition. Error bars represent standard error.

The target-acquisition training also significantly improved a subject's flicker perception or CFFT, t(5) = 5.23, p < 0.01, d = 2.49. Participants increased their CFFT from an average of 19.79 Hz to an average of 22.46 Hz. Thus, target-acquisition participants experienced, on average, a 14% ($=\frac{22.46-19.79}{19.79}$) improvement in their flicker perception.



Figure 12. Flicker perception thresholds for pre-tests and post-tests in the target-acquisition condition. Error bars represent standard error.

Target-acquisition training also significantly improved subjects' letter-decoding abilities, F(1,5) = 35.003, p < 0.01, $\eta^2 = 0.875$, from a pre-test mean of 45% to a post-test mean of 61%. Overall, participants demonstrated a 36% ($=\frac{61-45}{45}$) average improvement in their decoding performance.



Figure 13. Letter decoding accuracy for pre-tests and post-tests across three levels of distance from the focus point when motion was presented concurrently with target acquisition. Error bars represent standard error.

In the target-acquisition condition, there was no significant improvement in participants' tone discrimination, F(1,5) = 2.113, p = .206, $\eta^2 = .297$.



Figure 14. Tone discrimination accuracy for pre-tests and post-tests across five levels of tone difference when motion was presented concurrently with target acquisition. Error bars represent standard error, and the post-test trend line precisely overlays the pre-test trend line.

Target-recognition condition.

Training where non-essential, dim motion stimuli was paired with focal target recognition produced a significant but less robust improvement in motion detection, F(1, 5) = 82.332, p < 0.001, $\eta^2 = 0.943$. Participants experienced an improvement in motion detection from an overall mean of 39% correct in the pre-test to an overall mean of 56% correct in the post-test, showing, on average, a 43% ($=\frac{56-39}{39}$) improvement in motion perception.



Figure 15. Motion detection accuracy for pre-tests and post-tests across 10 levels of contrast brightness in the target-recognition condition. Error bars represent standard error.

Target-recognition training also improved participants' flicker perception,

t(5) = 3.54, p < 0.05, d = 1.12, increasing their CFFT from an average of 18.8 Hz to an average of 21.05 Hz. Thus target-recognition participants increased their flicker

perception by an average of 12% (= $\frac{21.05-18.8}{18.8}$).



Figure 16. Flicker perception thresholds for pre-tests and post-tests in the target-recognition condition. Error bars represent standard error.

Decoding performance significantly improved in subjects who completed the target-recognition training, F(1,5) = 15.539, p < 0.05, $\eta^2 = 0.757$, from a pre-test mean of 40% to a post-test mean of 55%. Similar to the target-acquisition group, the target-recognition group demonstrated a 37% ($=\frac{55-40}{40}$) average improvement in decoding performance.



Figure 17. Decoding accuracy for pre-tests and post-tests across three levels of distance from the focus point when motion was presented concurrently with target recognition. Error bars represent standard error.

In the target-recognition condition, there was no significant improvement in tone discrimination, F(1,5) = 1.746, p = .244, $\eta^2 = .259$.



Figure 18. Tone discrimination accuracy for pre-tests and post-tests across five levels of tone difference when motion was presented concurrently with target recognition. Error bars represent standard error, and the post-test trend line precisely overlays the pre-test trend line.

Comparison of the acquisition and recognition conditions.

To directly assess the levels of improvement observed in the target-acquisition group and those observed in the target-recognition group, each participant's pre-test scores were subtracted from his post-test scores for every condition. Then, a multivariate regression analysis of variance was calculated, comparing the target-acquisition group with the target-recognition group. Overall, the improvement seen in the targetacquisition group was significantly greater than the improvement observed in the targetrecognition group, F(9, 90) = 5.586, p < .001, $\eta^2 = 0.313$, with the target-acquisition group showing nearly a 27% base improvement between the pre-test and post-test as compared to a 17% base improvement observed in the target-recognition group.



Figure 19. Improvement in motion detection comparing the target-acquisition and target-recognition groups' post-test minus pre-test performance levels across 10 levels of contrast brightness. Error bars represent standard error.

Experiment 2

Motion presented 350 ms before target-recognition condition.

When non-essential, dim motion stimuli were presented 350 ms before the target in the focal target-recognition task, participants showed improvement in motion detection, F(1, 5) = 10.53, p < 0.01, $\eta^2 = 0.678$, advancing from an overall mean of 44% correct in the pre-test to an overall mean of 54% correct in the post-test. Specifically, they demonstrated an average improvement in motion detection of 23% ($=\frac{54-44}{44}$).



Figure 20. Motion detection accuracy for pre-tests and post-tests across 10 levels of contrast brightness when motion was presented 350 ms before target recognition. Error bars represent standard error.

When non-essential, dim motion stimuli were presented 350 ms before the focal target, an increase was also observed in participants' flicker perception, t(5) = 2.9, p < 0.05, d = 0.34, whereby their CFFT increased from an average of 20.28 Hz to an average of 21.31 Hz. Thus, target-acquisition participants' CFFT improved by an average of 5% ($=\frac{21.31-20.28}{20.28}$).



Figure 21. Flicker perception thresholds for pre-tests and post-tests when motion was presented 350 ms before target recognition. Error bars represent standard error.

When non-essential, dim motion stimuli were presented 350 ms before the focal target, decoding performance was also significantly improved, F(1,5) = 27.770, p < 0.01, $\eta^2 = 0.820$, from a pre-test mean of 45.15% to a post-test mean of 53.63%, with participants experiencing an average improvement of 18.7% (= $\frac{53.63-45.15}{45.15}$).



