Title
Mechanisms of Sensory Learning Processes

Permalink
https://escholarship.org/uc/item/97s8n38r

Author
Bays, Brett Christopher

Publication Date
2016

UNIVERSITY OF CALIFORNIA
RIVERSIDE

Mechanisms of Sensory Learning Processes

A Dissertation submitted in partial satisfaction
of the requirements for the degree of

Doctor of Philosophy

in

Psychology

by

Brett Christopher Bays

August 2016

Dissertation Committee:
Dr. Aaron R. Seitz, Chairperson
Dr. George J. Andersen
Dr. Steven E. Clark

The Dissertation of Brett Christopher Bays is approved:

Committee Chairperson

University of California, Riverside

Acknowledgements

I would like to thank my committee – Dr. Aaron Seitz, Dr. Steve Clark, and Dr. G. John Andersen – for their time and support. I would especially like to thank Aaron, who has been a phenomenal PhD advisor. He taught me what it means to be a researcher, always pushed me to seek out new solutions to seemingly insurmountable problems, and was an indefatigable source of wisdom and inspiration. In six years of collaboration he exercised extraordinary patience with me and was continuously available for help, often with a smile and a joke to go along with it. I hope that future students appreciate him as much as I do.

My mother deserves more thanks than I can give here. She has supported me throughout my life, no matter the cost to herself, and has always been as proud of me as humanly possible. I rarely show her enough gratitude but I will always be thankful for the help she has given me.

Faye Harmer and Renee Young in the administrative office were crucial to my success obtaining a PhD. Without them I would still be trying to register for my first year classes and fruitlessly pushing buttons on a fax machine.

Dr. Bir Bhanu and the IGERT on Video Bioinformatics supported me financially for two years and provided me with invaluable interdisciplinary experience.

Countless friends helped me throughout my time in the program, whether they knew it or not. While there are too many to mention, some of them deserve special acknowledgement. Lauren Ko has been one of my closest friends for two decades now.

She brought me donuts in high school, lets me relax at her house and ride horses whenever I visit, and has always listened to me when I felt discouraged. Alan Metoskie helped me survive both high school and college, was the best first roommate anyone could have, and is the funniest comedian of this generation. Chris Pfeffer has inspired me since I first met him and throughout our friendship together. He probably doesn't know it but he taught me how to remain calm when life is trying its best to drive you insane. Anthony Davis is the finest engineer, musician, and friend that a person could ask for. He has also been an inspiration to me for as long as I've known him and has only grown more inspiring with every challenge I've seen him overcome. Erica Baranski is one of the most caring roommates I've ever had and I will never be able to repay her for all of her help while I was injured and writing this dissertation. Every friend I've made in California since beginning my PhD has helped me to keep a few shreds of sanity during these six years and I'm thankful for every one of them. And certainly not least, Paloma LeVie has provided me with more help and support throughout this year, and especially throughout my injury, than I ever thought would be possible, which is all the more remarkable considering she is normally 2,700 miles away. She's the rarest combination of intelligence, humor, and charm, and I'm lucky to know her.

Finally, I would like to thank Odin and Loki, who were always there for me even when I was too busy to pet them. I should really buy you two some cat toys.

BRETT BAYS

Curriculum Vitae

Department of Psychology
University of California, Riverside
3209 Psychology Building
Riverside, California 92521
brett.bays@email.ucr.edu

EDUCATION

Ph.D.	Psychology (Cognitive Neuroscience) University of California, Riverside
B.A.	Psychology & Philosophy (double major) - 2005 University of Texas at Austin Graduated with honors

---

RESEARCH EXPERIENCE

- Designed and conducted dozens of independent and collaborative research studies in Dr. Aaron Seitz's cognitive neuroscience lab as a graduate student, in addition to other cognitive research performed as an undergraduate student
- Collected data from hundreds of participants in experiments; analyzed and evaluated data; reported on numerous significant findings in peer-reviewed journal publications, abstracts, and posters (see respective sections below)
- Gained extensive experience utilizing electrophysiological methods for neurological investigations with a focus on electroencephalography (EEG)
- Programmed behavioral and neurological studies continuously, creating hundreds of experimental programs and analysis scripts in Matlab, R, SPSS, and other languages/software
- Utilized multiple hardware systems, including hardware from Cortech Solutions, VPixx Technologies, Cambridge Research Systems, SR Research, and others
- Taught research methods and statistical analyses for multiple years at introductory, advanced, and graduate-student levels
- Mentored and trained fifteen undergraduate research assistants in lab protocols, methodology, computer programming, and research design

- Supervised four research assistants in their independent research, which lead to their acquisition of the Best Poster Award at the 2015 UCR Undergraduate Research Symposium
- Awarded the selective NSF IGERT for Video Bioinformatics fellowship from 2012-2014, which involved interdepartmental training and collaborative research of spatio-temporal data in engineering, biology, and bioengineering
- Gained early experience as a research assistant in Dr. Robert Josephs' Social Endocrinology Lab at the University of Texas as an undergraduate student

---

PROGRAMMING EXPERIENCE

- Matlab, including associated toolboxes such as PsychToolBox, EEGLab, FieldTrip, and the Machine Learning Toolbox
- R
- PASW/SPSS and other statistical software
- C++
- Taught Matlab programming for multiple years to undergraduate students in classes and research assistants in the laboratory
- Tutored, assisted, and problem-solved for numerous graduate students and faculty members who encountered programming difficulties in Matlab and R

CONFERENCES ATTENDED

- Vision Sciences Society, St. Pete Beach, Fl (formerly Fort Myers, Fl) – 2013, 2014, 2015
- UCR NSF IGERT for Video Bioinformatics, Lake Arrowhead, Ca – 2012, 2013, 2014
- Society for Neuroscience, San Diego, Ca – 2010, 2013
- Attention and Learning, La Jolla, Ca – 2013

TEACHING EXPERIENCE

University of California, Riverside. **Instructor**

- 2015 Psyc 11 Statistical Procedures

Assistant Instructor / Teaching Assistant

- 2016 Psyc 132 - Perception
- 2016 Psyc 182F - Experimental Design & Programming in Matlab
- 2015 Psyc 11 - Statistical Procedures
- 2015 Psyc 182F - Experimental Design & Programming in Matlab
- 2014 Psyc 211 - Statistical Inference (Graduate Level)
- 2012 Psyc 109 - Advanced Research Methods & Statistics
- 2012 Psyc 1 - Intro to Psychology
- 2011 Psyc 11 - Statistical Procedures
- 2011 Psyc 134 - Cognition

Independently Organized Courses

- 2013 - Programming in Matlab for research assistants from multiple labs

---

PUBLICATIONS

- **Bays, B.C.**, Visscher, K.M., Le Dantec, C.C., Seitz, A.R. (2015). Alpha-band EEG activity in perceptual learning. *Journal of Vision, 15(10), 7, DOI: 10.1167/15.10.7*

- **Bays, B.C.**, Turk-Browne, N.B., & Seitz, A.R. (2016). Dissociable behavioral outcomes of visual statistical learning. *Visual Cognition, 2016: 1-26, DOI: 10.1080/13506285.2016.1139647*

- Zahedi, A., On, V., Lin, S.C., **Bays, B.C.**, Omaiye, E., Bhanu, B., & Talbot, P. (2016). Computational Analysis of Human Embryonic Stem Cell Videos Predicts Health Index. *PLoS ONE, 11(2):e0148642, DOI: 10.1371/journal.pone.0148642*

ABSTRACTS AND POSTERS

- "Classifying EEG patterns of visual statistical learning", **Brett C. Bays** and Aaron R. Seitz, *Vision Sciences Society 2015* [abstract and poster]

- "Classifying EEG patterns of visual learning processes", **Brett C. Bays** and Aaron R. Seitz, *UCR NSF IGERT for Video Bioinformatics 2014 Conference and Retreat* [poster and video]

- "Alpha-band EEG activity as a signature of automaticity in perceptual learning", **Brett C. Bays**, Kristina M. Visscher, Christophe C. Le Dantec, Aaron R. Seitz, *Vision Sciences Society 2014* [abstract and poster]

- "What is the relation of alpha band activity in human EEG to perceptual and contextual learning?", **Brett C. Bays**, Christophe C. Le Dantec, Aaron R. Seitz, *UCR NSF IGERT for Video Bioinformatics 2013 Conference and Retreat* [poster and video]

- "Is the BDNF val66met polymorphism associated with differential statistical learning?", **Brett C. Bays**, Craig M. Bula, Christophe C. Le Dantec, Aaron R. Seitz, *Society for Neuroscience 2013* [abstract and poster]

- "Statistical learning, a singular process? Dissociating behavioral outcomes of visuo-temporal statistical learning", **Brett C. Bays**, Nicholas B. Turk-Browne, Aaron R. Seitz, *Vision Sciences Society 2013* [abstract and poster]

- "Dissociable neural processes underlying statistical learning", **Brett C. Bays**, Christophe Le Dantec, Aaron R. Seitz, *UCR NSF IGERT for Video Bioinformatics 2012 Conference and Retreat* [poster and video]

- "Men need a nap to show perceptual learning of motion direction discrimination, but women do not", Elizabeth A. McDevitt, **Brett C. Bays**, Ariel Rokem, Michael A. Silver, Sara C. Mednick, *Vision Sciences Society 2012* [abstract and poster]

TALKS AND PRESENTATIONS

- "Classifying EEG patterns of visual learning processes", **Brett C. Bays** and Aaron R. Seitz, *UCR IGERT on Video Bioinformatics annual retreat, October 11, 2014, Lake Arrowhead, CA* [video presentation and talk]

- "The non-specificity of automaticity: Alpha-band EEG activity in perceptual learning", **Brett C. Bays**, Kristina M. Visscher, Christophe C. Le Dantec, Aaron R. Seitz, *UCR Psychology cognitive area colloquium, May 28, 2014, UCR, Riverside, CA* [invited talk]

- "Alpha-band EEG activity in humans and visual perceptual learning", **Brett C. Bays**, Christophe C. Le Dantec, Aaron R. Seitz, *UCR IGERT on Video Bioinformatics colloquium, January 24, 2014, UCR, Riverside, CA* [video presentation and talk]

- "Spatio-temporal patterns of alpha band EEG activity in a perceptual learning paradigm: An in-progress analysis", **Brett C. Bays**, Christophe C. Le Dantec, Aaron R. Seitz, *UCR IGERT on Video Bioinformatics colloquium, January 17, 2014, UCR, Riverside, CA* [invited talk]

- "What is the relation of alpha band activity in human EEG to perceptual and contextual learning?", **Brett C. Bays**, Christophe C. Le Dantec, Aaron R. Seitz, *UCR IGERT on Video Bioinformatics annual retreat, December 7, 2013, Lake Arrowhead, CA* [video presentation and talk]

- "Dissociating behavioral outcomes of visuo-temporal statistical learning", **Brett C. Bays**, Nicholas Turk-Browne, Aaron R. Seitz, *UCR Psychology cognitive area colloquium, April 10, 2013, UCR, Riverside, CA* [invited talk]

- "Computational analysis of human embryonic stem cell videos predicts health index", **Brett C. Bays**, Vincent On, Atena Zahedi, *UCR IGERT on Video Bioinformatics colloquium, April 1, 2013, UCR, Riverside, CA* [invited talk]

- "Competing neural processes underlying statistical learning", **Brett C. Bays**, Nicholas Turk-Browne, Aaron R. Seitz, *UCR IGERT on Video Bioinformatics annual retreat, December 1, 2012, Lake Arrowhead, CA* [video presentation and talk]

- "The interaction of attention and visual statistical learning", **Brett C. Bays**, Nicholas Turk-Browne, Aaron R. Seitz, *UCR Psychology cognitive area colloquium, March 14, 2012, UCR, Riverside, CA* [invited talk]

PROFESSIONAL SOCIETIES

- Vision Sciences Society
- Society for Neuroscience

PEER REVIEWER

- Journal of Experimental Psychology: Learning, Memory, and Cognition
- Cognition
- Visual Cognition
- Frontiers in Human Neuroscience
- Psychonomic Bulletin and Review

FELLOWSHIPS AND AWARDS

- NASA/JPL FIELDS (Fellowships and Internships in Extremely Large Data Sets), Awarded full funding for one year, 2015
- UCR Outstanding Teaching Award, 2015
- NSF IGERT for Video Bioinformatics Fellowship, 2012-2014 ($30,000/year + travel expenses)
- National Science Foundation Graduate Research Fellowship, applied for in 2010 and 2011
- UCR Chancellor’s Distinguished Fellowship, 2010

ABSTRACT OF THE DISSERTATION

Mechanisms of Sensory Learning Processes

by

Brett Christopher Bays

Doctor of Philosophy, Graduate Program in Psychology
University of California, Riverside, August 2016
Dr. Aaron R. Seitz, Chairperson

Sensory learning – the ability of our perceptual systems to exhibit change and improvement in response to sensory input – is an important class of processes that allows perception to adapt meaningfully to the environment. It can include improvements based on repeated exposure to stimuli, called perceptual learning (PL), and learning patterns governing stimuli, called statistical learning (SL). Efficiently combining information from multiple modalities, called multisensory integration (MI), has also been shown to interact with these processes. In a series of experiments, we investigate whether PL, SL, and MI might each comprise multiple underlying mechanisms and whether those mechanisms might intersect, using behavioral and neurological methodology.