Figure 22. Decoding accuracy for pre-tests and post-tests across three levels of distance from the focus point when motion was presented 350 ms before target recognition. Error bars represent standard error.

When non-essential, dim motion stimuli were presented 350 ms before focal target recognition, no significant improvement was observed for the tone-discrimination measures, F(1,5) = 3.827, p = .108, $\eta^2 = .434$.



Figure 23. Tone discrimination accuracy for pre-tests and post-tests across five levels of tone difference when motion was presented 350 ms before target recognition. Error bars represent standard error.

Motion presented 350 ms after target-recognition condition.

When non-essential, dim motion stimuli were presented 350 ms after the focal target in the target-recognition training sessions, participants showed improvement in motion detection very similar to that observed in the original target-recognition condition, F(1, 5) = 93.24, p < 0.001, $\eta^2 = 0.949$, demonstrating an improvement in motion detection from an overall mean of 38% correct in the pre-test to an overall mean of 50% correct in the post-test, an improvement of 31% ($=\frac{50-38}{38}$) on average.



Figure 24. Motion detection accuracy for pre-tests and post-tests across 10 levels of contrast brightness when motion was presented 350 ms after target recognition. Error bars represent standard error.

When non-essential, dim motion stimuli were presented 350 ms after the focal target, an increase was observed in participants' flicker perception, t(5) = 3.68, p < 0.05, d = 1.79. Specifically, their CFFT increased from an average of 19.38 Hz to an average of 21.57 Hz. Thus, target-acquisition participants' CFFT improved by an average of 11% $(=\frac{21.57-19.38}{19.38}).$



Figure 25. Flicker perception thresholds for pre-tests and post-tests when motion was presented 350 ms after target recognition. Error bars represent standard error.

When non-essential, dim motion stimuli were presented 350 ms after the focal target, decoding performance was also significantly improved, F(1,5) = 20.066, p < 0.01, $\eta^2 = 0.801$, from a pre-test mean of 46% to a post-test mean of 58%. Similar to the target-acquisition group, decoding performance of participants in the 350 ms post-target presentation group improved by an average of 26% ($=\frac{58-46}{46}$).



Figure 26. Decoding accuracy for pre-tests and post-tests across three levels of distance from the focus point when motion was presented 350 ms after target recognition. Error bars represent standard error.

When non-essential, dim motion stimuli were presented 350 ms after focal target- recognition, no significant difference was observed in tone discrimination,



 $F(1,5) = 2.877, p = .151, \eta^2 = .365.$

Figure 27. Tone discrimination accuracy for pre-tests and post-tests across five levels of tone difference when motion was presented 350 ms after target recognition. Error bars represent standard error.

Comparison of the 350 ms before and 350 ms after conditions.

To directly assess the levels of improvement observed in the 350 ms before group and those observed in the 350 ms after group, each participant's pre-test scores were subtracted from his post-test scores for every condition. Then, a multivariate regression analysis of variance was calculated. Overall, the improvement seen in the 350 ms after group was significantly greater than the improvement observed in the 350 ms before group, F(9, 90) = 5.09, p < .001, $\eta^2 = 0.295$, with the 350 ms after group showing nearly a 13% base improvement between the pre-test and post-test as compared to a 9% base improvement observed in the 350 ms before group.



Figure 28. Improvement in motion detection comparing the 350 ms before and 350 ms after groups' post-test minus pre-test performance levels across 10 levels of contrast brightness. Error bars represent standard error.

Experiment 3

Reading disabled target-acquisition condition.

Participants with reading difficulties who were trained with non-essential, dim motion stimuli paired with the focal target that the participant needed to remember showed significant improvement in motion detection, F(1, 3) = 24.53, p < 0.05, $\eta^2 = 0.891$. An improvement in motion detection from an overall mean of 38% correct in the pre-test to an overall mean of 47% correct in the post-test was observed, showing, on average, that these reading disabled participants experienced a 24% ($=\frac{47-38}{38}$) improvement in motion perception.



Figure 29. Reading disabled motion detection accuracy for pre-tests and post-tests across 10 levels of contrast brightness when motion was presented concurrently with target acquisition. Error bars represent standard error.

The reading disabled target-acquisition participants' flicker perception levels were also significantly improved, t(3) = 10.65, p < 0.01, d = 2.67. Participants experienced an increase in their CFFT from an average of 17.71 Hz to an average of 21.08 Hz. Thus, participants with reading difficulties who had dim motion presented in conjunction with paired-shape targets that they were asked to remember improved their ability to see flicker by an average of 19% ($=\frac{21.08-17.71}{17.71}$).



Figure 30. Reading disabled flicker perception thresholds for pre-tests and post-tests in the target-acquisition condition. Error bars represent standard error.

Remarkably, reading disabled subjects who engaged in target-acquisition training showed an extremely robust improvement in their decoding performance, F(1,3) = 54.247, p < 0.001, $\eta^2 = 0.948$, from a pre-test mean of 37% to a post-test mean of 59%. Overall, these participants improved by an average of 59% ($=\frac{59-37}{37}$) on decoding performance.



Figure 31. Reading disabled decoding accuracy for pre-tests and post-tests across three levels of distance from the focus point when motion was presented concurrently with target acquisition. Error bars represent standard error.

For the reading disabled in the target-acquisition condition, there was no

significant improvement in tone discrimination, F(1,3) = 3.006, p = .144, $\eta^2 = .375$.



Figure 32. Reading disabled tone discrimination accuracy for pre-tests and post-tests across five levels of tone difference when motion was presented with target acquisition. Error bars represent standard error.

Reading disabled tone-recognition condition.

When reading disabled participants experienced non-essential, tone stimuli paired with the focal target-recognition task, there was no significant difference observed in: motion detection, F(1,3) = 8.176, p = .085, $\eta^2 = .732$ (see Figure 33); flicker, t(3) = 0.418, p = 0.703 (see Figure 34); or decoding, F(1,3) = 4.158, p = .134, $\eta^2 = .581$ (see Figure 35).



Figure 33. Reading disabled motion detection accuracy for pre-tests and post-tests across 10 levels of contrast brightness when tone was presented concurrently with target recognition. Error bars represent standard error.



Figure 34. Reading disabled flicker perception thresholds for pre-tests and post-tests when tone was presented concurrently with target recognition. Error bars represent standard error.



Figure 35. Reading disabled decoding accuracy for pre-tests and post-tests across three levels of distance from the focus point when tone was presented concurrently with target recognition. Error bars represent standard error.

On the contrary, reading disabled participants who experienced tone paired with the target-recognition task demonstrated a significant increase in tone discrimination, F(1, 3) = 47.958, p < 0.01, $\eta^2 = 0.941$, from a pre-test mean of 64.62% to a post-test mean of 76.36%. Indeed, these reading disabled participants improved their ability to discriminate tone by an average of 18.12% (= $\frac{76.36-64.62}{64.62}$).



Figure 36. Reading disabled tone discrimination accuracy for pre-tests and post-tests across five levels of tone difference when tone was presented concurrently with target recognition. Error bars represent standard error.

Experiment 4

Tone-discrimination condition (control).

When non-reading-disabled participants readers had non-essential tone paired with the focal target-recognition task, there was no significant difference observed in: motion detection, F(1,5) = 3.164, p = .163, $\eta^2 = .432$ (see Figure 37); flicker, t(5) = 1.03, p = 0.363 (see Figure 38); or decoding, F(1,3) = 4.336, p = .092, $\eta^2 = .464$ (see Figure 39).



Figure 37. Motion detection accuracy for pre-tests and post-tests across 10 levels of contrast brightness when tone was presented concurrently with target recognition. Error bars represent standard error.



Figure 38. Flicker perception thresholds for pre-tests and post-tests when tone was presented concurrently with target recognition. Error bars represent standard error.



Figure 39. Decoding accuracy for pre-tests and post-tests across three levels of distance from the focus point when tone was presented concurrently with target recognition. Error bars represent standard error.

However, when non-reading-disabled participants experienced tone paired with the target-recognition task, they demonstrated a significant increase in tone discrimination, F(1, 5) = 33.09, p < 0.01, $\eta^2 = 0.869$, from a pre-test mean of 62% to a post-test mean of 73%. Specifically, these participants showed an average improvement of 18% ($=\frac{73-62}{62}$) in tone discrimination.



Figure 40. Tone discrimination accuracy for pre-tests and post-tests across five levels of tone difference when tone was presented concurrently with target recognition. Error bars represent standard error.

Table 1

Overall Relation across P-values and Effect Size

	Measures			
Condition	Motion Perception	Flicker Perception	Decoding	Tone discrimination
Motion Paired with Acquisition	F(1,5) = 264.931 p≈ 0.000016 η ² = 0.981 54% Improvement	t(5) = 5.23 p≈ 0.006 d = 2.49 14% Improvement	F(1,5) = 35.003 p≈ 0.002 η ² = 0.875 36% Improvement	NS
Motion Paired with Recognition	F(1,5) = 82.323 p≈ 0.000272 η ² = 0.943 43% Improvement	t(5) = 3.54 p≈ 0.0164 d = 1.12 12% Improvement	F(1,5) = 15.539 p≈ 0.011 η ² = 0.757 37% Improvement	NS
Motion Paired 350 ms before Recognition	F(1,5) = 10.530 p≈ 0.023 η ² = 0.678 23% Improvement	t(5) = 2.895 p≈ 0.0342 d = 0.34 5% Improvement	F(1,5) = 22.770 p≈ 0.005 η ² = 0.820 18.7% Improvement	NS
Motion Paired 350 ms after Recognition	F(1,5) = 93.244 p≈ 0.000202 q ² = 0.949 31% Improvement	t(5) = 3.68 p≈ 0.0203 d = 1.79 11% Improvement	F(1,5) = 20.066 p≈ 0.007 η ² = 0.801 35.5% Improvement	NS
Reading Disabled Motion Paired with Acquisition	F(1,3) = 24.529 p≈ 0.016 η ² = 0.891 24% Improvement	t(3) = 10.65 p≈ 0.0077 d = 2.67 19% Improvement	F(1,3) = 54.247 p≈ 0.005 η ² = 0.948 59% Improvement	NS
Reading Disabled Tone Paired with Recognition	NS	NS	NS	F(1,3) = 47.958 p≈ 0.006 η ² = 0.941 18.12% Improvement
Tone Paired with Recognition	NS	NS	NS	F(1,5) = 33.088 p≈ 0.002 η ² = 0.869 18% Improvement

Discussion

In the present study, we tested the process by which the "task-irrelevant" (or associated near-threshold stimulus) learning paradigm subserves neural plasticity. We found that participants can learn from the modified learning paradigm that was created and employed for this study. This paradigm consisted of a visual paired-shape recognition task, using colored polygon targets as salient attended stimuli. In all of the motion-training groups, we observed sensitivity improvements in motion perception, flicker perception, and decoding, but not in tone discrimination. In the tone-training control group, we did not observe any sensitivity improvements in motion detection, flicker perception, or decoding, but we did observe significant improvement in tone discrimination.