In the first chapter, we conduct three experiments using an SL paradigm to show that SL may comprise multiple processes. Experiment 1 demonstrates our ability to find a dissociation between behavioral outcome measures; Experiment 2 replicates Experiment 1 using a different task; and Experiment 3 replicates it further while investigating whether the learning is associative or representational. In the second chapter, we analyze electroencephalogram (EEG) alpha power as a proxy for attentional resources during PL training. Behavioral results suggest that PL occurred and electrophysiological results suggest that after training, participants were able to perform the task using fewer resources and to allocate those resources more efficiently. This latter result did not apply specifically to trained stimuli, suggesting that multiple mechanisms may be at work during PL. The third chapter uses a novel training paradigm that combines PL, SL, and MI to investigate the extent to which these processes share common mechanisms and how their interactions impact perception. Across two sets of experiments, participants performed a discrimination task on audio-visual stimuli that appeared according to controlled spatio-temporal statistics. Behavioral data show some PL, SL, and MI effects, and EEG data hint at an SL and PL relationship with alpha power. The results of this study, although not all statistically significant, provide insight into the underlying mechanisms of PL, SL, MI.

Altogether, we provide evidence that sensory learning and other perceptual processes should not be treated as unitary mechanisms but instead should be investigated in terms of their manifold natures.

TABLE OF CONTENTS

GENERAL INTRODUCTION 1

References 12

CHAPTER 1 24

Abstract 25

Introduction 26

Experiment 1 30

Experiment 2 41

Experiment 3 46

General Discussion 52

References 57

Supplemental Data 62

Figures 67

Tables of Means 84

CHAPTER 2 89

Abstract 90

Introduction 91

Methods 95

Results 101

Discussion 104

References.....111
Figures.....118
Table of Means.....125

CHAPTER 3.....126
Abstract.....127
Introduction.....128
Experiment 1.....132
Experiment 2.....146
Discussion.....156
References.....163
Figures.....170
Tables of Means.....189

GENERAL DISCUSSION.....198
References.....205

COMPLETE REFERENCES.....208
COMPLETE TABLES OF MEANS.....223

LIST OF FIGURES

Figure 1 Experimental design....67

Figure 2 Exp. 1 – Accuracy and contrast by block....68

Figure 3 Exp. 1 – Mean RTs of each pair for each participant....69

Figure 4 Exp. 1 – Search task....70

Figure 5 Exp. 1 – Detection task split by search task....71

Figure 6 Exp. 2 – Response scale for recognition task....72

Figure 7 Exp. 2 – Detection task split by recognition task....73

Figure 8 Exp. 2 – Detection task split by Familiar/Remember ratings....74

Figure 9 Exp. 3 – Search task....75

Figure 10 Exp. 3 – Detection task split by search task....76

Figure S1 Exp. 1 – Histograms for learned/non-learned classifications....77

Figure S2 Exp. 1 – Detection task....78

Figure S3 Exp. 2 – Detection task....79

Figure S4 Exp. 3 – Detection task....80

Figure S5 Exp. 1 – Search task with triplet structure....81

Figure S6 Exp. 1 – Detection task with triplet structure split by search task....82

Figure S7 Exp. 2 – Detection task with triplet structure split by recognition task....83

Figure 11 Schedule of experimental sessions....118

Figure 12 Diagram of a single trial....119

Figure 13 Electrode placement and diagram of analysis periods....120

Figure 14 Orientation offset threshold across training days....121

Figure 15 Accuracy and RT before and after training 122

Figure 16 Alpha power before and after training with scalp distributions 123

Figure 17 Alpha power in trained and untrained targets in the post-test 124

Figure 18 Example of a modified Markov chain 170

Figure 19 Electrode placement 171

Figure 20 Exp. 1 – Trained vs. untrained positions in 2nd session 172

Figure 21 Exp. 1 – SL during training session 173

Figure 22 Exp. 1 – Trained vs. untrained statistics in 2nd session 174

Figure 23 Exp. 1 – Trials with sound vs. no sound in 2nd session 175

Figure 24 Exp. 1 – Alpha power split by transition probability 176

Figure 25 Exp. 1 – Control study – SL during training session 177

Figure 26 Exp. 2 – Schedule of experimental sessions 178

Figure 27 Exp. 2 – Contrast thresholds 179

Figure 28 Exp. 2 – Trained vs. untrained positions pre- and post-training 180

Figure 29 Exp. 2 – Landolt C results pre- and post-training 181

Figure 30 Exp. 2 – Cutoff spatial frequency results pre- and post-training 182

Figure 31 Exp. 2 – MN Read results pre- and post-training 183

Figure 32 Exp. 2 – SL effects across session days 184

Figure 33 Exp. 2 – Trained vs. untrained statistics pre- and post-training 185

Figure 34 Exp. 2 – Trials with sound vs. no sound pre- and post-training 186

Figure 35 Exp. 2 – Alpha power split by transition probability and test session 187

Figure 36 Exp. 2 – Alpha power for all visible trials pre- and post-training 188

LIST OF TABLES

Table 1 Chapter 1 – Experiment 1 Means and Standard Deviations 84

Table 2 Chapter 1 – Experiment 2 Means and Standard Deviations 85

Table 3 Chapter 1 – Experiment 3 Means and Standard Deviations 86

Table 4 Chapter 1 – Supplemental Data Means and Standard Deviations 87

Table 5 Chapter 2 – Means and Standard Deviations..125

Table 6 Chapter 3 – Experiment 1 & Control Study Means and Std. Dev. 189

Table 7 Chapter 3 – Experiment 2 Means and Standard Deviations 192

GENERAL INTRODUCTION

Sensory learning and plasticity

Adapting to our environment is essential to human functioning. Without this ability there could be no learning, no changes to our perceptual abilities, and no development throughout our lifetimes. The ability for a sensory system to learn and adapt to the environment is broadly known as "sensory plasticity" at the cellular level or "sensory learning" at the behavioral level, and involves the system's ability to change in response to perceptual input. Plasticity in the brain and its connection to learning has been postulated for over a hundred years, dating back to groundbreaking work such as Santiago Ramón y Cajal's "theory of neurotropism" (Ramón y Cajal, 1894, 1959) and Donald Hebb's investigations of the neural mechanisms underlying learning and behavior (Hebb, 1949). Experience-dependent plasticity has been more recently studied in a variety of paradigms (e.g., Buonomano & Merzenich, 1998; Johnson, 2001) and importantly has been discussed with respect to fully developed adult brains instead of solely with respect to younger, developing systems. This is important because early evidence suggested a lack of neuroplasticity in adult brains and evidence for critical periods of brain plasticity that occurred in developing neurological systems lent additional weight to this idea (Berardi, Pizzorusso, & Maffei, 2000; Hubel & Wiesel, 1962, 1970; Ramón y Cajal, 1959). These studies served to reinforce a view among many that mature, adult brains are incapable of further plasticity. However, a large number of studies soon provided evidence for adult plasticity in different perceptual modalities (Calford et al., 2005; Kaas, 1991). In the somatosensory modality, reorganization of adult brains has been observed in monkeys

(Merzenich et al., 1984), flying-fox bats (Calford & Tweedale, 1988), and in humans (Elbert et al., 1994; T. T. Yang et al., 1994). Similarly, in the visual modality adult neural plasticity has been observed in rats (Baroncelli et al., 2010; Sale et al., 2010), cats (Hua et al., 2010), monkeys (Heinen & Skavenski, 1991), humans (Fine et al., 2003; Gilbert, Li, & Piech, 2009; Yotsumoto et al., 2014), and correlates have been observed at both the molecular level (Obata, Obata, Das, & Gilbert, 1999) and at the behavioral level (e.g., Andersen, Ni, Bower, & Watanabe, 2010; Deveau, Ozer, & Seitz, 2014; Levi, 2005).

The evidence for adult plasticity is especially important for the types of sensory learning that we will discuss, namely perceptual learning (PL) and statistical learning (SL), and for the process of multisensory integration (MI) which can interact with perception. These three facets of learning and perception deal with a variety of situations in which mature sensory systems are exposed to new stimuli, patterns of stimuli, or combinations of stimuli, and produce improved or otherwise changed responses. For example, these changes might be improvements in visual acuity (PL), improved detection of patterns in the environment (SL), or integration of different modalities leading to improved detection of stimuli (MI). There is an open question in the literature, however, as to whether these processes are unitary, as they are often treated, or whether they each comprise multiple underlying mechanisms. Investigating the multifaceted nature of these processes is central to this dissertation and the evidence for predicting such a nature is discussed along with each process below. We then describe the experiments that were used to investigate the neural and behavioral mechanisms underlying these processes and how those mechanisms may intersect.

Perceptual learning

Perceptual learning refers to an improvement in performance for perceptual tasks after repeated exposure or training with stimuli related to those tasks. PL has been studied for over a century, has been documented in both non-human and human animals, and is typically considered an implicit process that can occur in multiple sensory modalities (for reviews see, Fahle, 2005; Ghose, 2004; Gilbert, Sigman, & Crist, 2001; Sagi, 2011; Sasaki, Náñez, & Watanabe, 2012; Seitz & Dinse, 2007; Watanabe & Sasaki, 2015). PL has retained its investigative importance because of its relationship to a sensory system's ability to adapt and improve in response to the environment and has been particularly well-studied in the visual modality. In visual PL, laboratory stimuli are often composed of simple features which can be manipulated and measured easily. For example, visual PL has been investigated using oriented gratings (Dobres & Seitz, 2010; Schoups, Vogels, Qian, & Orban, 2001; T. Yang & Maunsell, 2004), line or dot offset (Fahle, Edelman, & Poggio, 1995; Hung & Seitz, 2014; Poggio, Fahle, & Edelman, 1992), motion (Seitz, Nanez, Holloway, & Watanabe, 2006; Seitz & Watanabe, 2005, 2008; Zohary, Celebrini, Britten, & Newsome, 1994), and contrast (Adini, Sagi, & Tsodyks, 2002; Hua et al., 2010; Yu, Klein, & Levi, 2004). More complex stimuli and training paradigms have also been used to study PL, such as action video games (Green & Bavelier, 2007; Green, Li, & Bavelier, 2010), human faces (Hussain, Sekuler, & Bennett, 2011), and training designed to evoke perceptual gains outside of the laboratory (Deveau, Lovcik, & Seitz, 2014; Deveau, Ozer, & Seitz, 2014).

A highly debated topic within PL over the last two decades has involved the issue of specificity. Classically, behavioral improvements seen after training have been specific to the stimuli, location, and task used during training, leading many to theorize that neural correlates of PL occur in early visual areas, where neurons are sharply tuned to features such as orientation, location, and size (De Valois, 1977; Fahle, 2004; Fiorentini & Berardi, 1980; Ramachandran & Braddick, 1973). Evidence of neuronal changes in early visual areas that are specific to trained features has also provided support for this view (Bao, Yang, Rios, He, & Engel, 2010; Gilbert et al., 2009, 2001; Hua et al., 2010). However, a growing body of research has demonstrated that under certain conditions, PL can transfer to untrained locations and stimuli (Ahissar & Hochstein, 2004; Deveau, Ozer, et al., 2014; Hung & Seitz, 2014; Xiao et al., 2008; Zhang et al., 2010). Evidence such as this has been used to argue against early plasticity as the seat of PL, and there is currently a great deal of debate as to how to model the available evidence (Ahissar & Hochstein, 2004; Byers & Serences, 2012; Dosher & Lu, 1998; Fahle, 2005; Hung & Seitz, 2014; Jeter, Dosher, Liu, & Lu, 2010; Petrov, Dosher, & Lu, 2005; Pilly, Grossberg, & Seitz, 2010; Xiao et al., 2008; Zhang et al., 2010). We propose that one possible explanation would be the existence of multiple mechanisms subserving PL at different stages of perceptual processing. Thus, Chapter 2 of this dissertation adds to the discussion by examining neuronal and attentional mechanisms that might change due to PL training, how those changes provide evidence for different mechanisms supporting PL, and how those mechanisms might affect different explanations of PL specificity and non-specificity. Chapter 3 also examines whether the underlying mechanisms might interact with other perceptual processes and investigates specificity in PL by measuring transfer to untrained tasks after training.

Statistical learning

Statistical learning refers to the perceptual process of learning patterns among probabilistically organized stimuli, normally without any conscious awareness that there are patterns to be learned (for a review see, Turk-Browne, 2012). Like PL, the process of SL can occur in various modalities (e.g., Conway & Christiansen, 2006; Fiser & Aslin, 2001; Saffran, Aslin, & Newport, 1996), is thought to occur implicitly (Fiser & Aslin, 2002; Kim, Seitz, Feenstra, & Shams, 2009) and can influence our perception of stimuli (Barakat, Seitz, & Shams, 2013; Chalk, Seitz, & Seriès, 2010). Unlike PL, which normally occurs on a time-scale of days, SL can occur in a matter of minutes (Aslin, Saffran, & Newport, 1998; Kim et al., 2009; Saffran et al., 1996; Turk-Browne, Scholl, Chun, & Johnson, 2009) and in the visual modality can transfer across spatial and temporal dimensions (Turk-Browne & Scholl, 2009). Auditory SL is thought to underlie aspects of language development in humans (Saffran et al., 1996; Saffran, Johnson, Aslin, & Newport, 1999; Saffran & Thiessen, 2003; C. D. Yang, 2004) and visual SL has been implicated in the binding of features and objects (Turk-Browne, Isola, Scholl, & Treat, 2008) and defining the scale of objects (Fiser & Aslin, 2001, 2005).

The mechanisms underlying SL are not as well modeled as the mechanisms underlying PL. This is possibly due to SL becoming a research topic more recently than PL and also the wide variety of paradigms used to investigate SL, which can include exposure with cover tasks (Saffran, Newport, Aslin, Tunick, & Barrueco, 1997; Toro, Sinnett, & Soto-Faraco, 2005), exposure without cover tasks (Fiser & Aslin, 2001; Saffran et al., 1996), familiarity tests (Fiser & Aslin, 2001, 2002; Saffran et al., 1999; Turk-Browne et al., 2008), reaction time tests (Hunt & Aslin, 2001; Kim et al., 2009; Turk-Browne, Jungé, & Scholl, 2005), and different patterns governing the stimuli, such as visuo-spatial patterns, visuo-temporal patterns, and audio-temporal patterns (Fiser & Aslin, 2005; Saffran et al., 1999; Zhao, Al-Aidroos, & Turk-Browne, 2013). Neurological evidence for SL comes mostly from fMRI studies (for a review see, Karuza, Emberson, & Aslin, 2014) and suggests two main brain regions supporting SL – the medial temporal lobe (Schapiro, Gregory, Landau, McCloskey, & Turk-Browne, 2014; Schapiro, Kustner, & Turk-Browne, 2012; Turk-Browne et al., 2009; Turk-Browne, Scholl, Johnson, & Chun, 2010) and the striatum (Durrant, Cairney, & Lewis, 2013; Turk-Browne et al., 2009). Additionally, there is fMRI and near-infrared spectroscopy evidence for support from the left inferior frontal gyrus (Abla & Okanoya, 2008; Karuza et al., 2013; Turk-Browne et al., 2009) and activity in other regions, such as the occipital cortex, has also been correlated with SL (Turk-Browne et al., 2009, 2010). Taken together, this evidence points towards a learning process that likely involves higher brain regions than PL but which also demonstrates a fair amount of overlap, suggesting that there may be common components to both processes.

Although there are clearly many behavioral aspects of SL and multiple brain regions subserving it, the literature is fairly silent on whether SL is a unitary process or whether is comprises multiple processes. Based on evidence from SL in different modalities, Conway and Christiansen (2005) argue that multiple mechanisms compose SL, but few others discuss the topic. There is behavioral evidence that multiple processes may affect results of visual SL (Zhao, Ngo, McKendrick, & Turk-Browne, 2011), that the consolidation of SL may have multiple components (Durrant, Taylor, Cairney, & Lewis, 2011), and that SL may affect attentional processes (Zhao et al., 2013) and perceptual processes such as PL (Barakat et al., 2013). Additionally, there is neurological evidence for different time-courses of medial temporal lobe and striatal activation during SL, which might correspond to multiple memory systems at work (Durrant et al., 2013; Turk-Browne et al., 2009, 2010). Chapter 1 investigates this question further by using a novel analysis technique designed to find behavioral evidence of multiple processes underlying SL. Additionally, Chapter 3 investigates the relationship between SL and other perceptual processes such as PL and MI.

Multisensory integration

Multisensory integration is the process of combining information from different sensory modalities into a single multisensory unit. Although not utilized in the experiments of this dissertation as much as PL or SL, it is an important perceptual process that can affect both PL and SL, is involved in the experiments of Chapter 3, and thus deserves a brief introduction here. Historically, unisensory input has been considered the brain's primary source of perceptual information but growing evidence suggests that MI plays an important role as well (for reviews see, Koelewijn, Bronkhorst, & Theeuwes, 2010; Shams & Seitz, 2008; Shimojo & Shams, 2001; Stein & Stanford, 2008). For example, it is possible to obtain enhanced performance in visual learning tasks by using integrated visual and auditory stimuli (Kim, Seitz, & Shams, 2008; Raposo, Sheppard, Schrater, & Churchland, 2012; Seitz, Kim, & Shams, 2006; Shams & Seitz, 2008; Sheppard, Raposo, & Churchland, 2013). There is also a large body of evidence suggesting that MI may take place at very early processing stages in the brain, including primary visual and auditory cortex (Calvert et al., 1997, 1999; Cohen et al., 1997; Macaluso, Frith, & Driver, 2000; Powers, Hevey, & Wallace, 2012; Sadato et al., 1996; Shams, Kamitani, Thompson, & Shimojo, 2001).

For the purposes of this dissertation, MI is important because it has been shown that it can affect and improve PL performance (Deveau, Lovcik, et al., 2014; Kim et al., 2008; Seitz, Kim, et al., 2006; Shams & Seitz, 2008). For example, Kim, Seitz, and Shams (2008) found that using congruent auditory stimuli in conjunction with visual stimuli in a motion detection task increased the amount of learning and the rate of learning across training days. Multisensory stimuli have also been incorporated into vision-enhancing video games that utilize perceptual learning approaches (Deveau, Lovcik, et al., 2014). Additionally, multisensory stimuli have been used in studies of SL (Conway & Christiansen, 2006) although the results suggest that integration between modalities did not occur. These results suggest that there may be common mechanisms underlying MI and PL, and possibly MI and SL, and thus Chapter 3 is designed to investigate the question of how MI, PL, and SL might interact by incorporating all three processes in a single experimental paradigm.

Methodology

The methods used to investigate PL, SL, and MI are extremely varied and include behavioral measures such as reaction times and accuracy, electrophysiology such as single unit recordings and electroencephalography (EEG), and imaging based techniques such as MRI and fMRI (e.g., Abla & Okanoya, 2009; Bays, Visscher, Le Dantec, & Seitz, 2015; Le Dantec, Melton, & Seitz, 2012; Powers et al., 2012; Schapiro et al., 2014; Schoups et al., 2001; Yotsumoto et al., 2014). In this dissertation we focus on using behavioral measures and EEG to understand underlying mechanisms. EEG has been used to study PL (Bao et al., 2010; Bays et al., 2015; Freyer, Becker, Dinse, & Ritter, 2013; Sigala, Haufe, Roy, Dinse, & Ritter, 2014), SL (Abla, Katahira, & Okanoya, 2008; Abla & Okanoya, 2009; Sanders, Newport, & Neville, 2002), and MI (Shams et al., 2001). Converting the EEG signal from the time domain, where it is a measure of voltages across time, to the time-frequency domain, where it is a measure of power at different frequencies across time, has become a popular and revealing method for analyzing EEG data (for reviews see, Hanslmayr, Gross, Klimesch, & Shapiro, 2011; Hughes & Crunelli, 2005; Klimesch, 1999; Samar, Bopardikar, Rao, & Swartz, 1999). In particular the alpha bandwidth, comprising frequencies 8-12Hz, has shown to be predictive of performance (Hanslmayr et al., 2011; Klimesch, Sauseng, & Hanslmayr, 2007; Payne & Sekuler, 2014) and to be negatively correlated with effort and attention to visual tasks (Bollimunta, Chen, Schroeder, & Ding, 2008; Ergenoglu et al., 2004; Hanslmayr et al., 2007; Nenert, Viswanathan, Dubuc, & Visscher, 2012; Snyder & Foxe, 2010; Vaden, Hutcheson, McCollum, Kentros, & Visscher, 2012). The question of what alpha power may reveal about PL and SL is addressed in Chapters 2 and 3 and all three chapters utilize behavioral measures to address their respective issues.

Dissertation structure

The overarching goal of this dissertation is to examine the underlying mechanisms of sensory learning and other perceptual processes in novel ways and to ultimately determine where they might intersect. Chapter 1 examines visual SL and investigates whether it might itself comprise multiple processes. In a series of three experiments we show that visual SL, commonly treated as a single process, is able to show dissociable behavioral effects which suggest an underlying family of processes. Chapter 2 examines visual PL and uses behavioral and time-frequency EEG methodology to investigate task automaticity, efficiency, and effort in a PL training paradigm. The results suggest that after training participants are able to perform a PL task with more efficient uses of cognitive resources, although these benefits were not specific to trained stimuli. These results imply that there might be multiple mechanisms at work during PL training and help to address unresolved issues within the PL area such as transfer of training. Chapter 3 combines SL, PL, and MI methodology into a novel training paradigm used to investigate the intersection of those perceptual processes, whether they can be combined to improve perceptual abilities, and whether the training can transfer to untrained tasks. Behavioral and time-frequency EEG results suggest that learning occurred and that some of it may have transferred to untrained tasks. Together, these three chapters serve to help us understand different underlying aspects of sensory learning and perception, what they might have in common, and what remains for us to learn about them.

References

Abla, D., Katahira, K., & Okanoya, K. (2008). On-line assessment of statistical learning by event-related potentials. *Journal of Cognitive Neuroscience*, *20*(6), 952–64. http://doi.org/10.1162/jocn.2008.20058

Abla, D., & Okanoya, K. (2008). Statistical segmentation of tone sequences activates the left inferior frontal cortex: A near-infrared spectroscopy study. *Neuropsychologia*, *46*(11), 2787–2795. http://doi.org/10.1016/j.neuropsychologia.2008.05.012

Abla, D., & Okanoya, K. (2009). Visual statistical learning of shape sequences: An ERP study. *Neuroscience Research*, *64*(2), 185–90. http://doi.org/10.1016/j.neures.2009.02.013

Adini, Y., Sagi, D., & Tsodyks, M. (2002). Context-enabled learning in the human visual system. *Nature*, *415*(6873), 790–793. http://doi.org/10.1038/415790a

Ahissar, M., & Hochstein, S. (2004). The reverse hierarchy theory of visual perceptual learning. *Trends in Cognitive Sciences*, *8*(10), 457–64. http://doi.org/10.1016/j.tics.2004.08.011

Andersen, G. J., Ni, R., Bower, J. D., & Watanabe, T. (2010). Perceptual learning, aging, and improved visual performance in early stages of visual processing. *Journal of Vision*, *10*(13:4), 1–13. http://doi.org/10.1167/10.13.4.Introduction

Aslin, R. N., Saffran, J. R., & Newport, E. L. (1998). Computation of conditional probability statistics by 8-month-old infants. *Psychological Science*, *9*(4), 321–324.

Bao, M., Yang, L., Rios, C., He, B., & Engel, S. A. (2010). Perceptual learning increases the strength of the earliest signals in visual cortex. *Journal of Neuroscience*, *30*(45), 15080–15084.