Seitz and Watanabe (2003) proposed that during a cognitively demanding undertaking, neuro-modulators flood the brain, strengthening neural activity in a global manner. This concept is supported by studies that show that the temporal pairing of sensory stimuli with electrical stimulation of areas causes the release of learning-related neuro-modulators, presumably resulting in an expanded cortical representation of neurons that respond to the paired stimuli (Bao et al., 2001; Kilgard & Merzenich, 1998). In the current study, the increase in motion perception, flicker, decoding, and tone discrimination may be the result of neuro-modulators inadvertently strengthening neurons that are active, yet unrelated, to the paired-shapes recognition task. These findings support the notion that the neural plasticity gating problem called the noise-saturation dilemma proposed by Grossberg (1980) can be solved by a neuro-modulator system that requires concentration to elicit plasticity at all levels of neural processing.

60

Experiment 1

The current study supported our prediction that the target-acquisition group would experience greater improvement in motion perception than the target-recognition group. Specifically, we showed that when near-threshold motion was paired with the target that participants were asked to remember, a significantly greater improvement in motion detection was observed as compared to a group who had dim, near-threshold motion paired with the target as it repeated in a series of distractors. In addition, participants showed improvement in flicker perception and letter decoding; increases that were substantially equivalent in both the target-acquisition and target-recognition groups. The effect sizes were greater in the target-acquisition condition, supporting the contention that the acquisition condition is a more efficient learning paradigm. The implication is that although both recognition and acquisition play a role in the learning of near-threshold stimuli, acquisition plays a more important role in affecting plasticity.

One weakness of this study is that the target-recognition group experienced the target repeating only 70% of the time. This was necessary in order to keep the participants focused and engaged. When the target repeated more often, participants realized that answering "yes" was correct most of the time, and they tended to let their attention drift and stopped putting forth much effort. The byproduct of this design was that in the target-recognition condition, only 70% of the trials were available to expose participants to the dim stimuli. Previous research has shown that fewer trials per session result in no difference in learning (Groth, 2013). Although it is unlikely that the difference observed between the target-acquisition and the target-recognition groups is

61
due to fewer trials in the recognition condition, we cannot completely discount the possibility as a result of this study.

Experiment 2

The results of this study support the Killeen and Fetterman (1988) behavior model of timing. Participants who had dim motion gradients presented 350 ms after target recognition showed greater performance improvement than those who had dim motion gradients presented 350 ms before target recognition. This finding also makes sense in the context of concentration-induced neuro-modulator release described by Schultz (2000) and Dalley et al. (2001). If dim motion is presented before a target is recognized, the neuro-modulator conditions that support neural plasticity are not present. Accordingly, the learning that was observed in the 350 ms before condition was likely due to the fact that the neurons that responded to the dim motion were still partially active and in a refractory stage of hyper-polarization. However, in the 350 ms after condition, neuro-modulators responsible for inducing plasticity were likely still present and supporting the neurons that were responding to the dim motion. This thesis is consistent with the results showing that the 350 ms after group performed similarly to the original target-recognition condition, whereas the 350 ms before group did not perform as well.

Experiment 3

This experiment found that participants with reading difficulties who experienced dim motion paired with the target shapes they were asked to remember improved their ability to see motion, perceive flicker, and decode. These results support the findings of Gori et al. (2015) that demonstrated that motion training related to near-threshold perceptual learning radically improved the reading ability of adults with dyslexia.

62

There are a few salient differences between the current experiment and what was done by Gori and his team. Following Seitz et al. (2006) and Holloway et al. (2013), Gori used the original "task-irrelevant" learning program that presented letters in a rapid serial presentation to test the affect of near-threshold learning on dyslexics. In the original paradigm, two of eight letters were presented in a slightly lighter or darker shade of grey and were paired with near-threshold motion gradients. Participants were required to recognize and then remember two letters, so that they could report them at the end of the series. This rapid serial letter task is very tedious and is difficult for most people to maintain concentration. Consequently, the task was modified for the current study such that letter identification was replaced with paired-shapes recognition, thereby making the learning task less tedious and burdensome. Another distinction of this project is that it utilized English-speaking participants. Gori's study was performed within the context of the Italian language. Italian is a phonologically shallow language as compared to other languages such as English. Here, we show that reading disabled English speakers improved in a manner similar to that of the dyslexic Italian-speakers involved in the Gori study.

All in all, these findings demonstrate that a psychophysical learning paradigm may be employed to mediate some effects of reading difficulties in adults, and it may well be an effective remediation for children, as well. Keep in mind that the basic premise of near-threshold associative learning for motion training is that pairing dim motion gradients with concentration can improve sensitivity to motion, and that by strengthening motion sensitivity, other perceptual functions such as CFFT are improved as well. It would be quite easy to nest this paradigm in an interactive video game that

63

would be enjoyable for a child. Consequently, a real world application of these findings may be that a new, non-reading intervention for reading disabilities is possible.

This unique approach might also provide an important insight into developmental reading disability. It is possible that one of the issues involved in dyslexia is a deficit in central dorsal stream processing. The dominant view in literature today is that developmental dyslexia is an impairment in the phonological awareness of a dyslexic (Peterson & Pennington, 2012). Phonological awareness refers to one's ability to perceive and manipulate the sounds of spoken words (Mattingly, 1972), and it involves not only discerning the sounds of speech (Goswami, 2002; Hornickel & Kraus, 2013; Tallal, 1980) but also explicitly acting upon them (Boets et al., 2013). So, a deficit in phonological awareness would impair a person's ability to map speech sounds onto the visual letters that they represent, thereby preventing fluent reading (Vellutino, Fletcher, Snowling, & Scanlon, 2004).