Barakat, B. K., Seitz, A. R., & Shams, L. (2013). The effect of statistical learning on internal stimulus representations: Predictable items are enhanced even when not predicted. *Cognition*, *129*(2), 205–211. http://doi.org/10.1016/j.cognition.2013.07.003

Baroncelli, L., Sale, A., Viegi, A., Maya Vetencourt, J. F., De Pasquale, R., Baldini, S., & Maffei, L. (2010). Experience-dependent reactivation of ocular dominance plasticity in the adult visual cortex. *Experimental Neurology*, *226*(1), 100–109. http://doi.org/10.1016/j.expneurol.2010.08.009

Bays, B. C., Visscher, K. M., Le Dantec, C. C., & Seitz, A. R. (2015). Alpha-band EEG activity in perceptual learning. *Journal of Vision*, *15*(10), 1–12. http://doi.org/10.1167/15.10.7.doi

Berardi, N., Pizzorusso, T., & Maffei, L. (2000). Critical periods during sensory development. *Current Opinion in Neurobiology*, *10*(1), 138–145. http://doi.org/10.1016/S0959-4388(99)00047-1

Bollimunta, A., Chen, Y., Schroeder, C. E., & Ding, M. (2008). Neuronal mechanisms of cortical alpha oscillations in awake-behaving macaques. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *28*(40), 9976–9988. http://doi.org/10.1523/JNEUROSCI.2699-08.2008

Buonomano, D. V, & Merzenich, M. M. (1998). Cortical plasticity: from synapses to maps. *Annual Review of Neuroscience*, *21*(149), 149–186. http://doi.org/10.1146/annurev.neuro.21.1.149

Byers, A., & Serences, J. T. (2012). Exploring the relationship between perceptual learning and top-down attentional control. *Vision Research*, *74*, 30–39. http://doi.org/10.1016/j.visres.2012.07.008

Calford, M. B., Chino, Y. M., Das, A., Eysel, U. T., Gilbert, C. D., Heinen, S. J., … Ullman, S. (2005). Rewiring the adult brain. *Nature*, *438*(November), 3–4. http://doi.org/10.1038/04359

Calford, M. B., & Tweedale, R. (1988). Immediate and chronic changes in responses of somatosensory cortex in adult flying-fox after digit amputation. *Nature*. http://doi.org/10.1038/332446a0

Calvert, G. A., Brammer, M. J., Bullmore, E. T., Campbell, R., Iversen, S. D., & David, A. S. (1999). Response amplification in sensory-specific cortices during crossmodal binding. *Neuroreport*, *10*(12), 2619–2623. http://doi.org/10.1097/00001756-199908200-00033

Calvert, G. A., Bullmore, E. T., Brammer, M. J., Campbell, R., Williams, S. C. R., McGuire, P. K., … David, A. S. (1997). Activation of auditory cortex during silent lipreading. *Science*, *276*(5312), 593–596. http://doi.org/10.1126/science.276.5312.593

Chalk, M., Seitz, A. R., & Seriès, P. (2010). Rapidly learned stimulus expectations alter perception of motion. *Journal of Vision*, *10*(8), 1–18. http://doi.org/10.1167/10.8.2

Cohen, L. G., Celnik, P., Pascual-Leone, A., Corwell, B., Falz, L., Dambrosia, J., … Hallett, M. (1997). Functional relevance of cross-modal plasticity in blind humans. *Nature*, *389*(6647), 180–183. http://doi.org/10.1038/38278

Conway, C. M., & Christiansen, M. H. (2005). Modality-constrained statistical learning of tactile, visual, and auditory sequences. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *31*(1), 24–39.

Conway, C. M., & Christiansen, M. H. (2006). Statistical learning within and between modalities. *Psychological Science*, *17*(10), 905–912.

De Valois, K. (1977). Spatial frequency adaptation can enhance contrast sensitivity. *Vision Research*, *17*(9), 1057–1065.

Deveau, J., Lovcik, G., & Seitz, A. R. (2014). Broad-based visual benefits from training with an integrated perceptual-learning video game. *Vision Research*, *99*, 134–140. http://doi.org/10.1016/j.visres.2013.12.015

Deveau, J., Ozer, D. J., & Seitz, A. R. (2014). Improved vision and on-field performance in baseball through perceptual learning. *Current Biology*, *24*(4), R146–R147. http://doi.org/10.1016/j.cub.2014.01.004

Dobres, J., & Seitz, A. R. (2010). Perceptual learning of oriented gratings as revealed by classification images. *Journal of Vision*, *10*(13), 8–11. http://doi.org/10.1167/10.13.8.Introduction

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 of the United States of America*, *95*(23), 13988–13993.

Durrant, S. J., Cairney, S. A., & Lewis, P. A. (2013). Overnight consolidation aids the transfer of statistical knowledge from the medial temporal lobe to the striatum. *Cerebral Cortex*, *23*(10), 2467–2478. http://doi.org/10.1093/cercor/bhs244

Durrant, S. J., Taylor, C., Cairney, S. A., & Lewis, P. A. (2011). Sleep-dependent consolidation of statistical learning. *Neuropsychologia*, *49*(5), 1322–1331. http://doi.org/10.1016/j.neuropsychologia.2011.02.015

Elbert, T., Flor, H., Birbaumer, N., Knecht, S., Hampson, S., Larbig, W., & Taub, E. (1994). Extensive reorganization of the somatosensory cortex in adult humans after nervous system injury. *Neuroreport*, *5*, 2593–2597.

Ergenoglu, T., Demiralp, T., Bayraktaroglu, Z., Ergen, M., Beydagi, H., & Uresin, Y. (2004). Alpha rhythm of the EEG modulates visual detection performance in humans. *Cognitive Brain Research*, *20*(3), 376–383. http://doi.org/10.1016/j.cogbrainres.2004.03.009

Fahle, M. (2004). Perceptual learning: a case for early selection. *Journal of Vision*, *4*(10), 879–890. http://doi.org/10.1167/4.10.4

Fahle, M. (2005). Perceptual learning: specificity versus generalization. *Current Opinion in Neurobiology*, *15*(2), 154–160. http://doi.org/10.1016/j.conb.2005.03.010

Fahle, M., Edelman, S., & Poggio, T. (1995). Fast perceptual learning in hyperacuity. *Vision Research*, *35*(21), 3003–3013.

Fine, I., Wade, A. R., Brewer, A. a, May, M. G., Goodman, D. F., Boynton, G. M., … MacLeod, D. I. a. (2003). Long-term deprivation affects visual perception and cortex. *Nature Neuroscience*, *6*(9), 915–916. http://doi.org/10.1038/nn1102

Fiorentini, A., & Berardi, N. (1980). Perceptual learning specific for orientation and spatial frequency. *Nature*, *287*(5777), 43–44.

Fiser, J., & Aslin, R. N. (2001). Unsupervised statistical learning of higher-order spatial structures from visual scenes. *Psychological Science*, *12*(6), 499–504.

Fiser, J., & Aslin, R. N. (2002). Statistical learning of higher-order temporal structure from visual shape sequences. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *28*(3), 458–467.

Fiser, J., & Aslin, R. N. (2005). Encoding multielement scenes: Statistical learning of visual feature hierarchies. *Journal of Experimental Psychology: General*, *134*(4), 521–537.

Freyer, F., Becker, R., Dinse, H. R., & Ritter, P. (2013). State-dependent perceptual learning. *The Journal of Neuroscience*, *33*(7), 2900–2907. http://doi.org/10.1523/JNEUROSCI.4039-12.2013

Ghose, G. M. (2004). Learning in mammalian sensory cortex. *Current Opinion in Neurobiology*, *14*(4), 513–8. http://doi.org/10.1016/j.conb.2004.07.003

Gilbert, C. D., Li, W., & Piech, V. (2009). Perceptual learning and adult cortical plasticity. *Journal of Physiology*, *587*(12), 2743–2751.

Gilbert, C. D., Sigman, M., & Crist, R. E. (2001). The Neural Basis of Perceptual Learning. *Neuron*, *31*, 681–697.

Green, C. S., & Bavelier, D. (2007). Action-Video-Game Experience Alters the Spatial Resolution of Vision. *Psychological Science*, *18*(1), 88–94.

Green, C. S., Li, R., & Bavelier, D. (2010). Perceptual Learning During Action Video Game Playing. *Topics in Cognitive Science*, *2*(2), 202–216. http://doi.org/10.1111/j.1756-8765.2009.01054.x

Hanslmayr, S., Aslan, A., Staudigl, T., Klimesch, W., Herrmann, C. S., & Bäuml, K.-H. (2007). Prestimulus oscillations predict visual perception performance between and within subjects. *NeuroImage*, *37*(4), 1465–1473. http://doi.org/10.1016/j.neuroimage.2007.07.011

Hanslmayr, S., Gross, J., Klimesch, W., & Shapiro, K. L. (2011). The role of alpha oscillations in temporal attention. *Brain Research Reviews*, *67*(1-2), 331–343. http://doi.org/10.1016/j.brainresrev.2011.04.002

Hebb, D. O. (1949). *The Organization of Behavior*. New York: Wiley.

Heinen, S. J., & Skavenski, a a. (1991). Recovery of visual responses in foveal V1 neurons following bilateral foveal lesions in adult monkey. *Experimental Brain Research. Experimentelle Hirnforschung. Experimentation Cerebrale*, *83*, 670–674. http://doi.org/10.1007/BF00229845

Hua, T., Bao, P., Huang, C.-B., Wang, Z., Xu, J., Zhou, Y., & Lu, Z.-L. (2010). Perceptual Learning Improves Contrast Sensitivity of V1 Neurons in Cats. *Current Biology*, *20*, 887–894.

Hubel, D. H., & Wiesel, T. N. (1962). Receptive Fields, Binocular Interaction and Function Architecture in the Cat's Visual Cortex. *Journal of Physiology*, *160*, 106–154. http://doi.org/10.1523/JNEUROSCI.1991-09.2009

Hubel, D. H., & Wiesel, T. N. (1970). The period of susceptibility to the physiological effects of unilateral eye closure in kittens. *The Journal of Physiology*, *206*(2), 419–436. http://doi.org/10.1113/jphysiol.1970.sp009022

Hughes, S. W., & Crunelli, V. (2005). Thalamic mechanisms of EEG alpha rhythms and their pathological implications. *The Neuroscientist*, *11*(4), 357–372. http://doi.org/10.1177/1073858405277450

Hung, S.-C., & Seitz, A. R. (2014). Prolonged training at threshold promotes robust retinotopic specificity in perceptual learning. *The Journal of Neuroscience*, *34*(25), 8423–8431. http://doi.org/10.1523/JNEUROSCI.0745-14.2014

Hunt, R., & Aslin, R. (2001). Statistical learning in a serial reaction time task: Access to separable statistical cues by individual learners. *Journal of Experimental Psychology: General*, *130*(4), 658–680.

Hussain, Z., Sekuler, A. B., & Bennett, P. J. (2011). Superior identification of familiar visual patterns a year after learning. *Psychological Science*, *22*(6), 724–730. http://doi.org/10.1177/0956797611409591

Jeter, P. E., Dosher, B. A., Liu, S.-H., & Lu, Z.-L. (2010). Specificity of perceptual learning increases with increased training. *Vision Research*, *50*(19), 1928–1940. http://doi.org/10.1016/j.visres.2010.06.016

Johnson, M. H. (2001). Functional Brain Development in Humans. *Nature Reviews Neuroscience*, *2*(7), 475–483. http://doi.org/10.1038/35081509

Kaas, J. H. (1991). Plasticity of sensory and motor maps in adult mammals. *Annual Review of Neuroscience*, *14*, 137–167.

Karuza, E. A., Emberson, L. L., & Aslin, R. N. (2014). Combining fMRI and behavioral measures to examine the process of human learning. *Neurobiology of Learning and Memory*, *109*, 193–206. http://doi.org/10.1016/j.nlm.2013.09.012

Karuza, E. A., Newport, E. L., Aslin, R. N., Starling, S. J., Tivarus, M. E., & Bavelier, D. (2013). The neural correlates of statistical learning in a word segmentation task: An fMRI study. *Brain and Language*, *127*(1), 46–54. http://doi.org/10.1016/j.bandl.2012.11.007

Kim, R., Seitz, A., Feenstra, H., & Shams, L. (2009). Testing assumptions of statistical learning: Is it long-term and implicit? *Neuroscience Letters*, *461*(2), 145–149. http://doi.org/10.1016/j.neulet.2009.06.030

Kim, R., Seitz, A., & Shams, L. (2008). Benefits of Stimulus Congruency for Multisensory Facilitation of Visual Learning. *PloS One*, *3*(1), e1532.

Klimesch, W. (1999). EEG alpha and theta oscillations reflect cognitive and memory performance: a review and analysis. *Brain Research. Brain Research Reviews*, *29*(2-3), 169–195.

Klimesch, W., Sauseng, P., & Hanslmayr, S. (2007). EEG alpha oscillations: the inhibition-timing hypothesis. *Brain Research Reviews*, *53*(1), 63–88. http://doi.org/10.1016/j.brainresrev.2006.06.003

Koelewijn, T., Bronkhorst, A., & Theeuwes, J. (2010). Attention and the multiple stages of multisensory integration: A review of audiovisual studies. *Acta Psychologica*, *134*(3), 372–384. http://doi.org/10.1016/j.actpsy.2010.03.010

Le Dantec, C. C., Melton, E. E., & Seitz, A. R. (2012). A triple dissociation between learning of target , distractors , and spatial contexts. *Journal of Vision*, *12*(2), 1–12. http://doi.org/10.1167/12.2.5.Introduction

Levi, D. M. (2005). Perceptual learning in adults with amblyopia: A reevaluation of critical periods in human vision. *Developmental Psychobiology*, *46*(3), 222–232. http://doi.org/10.1002/dev.20050

Macaluso, E., Frith, C. D., & Driver, J. (2000). Modulation of human visual cortex by crossmodal spatial attention. *Science*, *289*(5482), 1206–1208. http://doi.org/8750

Merzenich, M. M., Nelson, R. J., Stryker, M. P., Cynader, M. S., Schoppmann, A., & Zook, J. M. (1984). Somatosensory Cortical Map Changes Following Digit Amputation in Adult Monkeys. *The Journal of Comparative Neurology*, *224*, 591–605.