However, near-threshold perceptual learning improves several abilities that are associated with the central dorsal pathway of the visual system (Gori et al., 2015; Seitz et al., 2005; Seitz et al., 2006). This leads to the implication that the magnocellular-dorsal visual system is at least partially involved with reading disabilities (Boets et al., 2013; Galaburda & Livingstone, 1993; Gori, Cecchini, Bigoni, Molteni, & Facoetti, 2014; Gori & Facoetti, 2015; Holloway & McBeath, 2013; Kevan & Pammer, 2008; Kevan & Pammer, 2009; Menghini et al., 2010; Stein & Talcott, 1999; Tallal, 2004), and thus, it can be influenced by a perceptual learning paradigm. Future research should explore this possibility more directly.

64

Experiment 4

The fourth experiment was an active control for other conditions in which participants were exposed to dim motion gradients in conjunction with the training paradigm. Here, we paired a 1 Hz (4.32 cents) different tone with the recognition task, while having a baseline tone presented with distractor targets. These data show that the control participants did not improve in motion detection, flicker perception, or decoding, but they did improve in their ability to discriminate between tones. This is also a novel finding in that although previous research has used the "task- irrelevant" learning paradigm to train auditory signals, they used an auditory task to train near-threshold auditory signals, while we used a visual paradigm to train an auditory signal.

Take Home Message

We separated the acquisition phase from the recognition phase of the identification process in a near-threshold learning paradigm and demonstrated that the concentration required to remember paired shapes promotes learning better than recognizing that the paired-shapes target has repeated.

We varied the timing of the paring between the recognition and the background stimuli and found that motion presented after a target elicits plasticity better than motion presented before a target. Lingering neuro-modulator states likely subserve neural activity following the recognition of a target and are not likely present when motion is presented before the target is recognized.

Participants with reading difficulties experienced significantly improved sensitivity to motion, detection, flicker perception, and decoding. These findings support the notion that children who have been identified as having a reading disability might have their symptoms mediated through a video game that has a version of this paradigm nested within it.

Lastly, although sensitivity to tone discrimination was not observed in any condition where motion was presented in conjunction with a target, we were able to improve participants' tone discrimination by pairing an auditory signal with a visual shapes-recognition task.

Taken as a whole, this study confirms that pairing near-threshold stimuli with focal stimuli improved performance in just tone discrimination, or in motion detection, CFFT, and letter decoding; and that the act of trying to remember a focal target elicited greater associative learning of correlated near-threshold stimulus than the act of recognizing a target. Indeed, these data suggest that we can now effectively design a visual learning paradigm similar to the one used in these experiments, incorporate it into an enjoyable video game, and, potentially, use it to mitigate some of the visual deficits that are often experienced by the reading disabled.

REFERENCES

- Abbott, L. F., & Nelson, S. B. (2000). Synaptic plasticity: taming the beast. *Nature Neuroscience*, *3*, 1178–1183. doi:10.1038/81453
- Adini, Y., Sagi, D., & Tsodyks, M. (2002). Context-enabled learning in the human visual system. *Nature*, *415*(6873), 790–793. doi:10.1038/415790a
- Ahissar, M., & Hochstein, S. (1993). Attentional Control of Early Perceptual Learning. Proceedings of the National Academy of Sciences, USA, 90, 5718–5722. doi:10.1016/S0896-6273(01)00424-X
- Ahissar, M., & Hochstein, S. (1997). Task difficulty and the specificity of perceptual learning. *Nature*, 387(6631), 401-406. doi:10.1038/387401a0
- Arnsten, A. F. (1997). Catecholamine regulation of the prefrontal cortex. *Journal of Psychopharmacology*, *11*(2), 151–162. doi:10.1177/026988119701100208
- Ball, K., & Sekuler, R. (1981). Adaptive processing of visual motion. *Journal of Experimental Psychology. Human Perception and Performance*, 7(4), 780–794. doi:10.1037/0096-1523.7.4.780
- Bao, S., Chan, V. T., & Merzenich, M. M. (2001). Cortical remodelling induced by activity of ventral tegmental dopamine neurons. *Nature*, 412(6842), 79–83. doi:10.1038/35083586
- Bi, G. Q., & Poo, M. M. (1998). Synaptic modifications in cultured hippocampal neurons: dependence on spike timing, synaptic strength, and postsynaptic cell type. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, 18(24), 10464–10472.
- Boets, B., Op De Beeck, H. P., Vandermosten, M., Scott, S. K., Gillebert, C. R., Mantini, D., ... Ghesquière, P. (2013). Intact but less accessible phonetic representations in adults with dyslexia. *Science*, 342(6163), 1251–1254. doi:10.1126/science.1244333
- Cornelissen, P., Richardson, A., Mason, A., Fowler, S., & Stein, J. (1995). Contrast sensitivity and coherent motion detection measured at photopic luminance levels in dyslexics and controls. *Vision Research*, 35(10), 1483–1494. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/7645277
- Crist, R. E., Kapadia, M. K., Westheimer, G., & Gilbert, C. D. (1997). Perceptual learning of spatial localization: specificity for orientation, position, and context. *Journal of Neurophysiology*, 78(6), 2889–2894.

- Dalley, J. W., McGaughy, J., O'Connell, M. T., Cardinal, R. N., Levita, L., & Robbins, T. W. (2001). Distinct changes in cortical acetylcholine and noradrenaline efflux during contingent and noncontingent performance of a visual attentional task. *The Journal of Neuroscience*, 21(13), 4908–4914. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/11425918
- Dinse, H. R., Ragert, P., Pleger, B., Schwenkreis, P., & Tegenthoff, M. (2003). Pharmacological modulation of perceptual learning and associated cortical reorganization. *Science*, 301(5629), 91–94. doi:10.1126/science.1085423
- Dosher, B. A., & Lu, Z. L. (1998). Perceptual learning reflects external noise filtering and internal noise reduction through channel reweighting. *Proceedings of the National Academy of Sciences*, 95(23), 13988–13993. doi:10.1073/pnas.95.23.13988
- Eden, G. F., VanMeter, J. W., Rumsey, J. M., Maisog, J. M., Woods, R. P., & Zeffiro, T. A. (1996). Abnormal processing of visual motion in dyslexia revealed by functional brain imaging. *Nature*, 382, 66–69. doi:10.1038/382066a0
- Fahle, M., Edelman, S., & Poggio, T. (1995). Fast perceptual learning in hyperacuity. *Vision Research*, *35*(21), 3003–3013. doi:10.1016/0042-6989(95)00044-Z
- Felmingham, K. L., & Jakobson, L. S. (1995). Visual and visuomotor performance in dyslexic children. Experimental Brain Research. Experimentelle Hirnforschung. Expérimentation Cérébrale, 106(3), 467–474. doi:10.1007/BF00231069
- Fetterman, J. G., & Killeen, P. R. (1995). Categorical scaling of time: implications for clock-counter models. *Journal of Experimental Psychology. Animal Behavior Processes*, 21(1), 43–63. doi:10.1037/0097-7403.21.1.43
- Fiorentini, A., & Berardi, N. (1980). Perceptual learning specific for orientation and spatial frequency. *Nature*, 287, 43-44. doi:10.1038/287043a0
- Furmanski, C. S., Schluppeck, D., & Engel, S. A. (2004). Learning strengthens the response of primary visual cortex to simple patterns. *Current Biology*, 14(7), 573– 578. doi:10.1016/j.cub.2004.03.032
- Galaburda, A., & Livingstone, M. (1993). Evidence for a magnocellular defect in developmental dyslexia. Annals of the New York Academy of Sciences, 682, 70–82. doi:10.1111/j.1749-6632.1993.tb22960.x
- Gerstner, W., Kempter, R., van Hemmen, J. L., & Wagner, H. (1996). A neuronal learning rule for sub-millisecond temporal coding. *Nature*, *383*(6595) 76-81. doi:10.1038/383076a0
- Gilbert, C. D., Sigman, M., & Crist, R. E. (2001). The neural basis of perceptual learning. *Neuron*, *31*(5) 681-697. doi:10.1016/S0896-6273(01)00424-X

- Glenberg, A. M., Lopez-Mobilia, G., McBeath, M., Toma, M., Sato, M., & Cattaneo, L. (2010). Knowing beans: human mirror mechanisms revealed through motor adaptation. *Frontiers in Human Neuroscience*, 4, 206. doi:10.3389/fnhum.2010.00204
- Gori, S., Cecchini, P., Bigoni, A., Molteni, M., & Facoetti, A. (2014). Magnocellulardorsal pathway and sub-lexical route in developmental dyslexia. *Frontiers in Human Neuroscience*, 8(June), 460. doi:10.3389/fnhum.2014.00460
- Gori, S., & Facoetti, A. (2015). How the visual aspects can be crucial in reading acquisition? The intriguing case of crowding and developmental dyslexia. *Journal of Vision*, *15*(1), 8-8. doi:10.1167/15.1.8
- Gori, S., Seitz, A. R., Ronconi, L., Franceschini, S., & Facoetti, A. (2015). Multiple Causal Links Between Magnocellular–Dorsal Pathway Deficit and Developmental Dyslexia. *Cerebral Cortex*, 1-14. doi:10.1093/cercor/bhv206
- Goswami, U. (2002). Phonology, Reading Development, and Dyslexia: A Crosslinguistic Perspective. Annals of Dyslexia, 52, 141–163. doi:10.1007/s11881-002-0010-0
- Grondin, S. (2001). Discriminating time intervals presented in sequences marked by visual signals. *Perception & Psychophysics*, 63(7), 1214–1228. doi:10.3758/BF03194535
- Grossberg, S. (1980). How does a brain build a cognitive code? *Psychological Review*, 87(1), 1–51. doi:10.1037/0033-295X.87.1.1
- Groth, A. (2013). Neural Plasticity in Lower- and Higher-Level Visual Cortex Processing (Master's thesis). Available from ProQuest Dissertations and Theses database. (UMI No. 1536508)
- Holloway, S. R., & McBeath, M. K. (2013). Independent Objective Timing Tests Designed to Measure Processing Rates of the Dorsal and Ventral Visual Systems, 1(2), 15–20. doi:10.12966/jcen.11.01.2013
- Holloway, S. R., Náñez, J. E., & Seitz, A. R. (2013). Word-decoding as a function of temporal processing in the visual system. *PloS One*, 8(12), e84010. doi:10.1371/journal.pone.0084010
- Hornickel, J., & Kraus, N. (2013). Unstable representation of sound: a biological marker of dyslexia. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, 33(8), 3500–3504. doi:10.1523/JNEUROSCI.4205-12.2013
- Jiménez, L., & Méndez, C. (2001). Implicit sequence learning with competing explicit cues. The Quarterly Journal of Experimental Psychology. Section A: Human Experimental Psychology, 54(2), 345–369. doi:10.1080/713755964