Nenert, R., Viswanathan, S., Dubuc, D. M., & Visscher, K. M. (2012). Modulations of ongoing alpha oscillations predict successful short-term visual memory encoding. *Frontiers in Human Neuroscience*, *6*(May), 1–11. http://doi.org/10.3389/fnhum.2012.00127

Obata, S., Obata, J., Das, A., & Gilbert, C. D. (1999). Molecular correlates of topographic reorganization in primary visual cortex following retinal lesions. *Cerebral Cortex*, *9*(3), 238–248. http://doi.org/10.1093/cercor/9.3.238

Payne, L., & Sekuler, R. (2014). The Importance of Ignoring: Alpha Oscillations Protect Selectivity. *Current Directions in Psychological Science*, *23*(3), 171–177. http://doi.org/10.1177/0963721414529145

Petrov, A. A., Dosher, B. A., & Lu, Z.-L. (2005). The dynamics of perceptual learning: an incremental reweighting model. *Psychological Review*, *112*(4), 715–743. http://doi.org/10.1037/0033-295X.112.4.715

Pilly, P. K., Grossberg, S., & Seitz, A. R. (2010). Low-level sensory plasticity during task-irrelevant perceptual learning: evidence from conventional and double training procedures. *Vision Research*, *50*(4), 424–432. http://doi.org/10.1016/j.visres.2009.09.022

Poggio, T., Fahle, M., & Edelman, S. (1992). Fast perceptual learning in visual hyperacuity. *Science*, *256*(5059), 1018–1021.

Powers, A. R., Hevey, M. A., & Wallace, M. T. (2012). Neural Correlates of Multisensory Perceptual Learning. *Journal of Neuroscience*, *32*(18), 6263–6274. http://doi.org/10.1523/JNEUROSCI.6138-11.2012

Ramachandran, V. S., & Braddick, O. (1973). Orientation-specific learning in stereopsis. *Perception*, *2*(3), 371–376.

Ramón y Cajal, S. (1894). The Croonian Lecture: La Fine Structure des Centres Nerveux. *Proceedings of the Royal Society of London*, *55*, 444–468. http://doi.org/10.2307/115494

Ramón y Cajal, S. (1959). *Degeneration & regeneration of the nervous system*. *Oxford University* (Vol. 1). New York: Hafner Publishing Co.

Raposo, D., Sheppard, J. P., Schrater, P. R., & Churchland, A. K. (2012). Multisensory decision-making in rats and humans. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *32*(11), 3726–35. http://doi.org/10.1523/JNEUROSCI.4998-11.2012

Sadato, N., Pascual-Leone, A., Grafman, J., Ibañez, V., Deiber, M.-P., Dold, G., & Hallett, M. (1996). Activation of the primary visual cortex by Braille reading in blind subjects. *Nature*, *380*, 526–528. http://doi.org/10.1093/acprof:oso/9780198528999.003.0022

Saffran, J. R., Aslin, R. N., & Newport, E. L. (1996). Statistical learning by 8-month-old infants. *Science*, *274*(5294), 1926–1928.

Saffran, J. R., Johnson, E., Aslin, R. N., & Newport, E. L. (1999). Statistical learning of tone sequences by human infants and adults. *Cognition*, *70*(1), 27–52.

Saffran, J. R., Newport, E. L., Aslin, R. N., Tunick, R. A., & Barrueco, S. (1997). Incidental language learning: Listening (and learning) out of the corner of your ear. *Psychological Science*, *8*(2), 101–105.

Saffran, J. R., & Thiessen, E. (2003). Pattern induction by infant language learners. *Developmental Psychology*, *39*(3), 484–494.

Sagi, D. (2011). Perceptual learning in Vision Research. *Vision Research*, *51*(13), 1552–1566. http://doi.org/10.1016/j.visres.2010.10.019

Sale, A., de Pasquale, R., Bonaccorsi, J., Pietra, G., Olivieri, D., Berardi, N., & Maffei, L. (2010). Visual Perceptual Learning Induces Long-Term Potentiation in the Visual Cortex. *Neuroscience*. http://doi.org/10.1016/j.neuroscience.2010.10.078

Samar, V. J., Bopardikar, a, Rao, R., & Swartz, K. (1999). Wavelet analysis of neuroelectric waveforms: a conceptual tutorial. *Brain and Language*, *66*(1), 7–60. http://doi.org/10.1006/brln.1998.2024

Sanders, L. D., Newport, E. L., & Neville, H. J. (2002). Segmenting nonsense: an event-related potential index of perceived onsets in continuous speech. *Nature Neuroscience*, *5*(7), 700–703. http://doi.org/10.1038/nn873

Sasaki, Y., Náñez, J., & Watanabe, T. (2012). Recent progress in perceptual learning research. *Wiley Interdisciplinary Reviews: Cognitive Science*, *3*(3), 293–299. http://doi.org/10.1002/wcs.1175.Recent

Schapiro, A. C., Gregory, E., Landau, B., McCloskey, M., & Turk-Browne, N. B. (2014). The necessity of the medial temporal lobe for statistical learning. *Journal of Cognitive Neuroscience*, *26*(8), 1736–1747. http://doi.org/doi:10.1162/jocn_a_00578

Schapiro, A. C., Kustner, L. V, & Turk-Browne, N. B. (2012). Shaping of object representations in the human medial temporal lobe based on temporal regularities. *Current Biology*, *22*(17), 1622–1627. http://doi.org/10.1016/j.cub.2012.06.056

Schoups, A., Vogels, R., Qian, N., & Orban, G. (2001). Practising orientation identification improves orientation coding in V1 neurons. *Nature*, *412*(August), 549–553.

Seitz, A. R., & Dinse, H. R. (2007). A common framework for perceptual learning. *Current Opinion in Neurobiology*, *17*, 148–153.

Seitz, A. R., Kim, R., & Shams, L. (2006). Sound facilitates visual learning. *Current Biology*, *16*, 1422–1427.

Seitz, A. R., Nanez, J. E., Holloway, S. R., & Watanabe, T. (2006). Perceptual Learning of Motion Leads to Faster Flicker Perception. *PloS One*, *1*(1), e28.

Seitz, A. R., & Watanabe, T. (2005). A unified model for perceptual learning. *Trends in Cognitive Sciences*, *9*(7), 329–334.

Seitz, A. R., & Watanabe, T. (2008). Is task-irrelevant learning really task-irrelevant? *PloS One*, *3*(11), e3792. http://doi.org/10.1371/journal.pone.0003792

Shams, L., Kamitani, Y., Thompson, S., & Shimojo, S. (2001). Sound alters visual evoked potentials in humans. *Neuroreport*, *12*(17), 3849–3852. http://doi.org/10.1097/00001756-200112040-00049

Shams, L., & Seitz, A. R. (2008). Benefits of Multisensory Learning. *Trends in Cognitive Sciences*, *12*(11), 411–417.

Sheppard, J., Raposo, D., & Churchland, A. (2013). Dynamic weighting of multisensory stimuli shapes decision-making in rats and humans. *Journal of Vision*, *13(6)*(4), 1–19. http://doi.org/10.1167/13.6.4.doi

Shimojo, S., & Shams, L. (2001). Sensory modalities are not seperate modalities: plasticity and interactions. *Current Opinion in Neurobiology*, *11*, 505–509.

Sigala, R., Haufe, S., Roy, D., Dinse, H. R., & Ritter, P. (2014). The role of alpha-rhythm states in perceptual learning: insights from experiments and computational models. *Frontiers in Computational Neuroscience*, *8*(36), 1–19. http://doi.org/10.3389/fncom.2014.00036

Snyder, A. C., & Foxe, J. J. (2010). Anticipatory attentional suppression of visual features indexed by oscillatory alpha-band power increases: a high-density electrical mapping study. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *30*(11), 4024–4032. http://doi.org/10.1523/JNEUROSCI.5684-09.2010

Stein, B. E., & Stanford, T. R. (2008). Multisensory integration: current issues from the perspective of the single neuron. *Nature Reviews. Neuroscience*, *9*(4), 255–266. http://doi.org/10.1038/nrn2377

Toro, J. M., Sinnett, S., & Soto-Faraco, S. (2005). Speech segmentation by statistical learning depends on attention. *Cognition*, *97*(2), B25–B34.

Turk-Browne, N. B. (2012). Statistical learning and its consequences. In M. D. Dodd & J. H. Flowers (Eds.), *The Influence of Attention, Learning, and Motivation on Visual Search* (pp. 117–146). New York, NY: Springer New York. http://doi.org/10.1007/978-1-4614-4794-8

Turk-Browne, N. B., Isola, P. J., Scholl, B., & Treat, T. A. (2008). Multidimensional visual statistical learning. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *34*(2), 399–407.

Turk-Browne, N. B., Jungé, J. A., & Scholl, B. J. (2005). The automaticity of visual statistical learning. *Journal of Experimental Psychology: General*, *134*(4), 552–564.

Turk-Browne, N. B., & Scholl, B. (2009). Flexible visual statistical learning: transfer across space and time. *Journal of Experimental Psychology: Human Perception and Performance*, *35*(1), 195–202.

Turk-Browne, N. B., Scholl, B. J., Chun, M. M., & Johnson, M. K. (2009). Neural evidence of statistical learning: Efficient detection of visual regularities without awareness. *Journal of Cognitive Neuroscience*, *21*(10), 1934–1945.

Turk-Browne, N. B., Scholl, B., Johnson, M. K., & Chun, M. M. (2010). Implicit perceptual anticipation triggered by statistical learning. *Journal of Neuroscience*, *30*(33), 11177–11187.

Vaden, R. J., Hutcheson, N. L., McCollum, L. a, Kentros, J., & Visscher, K. M. (2012). Older adults, unlike younger adults, do not modulate alpha power to suppress irrelevant information. *NeuroImage*, *63*(3), 1127–1133. http://doi.org/10.1016/j.neuroimage.2012.07.050

Watanabe, T., & Sasaki, Y. (2015). Perceptual learning: Toward a comprehensive theory. *Annual Review of Psychology*, *66*, 197–221. http://doi.org/10.1146/annurev-psych-010814-015214

Xiao, L.-Q., Zhang, J.-Y., Wang, R., Klein, S. a, Levi, D. M., & Yu, C. (2008). Complete transfer of perceptual learning across retinal locations enabled by double training. *Current Biology : CB*, *18*(24), 1922–1926. http://doi.org/10.1016/j.cub.2008.10.030

Yang, C. D. (2004). Universal Grammar, statistics or both? *Trends in Cognitive Sciences*, *8*(10), 451–456.

Yang, T., & Maunsell, J. H. R. (2004). The effect of perceptual learning on neuronal responses in monkey visual area V4. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *24*(7), 1617–1626. http://doi.org/10.1523/JNEUROSCI.4442-03.2004

Yang, T. T., Gallen, C. C., Ramachandran, V. S., Cobb, S., Schwartz, B. J., & Bloom, F. E. (1994). Noninvasive detection of cerebral plasticity in adult human somatosensory cortex. *Neuroreport*, *5*, 701–704.

Yotsumoto, Y., Chang, L. H., Ni, R., Pierce, R., Andersen, G. J., Watanabe, T., & Sasaki, Y. (2014). White matter in the older brain is more plastic than in the younger brain. *Nature Communications*, *5*(5504), 1–8. http://doi.org/10.1038/ncomms6504

Yu, C., Klein, S. A., & Levi, D. M. (2004). Perceptual learning in contrast discrimination and the (minimal) role of context. *Journal of Vision*, *4*, 169–182. http://doi.org/10.1167/4.3.4

Zhang, J.-Y., Zhang, G.-L., Xiao, L.-Q., Klein, S. a, Levi, D. M., & Yu, C. (2010). Rule-based learning explains visual perceptual learning and its specificity and transfer. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *30*(37), 12323–12328. http://doi.org/10.1523/JNEUROSCI.0704-10.2010

Zhao, J., Al-Aidroos, N., & Turk-Browne, N. B. (2013). Attention is spontaneously biased toward regularities. *Psychological Science*, *24*(5), 667–677. http://doi.org/10.1177/0956797612460407

Zhao, J., Ngo, N., McKendrick, R., & Turk-Browne, N. B. (2011). Mutual interference between statistical summary perception and statistical learning. *Psychological Science*, *22*(9), 1212–1219. http://doi.org/10.1177/0956797611419304

Zohary, E., Celebrini, S., Britten, K. H., & Newsome, W. T. (1994). Neuronal plasticity that underlies improvement in perceptual performance. *Science (New York, N.Y.)*, *263*(5151), 1289–1292.

Chapter 1

This chapter has previously been published as

Dissociable behavioral outcomes of visual statistical learning

Brett C. Bays[1], Nicholas B. Turk-Browne[2], Aaron R. Seitz[1]

[1]University of California, Riverside

[2]Princeton University

Visual Cognition (2016) February

DOI: 10.1080/13506285.2016.1139647

Abstract

Statistical learning refers to the extraction of probabilistic relationships between stimuli and is increasingly used as a method to understand learning processes. However, numerous cognitive processes are sensitive to statistical relationships between stimuli and any one measure of learning may conflate these processes; to date little research has focused on differentiating these processes. To understand how multiple processes underlie statistical learning, here we compared, within the same study, operational measures of learning from different tasks that may be differentially sensitive to these processes. In Experiment 1, participants were visually exposed to temporal regularities embedded in a stream of shapes. Their task was to periodically detect whether a shape, whose contrast was staircased to a threshold level, was present or absent. Afterwards, they completed a search task, where statistically predictable shapes were found more quickly. We used the search task to label shape pairs as "learned" or "non-learned", and then used these labels to analyze the detection task. We found a dissociation between learning on the search task and the detection task where only non-learned pairs showed learning effects in the detection task. This finding was replicated in further experiments with recognition memory (Experiment 2) and associative learning tasks (Experiment 3). Taken together, these findings are consistent with the view that statistical learning may comprise a family of processes that can produce dissociable effects on different aspects of behavior.

Introduction

An important cognitive function is to learn associative relationships between stimuli in our environment. However, our perceptual systems are oversaturated in terms of the number of stimuli we can attend to and remember. Thus, learning to associate stimuli into coherent perceptual objects may seem like a hopeless endeavor. One way that people learn associative relationships between environmental patterns is through statistical learning, a ubiquitous process that involves learning patterns among stimuli organized according to probabilistic relationships. It can occur extremely quickly in experimental settings, after only a few minutes (Aslin, Saffran, & Newport, 1998; Kim, Seitz, Feenstra, & Shams, 2009; Saffran, Aslin, & Newport, 1996), and without explicit awareness (Fiser & Aslin, 2002; Kim et al., 2009). Statistical learning has been found to underlie basic aspects of language development (Saffran et al., 1996; Saffran & Thiessen, 2003; C. D. Yang, 2004), as well as other aspects of cognitive development and psychology. For instance, it occurs in both children and adults (Saffran, Johnson, Aslin, & Newport, 1999), operates in multiple modalities (Conway & Christiansen, 2005), helps bind both features and objects (Turk-Browne, Isola, Scholl, & Treat, 2008), transfers across spatial and temporal dimensions (Turk-Browne & Scholl, 2009), defines the scale of visual objects (Fiser & Aslin, 2001, 2005), and can even alter our perception of stimuli (Chalk, Seitz, & Seriès, 2010).

Among the wide array of statistical learning studies, there is an equally wide array of exposure (acquisition of learning) and testing (assessment of learning) procedures. Exposure can occur passively with auditory stimuli (Saffran et al., 1996), passively with visual stimuli (Fiser & Aslin, 2001), actively with a cover task related to the stimuli (Toro, Sinnett, & Soto-Faraco, 2005), and actively with a cover task unrelated to the stimuli (Saffran, Newport, Aslin, Tunick, & Barrueco, 1997). Testing procedures used to assay learning include familiarity tests (e.g., Fiser & Aslin, 2001, 2002; Saffran et al., 1999; Turk-Browne et al., 2008), reaction time tests (Hunt & Aslin, 2001; Kim et al., 2009; Turk-Browne, Jungé, & Scholl, 2005), and functional magnetic resonance imaging (e.g., Karuza et al., 2013; Schapiro, Gregory, Landau, McCloskey, & Turk-Browne, 2014; Schapiro, Kustner, & Turk-Browne, 2012; Turk-Browne, Scholl, Chun, & Johnson, 2009).

Researchers often alternate between measures of statistical learning without differentiating between the general interpretations of the outcomes (Turk-Browne et al., 2008, 2005). For example, results obtained using a reaction time task have been discussed in the same terms as those obtained using a two-interval forced choice task with relation to what they reveal about statistical learning (Turk-Browne et al., 2008, 2005). Additionally, results from paradigms as varied as the learning of visuo-spatial patterns, visuo-temporal patterns, and audio-temporal patterns, are all labeled with the general name of "statistical learning" with little discussion of distinctions in the learning rate, mechanisms, and constraints (Fiser & Aslin, 2005; Saffran et al., 1999; Zhao, Al-Aidroos, & Turk-Browne, 2013). These results are sometimes explicitly theorized to represent the same underlying learning mechanism (Kirkham, Slemmer, & Johnson, 2002; Perruchet & Pacton, 2006) or occasionally theorized to stem from different cognitive mechanisms (Conway & Christiansen, 2005), but more often the literature has not discussed in detail what exactly statistical learning is.

Further, despite the myriad procedures that have been used to investigate statistical learning, researchers rarely address the possibility that different systems may be engaged and responsible for the learning observed across studies. Here we address the possibility that statistical learning comprises multiple cognitive processes. A "process" refers to a series of steps to achieve a particular end (process, 2015), and by "multiple processes" we mean that different systems act at once upon the stimuli — independently, cooperatively, or competitively — and that each can achieve its own end and learn independently.

Growing evidence suggests that numerous cognitive processes are sensitive to statistical relationships and that learning in even simple tasks can involve simultaneous dissociable processes (Frost, Siegelman, Narkiss, & Afek, 2013; Le Dantec, Melton, & Seitz, 2012; Zhao et al., 2013; Zhao, Ngo, McKendrick, & Turk-Browne, 2011). The consolidation of statistical learning has both sleep-dependent and time-dependent components (Durrant, Taylor, Cairney, & Lewis, 2011) and may lead to perceptual learning in addition to associative learning (Barakat, Seitz, & Shams, 2013). In artificial grammar learning (AGL) paradigms, which are closely related to statistical learning paradigms, fMRI studies have revealed different neural networks subserving the recognition of items and the learning of the grammar (Fletcher, Büchel, Josephs, Friston, & Dolan, 1999; Lieberman, Chang, Chiao, Bookheimer, & Knowlton, 2004; Seger, Prabhakaran, Poldrack, & Gabrieli, 2000) and dissociable overlapping networks of implicit and explicit learning during AGL have been demonstrated (J. Yang & Li, 2012). Similarly, in statistical learning paradigms, different time-courses of medial temporal lobe and striatal activation have been observed, which might correspond to competing memory systems at work (Durrant, Cairney, & Lewis, 2013; Turk-Browne et al., 2009; Turk-Browne, Scholl, Johnson, & Chun, 2010).

In the present study, we investigate how the utilization of multiple tasks that assay statistical learning may reveal different underlying cognitive processes. This involves using a novel 'item analysis' approach in which we quantify statistical learning with two different tests per experiment and then relate the amount of learning in each test on an item-by-item basis. This approach enables a more detailed characterization of statistical learning than is typically possible in studies using a single outcome measurement. Moreover, by using multiple tests of statistical learning, we can also examine whether learning manifests itself in a stable way across different behaviors for a given item. Although measuring different behavioral tasks does not provide conclusive evidence for or against multiple processes per se, this approach might nevertheless produce evidence useful for evaluating our hypothesis.

A single-process model of statistical learning predicts that multiple tests should reveal the same qualitative pattern of results. If one measure is more sensitive to learning than another, a single-process model would predict significant results from the more sensitive measure(s) and diminished or null results from the less sensitive measure(s). However, across three experiments, we found reversals between different behavioral outcomes of statistical learning; that is, qualitative patterns of learning opposite to each other. These findings undermine an implicit assumption in the field that a common process underlies all manifestations of statistical learning.

Experiment 1

Our first experiment was an investigation of whether different tasks can reveal different statistical learning outcomes from the same exposure. We conducted an item-level analysis where, for each statistical regularity (e.g., a single pair of items for a participant), we compared learning for that regularity across two outcome measures. Specifically, we used a search post-test to categorize regularities as “learned” or “non-learned”, and then examined performance for these categorized regularities during a detection task conducted concurrent with exposure.

In the detection task, a continuous stream of shapes was presented and participants responded to a periodic tone as to whether a shape was present or absent. This task occurred while participants learned the statistical regularities and then continued for a period of time after learning could reasonably be assumed to have occurred. In the search task, which occurred after the detection task, participants were presented with a target shape at the beginning of each trial and responded as soon as that shape appeared in a rapid-serial visual presentation (RSVP) of distractors and a target.

These tasks are described more fully below, but insofar as different measures of statistical learning reveal the same underlying process, then learned regularities from the search task should exhibit the same signatures of learning in the detection task. Alternatively, there may be no relationship or a negative relationship between learning effects during the detection task and the search task, which would be consistent with the existence of multiple processes in statistical learning that manifest different behavioral outcomes.

Methods

Participants

Thirty-seven undergraduates at the University of California, Riverside, aged 18-24 (24 females), were included in this study. The number of participants was determined based on how many students could be recruited for this study within one 10-week quarter in the UC Riverside undergraduate subject pool. This method introduces no statistical bias, as at no point were data analyzed in order to determine when to cease data collection. Inclusion required completion of all experimental procedures without technical errors and with responses to at least 70% of targets in both tasks (a criterion derived from pilot data). Inability to complete both tasks satisfactorily resulted in the exclusion of seven participants beyond the thirty-seven included in the study. The data of these participants were not analyzed beyond the point of determining their response rates and, importantly, these subject exclusion criteria are not related to the differential performance between items that form the critical analyses in this study. Participants received credit toward partial fulfillment of course requirements for an introductory psychology course, gave written informed consent as approved by the Human Research Review Board, and had normal or corrected-to-normal vision. These criteria also apply to the subsequent experiments reported below.

Stimuli

The stimuli consisted of 15 shapes that were novel to the participants. These shapes were adapted from or made to resemble shapes used in previous statistical learning studies (Fiser & Aslin, 2001; Turk-Browne et al., 2005), subtending approximately 2.5º visually, and were randomly grouped into five triplets on a participant-by-participant basis (see Figure 1A).

Apparatus

All stimuli were displayed on a 40.96cm wide ViewSonic PF817 CRT monitor connected to an Apple Mac Pro computer running OSX 10.6.8. Mediating the connection from monitor to computer was a Bits++ digital video processor (Cambridge Research Systems) that enables a 14-bit DAC, allowing for a 64-fold increase in the display's possible contrast values. Sennheiser HD 650 headphones, plugged into an AudioFire 2 (Echo Digital Audio) audio interface, were used to present the auditory stimuli. Participants' heads were restrained with a chin rest and forehead bar 69.22cm from the screen. Stimuli were controlled by custom code written in Matlab, using the Psychophysics Toolbox (http://psychtoolbox.org).

Detection Task

During exposure, participants performed a detection task on a stream of shapes appearing one at a time. Unbeknownst to them, the 15 shapes were grouped into 5 triplets — e.g., if shapes A, B, and C were grouped together, they always occurred in the order of

A-B-C. Triplets for each participant were mixed pseudorandomly within the presentation blocks, preserving relations within triplets and equating overall exposure of triplets. In each of the 20 exposure blocks, the 5 triplets were presented 18 times. The shapes were presented one at a time in the center of the screen, on a gray background, with duration of 300ms and ISI of 100ms. Shapes were filled with spatial white noise with pixel values above or below the gray background and thus were always presented at the same mean luminance as the background (54 cd/m^2). The luminance range was scaled according to a staircase (see Figure 1B and Figure 2B). The duration of each block was 1.8 minutes, and with breaks between blocks, the exposure phase typically lasted 40-45 minutes.

Within every block, each shape was paired twice with a tone that signaled the participants to press “1” on the keyboard if a shape was visible on the screen or “2” if there was no visible shape (Figure 1C). All shapes were used once as a “present” target (i.e., visible and requiring a “1” response from the participant) and once as an “absent” target (i.e., invisible and requiring a “2” response). That is, when a shape was an "absent" target, we presented a gray patch the same color and contrast as the background (and thus invisible) during the shape's normal presentation period. When the tone sounded the participant had to report whether there was a shape present or whether there was no shape present. To temporally distribute responses, 1-3 filler triplets were placed between triplets containing a target.

To ensure that the detection task was engaging and challenging, the contrast of the shapes was adjusted using a block-wise staircase (Le Dantec et al., 2012). If mean accuracy in the prior block was greater than .80, contrast was adjusted according to the formula

$C' = \frac{C}{(P - .75) + 1}$, where C' is the new contrast level for the upcoming block, C is the current contrast level, and P is the mean performance for the completed block. If mean accuracy for the block was .70 or less, then contrast was adjusted according to the formula $C' = C * (1 - (P - .75))$ with the constraint that the minimum value of P was set to .50 (i.e., chance level). This staircase brought participants' performance to an average of 75% accuracy (see Figure 2A) and converged after approximately 10 blocks.

To measure statistical learning, we examined data after the staircase on contrast converged. Based upon pilot experiments, and verified in the present experiment, this occurred after block 10. Thus, all analyses use only data from the second half of the detection task, blocks 11-20, where the change in contrast between blocks is minimal (see Figure 2B). The use of these later blocks ensured that there was minimal variance in stimulus contrast and subject performance and that there was sufficient time for the statistical regularities to be learned. As such, our analysis of blocks 11-20 is akin to post-tests used in other studies of statistical learning. For staircasing purposes accuracy was calculated over both present and absent targets, but because we were interested only in how statistical learning occurs for visible shapes and the effect of the absence of a shape is unknown, analyses were performed only on present targets. Since present trials had higher accuracy than absent trials overall, accuracy in subsequent analyses was slightly greater than the 75% level.