- Kaas, J. H., Merzenich, M. M., & Killackey, H. P. (1983). The reorganization of somatosensory cortex following peripheral nerve damage in adult and developing mammals. *Annual Review of Neuroscience*, 6, 325–356. doi:10.1146/annurev.ne.06.030183.001545
- Kevan, A., & Pammer, K. (2008). Visual deficits in pre-readers at familial risk for dyslexia. Vision Research, 48(28), 2835–2839. doi:10.1016/j.visres.2008.09.022
- Kevan, A., & Pammer, K. (2009). Predicting early reading skills from pre-reading measures of dorsal stream functioning. *Neuropsychologia*, 47(14), 3174–3181. doi:10.1016/j.neuropsychologia.2009.07.016
- Kilgard, M. P., & Merzenich, M. M. (1998). Cortical map reorganization enabled by nucleus basalis activity. *Science*, 279(5357), 1714–1718. doi:10.1126/science.279.5357.1714
- Killeen, P. R., & Fetterman, J. G. (1988). A behavioral theory of timing. *Psychological Review*, 95(2), 274–295. doi:10.1037/0033-295X.95.2.274
- Knight, R. T., Staines, W. R., Swick, D., & Chao, L. L. (1999). Prefrontal cortex regulates inhibition and excitation in distributed neural networks. *Acta Psychologica*, 101(2-3), 159–178. doi:10.1016/S0001-6918(99)00004-9
- Leonards, U., & Singer, W. (1997). Selective temporal interactions between processing streams with differential sensitivity for colour and luminance contrast. *Vision Research*, 37(9), 1129–1140. doi:10.1016/S0042-6989(96)00264-7
- Li, C.S., R., Padoa-Schioppa, C., & Bizzi, E. (2001). Neuronal Correlates of Motor Performance and Motor Learning in the Primary Motor Cortex of Monkeys Adapting to an External Force Field. *Neuron*, 30(2), 593–607. doi:10.1016/S0896-6273(01)00301-4
- Li, W., Thier, P., & Wehrhahn, C. (2000). Contextual influence on orientation discrimination of humans and responses of neurons in V1 of alert monkeys. *Journal* of Neurophysiology, 83(2), 941–954.
- Livingstone, M. S., Rosen, G. D., Drislane, F. W., & Galaburda, A. M. (1991). Physiological and anatomical evidence for a magnocellular defect in developmental dyslexia. *Proceedings of the National Academy of Sciences, USA*, 88(18), 7943– 7947. doi:10.1073/pnas.90.6.2556.e
- Markram, H., Lubke, J., Frotscher, M., & Sakmann, B. (1997). Regulation of synaptic efficacy by coincidence of postsynaptic APs and EPSPs. *Science*, 275(5297), 213–215. doi:10.1126/science.275.5297.213

- Marr, D. (1982). Vision: A Computational Investigation into the Human Representation and Processing of Visual Information. *Phenomenology and the Cognitive Sciences*, 8(4), 397. doi:10.1007/s11097-009-9141-7
- Martin, F., & Lovegrove, W. (1987). Flicker contrast sensitivity in normal and specifically disabled readers. *Perception*, *16*(2), 215–221. doi:10.1068/p160215
- Mattingly, I. (1972). Speech Cues and Sign Stimuli. American Scientist, 60(3), 327–337.
- Maunsell, J., Nealey, T., & DePriest, D. (1990). Magnocellular and parvocellular contributions to responses in the middle temporal visual area (MT) of the macaque monkey. *Journal of Neuroscience*, 10(October), 3323–3334. Retrieved from http://www.jneurosci.org/cgi/content/abstract/10/10/3323
- Menghini, D., Finzi, A., Benassi, M., Bolzani, R., Facoetti, A., Giovagnoli, S., ... Vicari, S. (2010). Different underlying neurocognitive deficits in developmental dyslexia: A comparative study. *Neuropsychologia*, 48(4), 863–872. doi:10.1016/j.neuropsychologia.2009.11.003
- Merzenich, M. M., Jenkins, W. M., Johnston, P., Schreiner, C., Miller, S. L., & Tallal, P. (1996). Temporal processing deficits of language-learning impaired children ameliorated by training. *Science*, 271(5245), 77–81. doi:10.1126/science.271.5245.77
- Morikawa, K., & McBeath, M. K. (1992). Lateral motion bias associated with reading direction. Vision Research, 32(6), 1137–1141. doi:10.1016/0042-6989(92)90014-A
- Nissen, M. J., & Bullemer, P. (1987). Attentional requirements of learning: Evidence from performance measures. *Cognitive Psychology*, 19(1), 1–32. doi:10.1016/0010-0285(87)90002-8
- Olson, I. R., & Chun, M. M. (2001). Temporal contextual cuing of visual attention. Journal of Experimental Psychology. Learning, Memory, and Cognition, 27(5), 1299–1313. doi:10.1037/0278-7393.27.5.1299
- Pantev, C., Oostenveld, R., Engelien, A., Ross, B., Roberts, L. E., & Hoke, M. (1998). Increased auditory cortical representation in musicians. *Nature*, 392(6678), 811– 814. doi:10.1038/33918
- Pascual-Leone, A., Bartres-Faz, D., & Keenan, J. P. (1999). Transcranial magnetic stimulation: studying the brain-behaviour relationship by induction of "virtual lesions." *Philosophical Transactions of the Royal Society of London. Series B*, *Biological Sciences*, 354(1387), 1229–1238. doi:10.1098/rstb.1999.0476