In both the detection task and in the search task (below), RTs more than two standard deviations from the mean of each subject were excluded from analyses.

Search Task

Immediately following exposure, a "search task", adapted from previous studies (Kim et al., 2009; Turk-Browne et al., 2005), was performed. At the beginning of each trial of the search task, a target shape (one of the 15 seen in the exposure phase) was displayed at the top of the screen and the participant pressed any key to begin the trial. After the target shape disappeared, a pseudorandomly ordered stream of the 5 triplets was shown at the same sequential presentation rate as in exposure, with the constraint that the triplet containing the target could not be the first or last triplet shown in that trial. The participant's task was to press the space bar as soon as the target shape appeared. Each of the 15 shapes served as a target once per block, and all shapes were displayed at a suprathreshold contrast level. The search task consisted of six blocks with 15 trials each, which lasted 12 minutes total.

Analysis of shape groupings

The goal of the study was to determine statistical learning on an item level — that is, at the level of individual shape groupings — and determine whether different shape groupings were learned in different ways (see “Analysis of learned and non-learned pairs”, below). To determine the proper items to use in the ultimate analyses, we first examined whether participants learned the full configuration of the triplets or whether participants learned two pairs — the first/second shape pair (pair 1) and the second/third shape pair (pair 2; Fiser & Aslin, 2002, 2005; Hunt & Aslin, 2001). We based this analysis on the search task, which is a more standard measure of visual statistical learning (Baker, Olson,

& Behrmann, 2004; Hunt & Aslin, 2001; Olson & Chun, 2001; Turk-Browne et al., 2005) than the detection task that we introduce for the first time in this paper. In this analysis, a negative correlation of $r=-0.5$ is expected by chance, simply because the same second-position RT is the negative part of the subtraction for pair 1 and the positive part of the subtraction for pair 2. Response latency in the search task measures the degree to which a target can be predicted based on associations with the preceding item(s) and previous studies using this task found monotonic decreases in RT as item position increases (e.g., Campbell, Healey, Lee, Zimerman, & Hasher, 2012; Kim et al., 2009; Turk-Browne et al., 2005, 2010). Insofar as a triplet has been well learned, there are strong associations between all items and the associative strength from the first to second item and the second to third item should be correlated. Thus, if the full triplet structure were learned, the RT differences between items 1 and 2 would correlate with RT differences between items 2 and 3 significantly more positively than $r=-0.5$. However, we found an even more negative correlation between the effects for the two pairs ($r=-0.77$, $p<0.00001$), which was more negative than all but 8.37% of iterations in non-parametric randomization test (i.e., randomly assigning the observed distribution of RTs to different triplet positions 10,000 times and computing the correlation in each iteration). We also ran additional correlational analyses and simulations on the difference between the first two items of the triplet and the difference between the first and last items of the triplet. Here we found a correlation of $r=0.47$, which is almost identical to the correlation of $r=0.50$ that is expected by chance. These analyses suggest a failure to learn at the triplet level and the trend in the opposite direction suggests that learning of the two pairs — which shared an element — may be competitive (see also Fiser & Aslin, 2002) rather than cooperative.

Given that the evidence suggested that learning did not occur on the level of the triplets, subsequent analyses were restricted to pairs, and in particular, to pair 1 of each triplet. The restriction of analyses to the first pair also provides uniformity across the studies, as Experiment 3 only included pairs (which were all first pairs, by definition). In addition, because the first pair appeared before the second, this decision helps mitigate any complications that might arise due to the possible competition between the pairs. For example, if there are negative interactions between pair 1 and pair 2 then including pair 2 in the analysis would introduce a lack of independence, which could complicate the interpretation of learning comparisons between the detection and search tasks. Of note, the correlational analysis described here is intended to determine which items should be included in subsequent comparisons of learning between the two tasks and does not itself argue for or against the multiple-process hypothesis of statistical learning.

Analysis of learned and non-learned pairs

A key novelty of the present study is that we split each participant's pairs into those that were learned and those that were not learned. We did this based on the search task, which represents the more typical measure of statistical learning and where the standard analysis is to compute the mean RT for all first position shapes and compare that to the mean RT for all second position shapes. Instead of averaging over all shapes in each position, our analysis conserved information about the pairings that the shapes were assigned to for each participant. Each pair for a participant was classified as "learned" if the mean RT during the search task was lower for the second position shape of that pair than for the first position (Figure 3, solid blue lines, negative slope). If the mean RT was not lower for the second position shape of a pair, then it was classified as "non-learned" (Figure 3, dashed red lines, zero or positive slope). Although this classification method may not capture all of the nuances of the extent to which a pair was learned, it provides a simple dichotomous measure of learning from the search task which can then be related to the independent data from the detection task (see Figure S1 for confirmation that this analysis is reliable and consistent with the number of times that the second position RTs are faster than that of the first position RTs within each of the six blocks of the search task).

To analyze learning of each pair separately (averaging across repetitions of each item in the detection and search tasks), we employed a modified 2x2 (position: first/second X learning status: learned/non-learned) factorial ANOVA (see Supplemental Data “Statistical analyses” for details). After the interaction had been calculated, we used planned paired-samples t-tests to analyze the simple effects of position across learned and non-learned pairs. Because the search and detection tasks were independent of one another, using this method to analyze the pairs did not raise any issues of spurious dependencies between the results of the search task and the results of the detection task. Additionally, we modeled these results using 10,000 permutations of the data to discover how often we would expect results similar to those reported below, in which the detection task reveals opposite patterns of RT than the search task. The resulting likelihood was less than 0.1% ($p<.001$) of obtaining an effect similar to this by chance.

Results and discussion

As a basic measure of statistical learning, we examined first vs. second shape position performance in the search and detection tasks. In accordance with the literature, the search task showed significantly faster RTs (Figure 4; planned one-tailed paired t-test, *t*(36)=1.69, *p*=0.05, Cohen's *d*=0.28) for the second (520.0 ms) compared to the first position (535.0 ms) of pairs. However, in the detection task no effect of position (see Supplemental Data), was observed in terms of RTs (666.7 vs. 674.5 ms, respectively; *t*(36)=1.08, *p*=0.29, Cohen's *d*=0.18) or accuracy for second vs. first positions (85.6 vs. 84.8%, respectively; *t*(36)=0.69, *p*=0.50, Cohen's *d*=0.12).

Although an overall effect of statistical learning was observed in the search task, the significance of this effect was borderline. This raises the question of whether all pairs were learned weakly and to the same extent, or whether some pairs were learned and others were not. This question gets to the heart of our multiple-process hypothesis and, as can be seen in Figure 3, evidence suggests that there was considerable variability across pairs in the search RT effect, with some pairs showing an effect consistent with learning and others showing the opposite. This variability may just be noise, unrelated to performance in the detection task for the same items. Alternatively, it may reflect true differences in item-level learning, such that our labeling of pairs as learned or non-learned retains meaning in the detection task.

To test the multiple-process hypothesis, we examined whether learned pairs from the search task (Figure 3, solid blue lines) elicited different performance in the detection task than non-learned pairs (Figure 3, dashed red lines). For results of this experiment and of Experiment 2 using the full triplet structure, see Supplemental Data. This pair-wise analysis differs from typical analyses in studies of statistical learning, in that we allow for the possibility that participants did not learn each pair that they were exposed to in the same manner.

This analysis revealed a dramatic and counterintuitive *negative* relationship between the detection task from exposure and the search task from the post-test (Figure 5). The pairs classified as learned in the search task (N=106 pairs, or 212 shapes) and the pairs classified as non-learned in the search task (N=79, or 158 shapes) showed a significant interaction (position X learning status) for RT ($F(1,366)=7.00$, $p=0.0085$, $\eta^2=0.019$) although not accuracy ($F(1,366)=1.36$, $p=0.24$, $\eta^2=0.0037$) in the detection task. For RTs, non-learned pairs (i.e., those not showing learning in the search task) *did* show learning in the detection task, with faster responses for second vs. first positions (645.7 vs. 670.7 ms, respectively; $t(78)=2.42$, $p=0.018$, Cohen's $d=0.27$). This finding of learning in the detection task for pairs not showing learning in the search task cannot be explained by a speed-accuracy tradeoff, as accuracy was numerically higher for the second vs. first positions (87.7 vs. 85.6%, respectively) of the non-learned pairs ($t(78)=1.46$, $p=0.15$, Cohen's $d=0.16$). In contrast, learned pairs (i.e., those showing learning in the search task) exhibited no learning in the detection task for second vs. first RTs (684.3 vs. 677.9 ms, respectively; $t(105)=0.79$, $p=0.43$, Cohen's $d=0.076$) or accuracy (84.0 vs. 84.2%, respectively; $t(105)=0.22$, $p=0.82$, Cohen's $d=0.015$). Notably, the reliable decrease in RT for non-learned second position in the detection task implies that statistical learning occurred for those pairs, as there was no information available to the participant about the upcoming shape except for the statistical regularities governing the presentations. These data, showing a dissociation between statistical learning as manifested in the detection and search tasks, are consistent with the predictions of the multiple-process hypothesis.

Experiment 2

Although Experiment 1 provides initial support for the multiple-process hypothesis, the counter-intuitive nature of the result compelled us to replicate the finding. Furthermore, to better understand the dissociation between learning on the detection and search tasks, and to validate the dissociation, in Experiment 2 we replaced the search task with a recognition task, in which participants were asked to judge whether a sequence had occurred during exposure or not, and to rate their confidence in the judgment.

The recognition task was selected as potentially being more sensitive to different components of memory than the classically described two-alternative-forced-choice familiarity test in statistical learning (e.g., Fiser & Aslin, 2002). Research indicates that familiarity and recognition judgments may correspond to different aspects of encoded memories (Wixted, 2007; Yonelinas, 1994) and we hypothesized that different memory judgments might map onto the learned/non-learned dissociations seen in Experiment 1. For example, pairs rated with "Remember" (see Methods below) might correspond to the learned pairs of Experiment 1 and pairs rated as “Familiar” might correspond to the non-learned pairs. However, regardless of information gained from the ratings, the main purpose of this experiment was to replicate the results of Experiment 1 and generalize the dissociation of statistical learning measures using a different learning measure.

Methods

Participants

Forty-one undergraduates at the University of California, Riverside, aged 18-22 (26 females), participated in this experiment (sample size again determined by how many students could be recruited within a quarter from the UC Riverside undergraduate subject pool). Inability to complete both tasks satisfactorily resulted in the exclusion of four participants beyond the forty-one included in the study. As in Experiment 1, if participants were excluded then their data were not analyzed beyond determining their response rate.

Stimuli and apparatus

The stimuli and display apparatus were identical to Experiment 1, except for the differences noted here. Stimuli were displayed on a 48.26cm wide Sony Trinitron CRT monitor connected to an Apple Mac mini computer running OSX 10.5.6. Mediating the connection from monitor to computer was a Datapixx processor (VPixx Technologies) that enables a 16-bit DAC, allowing for a 256-fold increase in the display's possible contrast values. Responses were collected using a RESPONSEPixx button box (VPixx Technologies) that enables microsecond precision of response latency measurement. Tones were presented using a small speaker placed behind the monitor. Participants' heads were restrained with a chin rest 69.85cm from the screen.

Detection Task

The exposure and detection task were identical to Experiment 1.

Recognition Task

A recognition task was used instead of the search task for the post-test. Responses were provided on a multidimensional "New/Old" and "Familiar/Remember" scale (Figure 6; adapted from Ingram, Mickes, & Wixted, 2012). On this scale, participants reported with a single response whether a sequence was new or old, rated their confidence, and, in the case of old responses, whether they recollected any details surrounding prior experiences with the sequence. If participants recalled any such details, for example a specific instance when that sequence occurred, they responded with the "R" scale for remember. If they did not recall specific details but simply had a feeling that they had seen the sequence before, they responded with the "F" scale for familiar. Stickers were placed on the number-pad of the keyboard to match the scale shown in Figure 6.

In each of 10 trials, participants were exposed to a sequence of three of the shapes seen during exposure, presented with the same SOA and ISI as before. After the last shape was displayed, a response query appeared on screen and participants reported whether that sequence (i.e., those three shapes in that exact order) had occurred during exposure. The 10 trials consisted of the 5 intact triplets, which had occurred repeatedly during exposure, and 5 rearranged triplets, which contained the same exposed shapes but in an order that could not have occurred during exposure. After obtaining the recognition judgments, we confined our multiple-process analyses to the first two shapes, i.e., the first pair, of each triplet for the reasons provided in Experiment 1.