Pavlov, I. P. (1927). Conditioned Reflexes. [Vol. 17]. doi:10.2307/1134737

- Peterson, R. L., & Pennington, B. F. (2012). Developmental dyslexia. *Lancet*, 379(9830), 1997–2007. doi:10.1016/S0140-6736(12)60198-6
- Schoups, A., Vogels, R., Qian, N., & Orban, G. (2001). Practising orientation identification improves orientation coding in V1 neurons. *Nature*, 412(6846), 549– 553. doi:10.1038/35087601
- Schultz, W. (2000). Multiple Reward Signals. *Nature Reviews Neuroscience*, *1*(December), 199–207.
- Schwartz, S., Maquet, P., & Frith, C. (2002). Neural correlates of perceptual learning: a functional MRI study of visual texture discrimination. *Proceedings of the National Academy of Sciences of the United States of America*, 99(26), 17137–17142. doi:10.1073/pnas.242414599
- Seitz, A. R., Náñez, J. E., Holloway, S. R., & Watanabe, T. (2005). Visual experience can substantially alter critical flicker fusion thresholds. *Human Psychopharmacology*, 20(1), 55–60. doi:10.1002/hup.661
- Seitz, A. R., Náñez, J. E., Holloway, S. R., & Watanabe, T. (2006). Perceptual learning of motion leads to faster flicker perception. *PloS One*, 1(1), e28. doi:10.1371/journal.pone.0000028
- Seitz, A. R., Protopapas, A., Tsushima, Y., Vlahou, E. L., Gori, S., Grossberg, S., & Watanabe, T. (2010). Unattended exposure to components of speech sounds yields same benefits as explicit auditory training. *Cognition*, 115(3), 435–443. doi:10.1016/j.cognition.2010.03.004
- Seitz, A. R., & Watanabe, T. (2003). Psychophysics: Is subliminal learning really passive? *Nature*, 422(6927), 36. doi:10.1038/422036a
- Sjöström, P. J., Turrigiano, G. G., & Nelson, S. B. (2001). Rate, timing, and cooperativity jointly determine cortical synaptic plasticity. *Neuron*, *32*(6), 1149–1164. doi:10.1016/S0896-6273(01)00542-6
- Stein, J., & Talcott, J. (1999). Impaired neuronal timing in developmental dyslexia—the magnocellular hypothesis. *Dyslexia*, 5(June), 59–77. doi:10.1002/(SICI)1099-0909(199906)5:2<59::AID-DYS134>3.0.CO;2-F
- Tallal, P. (1980). Auditory temporal perception, phonics, and reading disabilities in children. *Brain and Language*, 9(2), 182–198. doi:10.1016/0093-934X(80)90139-X

- Tallal, P. (2004). Improving language and literacy is a matter of time. *Nature Reviews*. *Neuroscience*, *5*(9), 721–728. doi:10.1038/nrn1499
- Tipper, S. P., & Cranston, M. (1985). Selective attention and priming: Inhibitory and facilitatory effects of ignored primes. *The Quarterly Journal of Experimental Psychology, Section A: Human Experimental Psychology*, 37(4), 591–611. doi:10.1080/14640748508400921
- Tsushima, Y., Sasaki, Y., & Watanabe, T. (2006). Greater disruption due to failure of inhibitory control on an ambiguous distractor. *Science*, 314(5806), 1786–1788. doi:10.1126/science.1133197
- Tsushima, Y., Seitz, A. R., & Watanabe, T. (2008). Task-irrelevant learning occurs only when the irrelevant feature is weak. *Current Biology*, 18(12), R516-R517. doi:10.1016/j.cub.2008.04.029
- Vaina, L. M., Soloviev, S., Bienfang, D. C., & Cowey, A. (2000). A lesion of cortical area V2 selectively impairs the perception of the direction of first-order visual motion. *Neuroreport*, 11(5), 1039–1044. doi:10.1097/00001756-200004070-00028
- Vellutino, F. R., Fletcher, J. M., Snowling, M. J., & Scanlon, D. M. (2004). Specific reading disability (dyslexia): What have we learned in the past four decades? *Journal of Child Psychology and Psychiatry and Allied Disciplines*, 45(1), 2-40. doi:10.1046/j.0021-9630.2003.00305.x
- Watanabe, T., Náñez, J. E., 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. *Nature Neuroscience*, 5(10), 1003–1009. doi:10.1038/nn915
- Watanabe, T., Náñez, J. E., & Sasaki, Y. (2001). Perceptual learning without perception. *Nature*, *413*(6858), 844–848. doi:10.1038/35101601
- Wiesel, T. N., & Hubel, D. H. (1965). Extent of recovery from the effects of visual deprivation in kittens. *Journal of Neurophysiology*, 28(6), 1060–1072.
- Wiggs, C. L., & Martin, A. (1998). Properties and mechanisms of perceptual priming. *Current Opinion in Neurobiology*, 8(2), 227-233. doi:10.1016/S0959-4388(98)80144-X
- World Medical Association. (2008). World Medical Association Declaration of Helsinki: Ethical principles for medical research involving human subjects (amended by the 59th WMA General Assembly, Seoul, October 2008). Ferney-Voltaire: WMA World Medical Association (WMA).

- Yang, T., & Maunsell, J. H. R. (2004). The effect of perceptual learning on neuronal responses in monkey visual area V4. *Journal of Neuroscience*, 24, 1617–1626.
- Zohary, E., Shadlen, M. N., & Newsome, W. T. (1994). Correlated neuronal discharge rate and its implications for psychophysical performance. *Nature*, *370*, 140-143. doi:10.1038/370140a0