Results and discussion

To test the multiple-process hypothesis, we coded the detection task performance according to whether an intact pair was correctly identified as “Old” in the recognition task ("Recognition learned") or incorrectly identified as “New” ("Recognition non-learned"). Consistent with the hypothesis (see Figure 7), learned pairs (N=139 pairs, or 278 shapes) and non-learned pairs (N=66 pairs, or 132 shapes) showed a significant interaction (position X learning status) for RT ($F(1,406)=10.41$, $p=0.0014$, $\eta^2=0.025$) and a marginal interaction for accuracy ($F(1,406)=2.90$, $p=0.089$, $\eta^2=0.007$). Learned pairs (i.e., those that were correctly identified in the recognition task) showed a significant drop in detection accuracy for the second vs. first positions (87.2 vs. 90.6%, respectively; $t(138)=3.15$, $p=0.002$, Cohen's $d=0.27$) and no significant difference in RT for the second vs. first positions (603.4 vs. 601.0 ms, respectively; $t(138)=0.41$, $p=0.68$, Cohen's $d=0.036$). For non-learned pairs (i.e., those that were *not* correctly identified in the recognition task), RT showed a significant decrease for the second vs. first positions (579.9 vs. 608.4 ms, respectively; $t(65)=3.32$, $p=0.0015$, Cohen's $d=0.41$) and no significant difference in accuracy for the second vs. first positions (90.8 vs. 91.1%, respectively; $t(65)=0.20$, $p=0.84$, Cohen's $d=0.024$). These results conceptually replicate those of Experiment 1 and suggest that, unlike the detection task, the recognition task from this experiment and the search task from Experiment 1 may tap into the same statistical learning process — at least based on their shared opposition to the detection task.

To understand these results in greater detail, learned pairs were further subdivided into "Familiar" or "Remember" retrieval modes (Figure 8). Treating learning status as a three-level factor (Familiar, N=78 pairs, or 156 shapes; Remember, N=61 pairs, or 122 shapes; and New, N=66, or 132 shapes), there was a significant interaction (position X learning status) for RT ($F(2,404)=5.44$, $p=0.0047$, $\eta^2=0.026$) and a marginal interaction for accuracy ($F(2,404)=2.40$, $p=0.092$, $\eta^2=0.011$). The decrease in accuracy for the second position vs. the first position in learned pairs was driven by Familiar (84.7 vs. 89.4%, respectively; $t(77)=2.89$, $p=0.005$, Cohen's $d=0.33$) but not Remember pairs (90.3 vs. 92.1%, respectively; $t(60)=1.35$, $p=0.18$, Cohen's $d=0.17$). The difference in RT for the second position as compared to the first was not reliable for Familiar (615.7 vs. 616.8 ms, respectively; $t(77)=0.13$, $p=0.90$, Cohen's $d=0.015$) nor Remember (587.5 vs. 580.9 ms, respectively; $t(60)=0.90$, $p=0.37$, Cohen's $d=0.11$) pairs. As reported above, only the non-learned pairs showed a decrease in RT for the second position.

These results suggest a potential dissociation between remembered and familiar pairs with the primary distinction being faster and more accurate detection for the remembered pairs. Although we had hypothesized that a familiar/remember dissociation might be linked to the learned/non-learned dissociation seen in Experiment 1, the data did not support this hypothesis. Instead, both the familiar and remember pairs are consistent with the learned pairs of Experiment 1 and the results as a whole replicate the learned/non-learned dissociation found in Experiment 1.

Experiment 3

Although Experiment 2 replicated Experiment 1, it failed to provide additional clarity about the mechanisms underlying our results. Experiment 3 was run for this purpose, to determine whether the facilitation for the second shape position in the search task reflects an enhanced representation of the second shape, the learning of an association between the first and second shapes, or a combination of the two.

Statistical learning is typically assumed to reflect an association between stimuli A and B, where perceiving A enables one to predict the subsequent appearance of B (Schapiro et al., 2012). However, recent work suggests that statistical learning can give rise to an enhanced salience of the second stimulus of a pair even outside of its exposed context, and that this enhanced salience can account for second position effects in the search task (Barakat et al., 2013). We therefore examined whether learning in the detection and search tasks reflects an associative and/or representational form of learning. If learning is associative, then replacing the second shape with an out-of-context shape (a misplaced second shape or a foil, see Methods below) should result in slower RTs. On the other hand, if the learning reflects an enhanced representation of the second shape, then misplaced second shapes should elicit speeded responses even when presented out of context; in contrast, foils, which are shapes not shown during exposure, should receive no such benefit. A combination of associative effects and enhancement is also possible.

Methods

Participants

Fifty-six undergraduates at the University of California, Riverside, aged 17-32 (25 females), participated in this experiment (sample size again determined by how many students could be recruited within a quarter from the UC Riverside undergraduate subject pool). Inability to complete both tasks satisfactorily resulted in the exclusion of five participants beyond the fifty-six included in the study. As in Experiments 1 and 2, if participants were excluded then their data were not analyzed beyond determining their response rate.

Stimuli and apparatus

The stimuli and apparatus were identical to Experiment 2, except that three additional shapes were used to accommodate the conditions of this experiment.

Detection Task

The detection task during exposure was the same as Experiment 1, except as noted. First, the stimulus regularities in Experiment 3 consisted of six pairs rather than five triplets. Second, in blocks 11-20, one of five conditions occurred when a target appeared on the screen (blocks 1-10 were the same as in Experiment 1 other than the use of pairs rather than triplets). The two "intact" target conditions were the same as in the previous experiments and as in the first 10 blocks of the current experiment: the target was either the correct first or second shape of a pair. The two "foil" target conditions involved six foil shapes that were never shown in the first half of exposure. Foils could occur as targets in either the first or second position of a pair with equal frequency. That is, in each of the latter 10 blocks, each of the six foil items occurred in place of the first item of a pseudorandomly determined intact pair and during a different trial would also appear in place of the second item of a pseudorandomly determined intact pair. The particular foil used with each pair was randomized and counterbalanced across blocks. The “mismatched” condition replaced a pair's second shape with the second shape from a different pair as was done in Barakat et al. (2013). That is, a shape that had been seen in the first half of the exposure task occupying a second position appeared as a target after a different first shape. All conditions and shapes were counterbalanced to equate the exposure of shapes and pairs.

As in Experiment 1, there were twenty blocks of exposure. In the first ten blocks, all pairs were presented as intact pairs. Each shape position of the six pairs was used as a target twice, resulting in twenty-four pairs that contained a target. In half of these, the target was present and in the other half, the target was absent. The shape used as the target was counterbalanced. 1-3 intact filler pairs were presented between target-containing pairs, which amounted to a total of 72 pairs, or 144 shapes, per block. In the second ten blocks, there were sixty targets per block, again half present and half absent. The thirty present targets consisted of six instances of each of the following: intact first position, intact second position, foil first position, foil second position, and mismatched second position. Combined with 1-3 intact filler pairs between each target-containing pair, this amounted to a total of 180 pairs, or 360 shapes, per block.

Search Task

The search task was similar to Experiment 1, except as noted. There were five blocks of 30 trials each. Within a block, every shape from each condition (first and second intact, first and second foil, mismatch) was used once as a target, including the six foils when the trial called for one of those two conditions. Given that the mismatched condition required the second shape of a pair to be replaced with another pair's second shape, the pair from which the second shape was drawn could not be displayed on that trial (or else the target would be displayed twice in a single trial, once as an intact second shape and once as a mismatched second shape). Thus, each trial of the search task displayed five of the pairs instead of all six. The omitted pair was counterbalanced across trials, and when the mismatched condition occurred, the missing pair was always the pair from which the replacement shape had been drawn.

Results and discussion

Search task

We first sought overall evidence of statistical learning in the search task (Figure 9). The intact pairs showed reliably faster RTs for the second vs. first positions (424.7 vs. 441.9 ms, respectively; $t(55)=5.38$, $p<0.0001$, Cohen's $d=0.72$). The second position foils (422.0 ms) and mismatched second shapes (429.9 ms) were also found more quickly than the first intact shape (441.9 ms; $t(55)=5.93$, $p<0.0001$, Cohen's $d=0.80$ and $t(55)=3.64$, $p=0.0006$, Cohen's $d=0.48$, respectively). Furthermore, RTs were faster for second position vs. first position foils (422.0 vs. 434.9 ms, respectively; $t(55)=4.14$, $p=0.00012$, Cohen's *d*=0.55), suggesting that there may have been some learning for position, regardless of item presented. These results demonstrate that statistical learning occurred and replicate the findings of Barakat et al. (2013), showing a benefit for shapes in the second position even outside of their pair context.

However, our primary interest was to test the multiple-process hypothesis by examining performance in the detection task. As in Experiment 1, we split pairs according to whether they displayed a negative slope (learned) or a flat/positive slope (non-learned) in the search task. We did this separately for each condition.

Learned vs. non-learned pairs – intact conditions

For intact conditions, learning was measured as intact first shape RT minus intact second shape RT, resulting in N=179 learned pairs, or 358 shapes, and N=157 non-learned pairs, or 314 shapes. Results for the intact pairs replicated those of Experiment 1 (Figure 10) and provide additional support for the multiple-process hypothesis. Although neither interaction (position X learning status) reached significance (accuracy: $F(1,668)<0.1$, $p=0.95$, $\eta^2<0.001$; RT: $F(1,668)=1.01$, $p=0.31$, $\eta^2=0.0015$), non-learned pairs showed a simple RT effect for second vs. first position in the detection task (542.6 vs. 553.6 ms, respectively; $t(156)=2.24$, $p=0.026$, Cohen's $d=0.18$), whereas learned pairs did not (556.6 vs. 561.0 ms, respectively; $t(178)=0.92$, $p=0.36$, Cohen's $d=0.068$). There was no effect in accuracy for second vs. first in either learned pairs (89.0 vs. 88.7%, respectively; $t(178)=0.25$, $p=0.80$, Cohen's $d=0.020$) or non-learned pairs (88.3 vs. 87.9%, respectively; $t(156)=0.32$, $p=0.75$, Cohen's $d=0.027$).

Learned vs. non-learned pairs – foil and mismatched conditions

As in the search task, analyses of the foil and mismatched conditions in the detection task can provide additional evidence on whether the faster performance for second shapes is an associative effect rather than just a speeded response for any item presented after a learned first item. The foil and mismatched conditions indicated that both the learned and non-learned pairs displayed some learning in the detection task (Figure 10). However, the nature of these effects differed. For the learned pairs, the overall pattern was slower RTs for second shapes relative to intact first shapes. This was only significant for foil second shapes (571.2 vs. 561.0 ms; $t(178)=2.10$, $p=0.037$, Cohen's $d=0.16$), not mismatched second shapes (564.1 vs. 561.0 ms; $t(178)=0.70$, $p=0.49$, Cohen's $d=0.052$). Comparing just second positions of the learned pairs, RTs were significantly slower for foil vs. intact shapes (571.2 vs. 556.6 ms, respectively; $t(178)=3.14$, $p=0.002$, Cohen's $d=0.23$) and marginally slower for mismatched vs. intact shapes (564.1 vs. 556.6 ms, respectively; $t(178)=1.68$, $p=0.094$, Cohen's $d=0.12$). These results provide support for the hypothesis that associative learning occurred between the first and second positions of the learned pairs.

For the non-learned pairs, the overall pattern was equivalent RTs for second shapes relative to first intact shapes. This was true for both foil second shapes (549.1 vs. 553.6 ms; $t(156)=0.91$, $p=0.36$, Cohen's $d=0.072$) and mismatched second shapes (553.8 vs. 553.6 ms; $t(156)=0.04$, $p=0.97$, Cohen's $d=0.0033$). Comparing just second positions, RTs were significantly slower for mismatched vs. intact shapes (553.8 vs. 542.6 ms, respectively; *t*(156)=2.41, *p*=0.017, Cohen's *d*=0.19) and not significantly different for foil vs. intact shapes (549.1 vs. 542.6 ms, respectively; *t*(156)=1.46, *p*=0.15, Cohen's *d*=0.12). This can be considered a lack of facilitation for the mismatched second shapes and is also suggestive of associative learning being displayed in the detection task for the non-learned-pairs.

Considering the learned and non-learned pairs together, our data are consistent with the associative learning hypothesis. Whenever the second shape in a pair is replaced, the response is slowed. Using this measure of learning, there was a comparable magnitude of associative learning displayed in the detection task for both learned pairs (11.1ms) and non-learned pairs (8.9ms). However, the manner in which the violation of the associative prediction manifested itself (slowing for learned but a lack of speeding for non-learned) provides further evidence of dissociation between detection and search measures of statistical learning. Combined with the pattern of results for the intact conditions, which are analogous to the conditions of Experiments 1 and 2 and replicate those patterns of results, these data again are consistent with the predictions of the multiple-process hypothesis for statistical learning.

General Discussion

For most studies of statistical learning, a single test is used to index learning. Here we show that this approach underestimates the extent of learning that has taken place. Specifically, we found that statistical learning can be reflected in multiple behavioral tasks, and critically, that these tasks do not provide redundant information. One aspect of learning was revealed in the search task, where lower latencies were found for predictable shapes. A dissociated aspect of learning was observed in the detection task, again indicated by better performance for predictable shapes, but only for those items that did not display learning in the search task. Similar results were obtained for recognition memory judgments, where correctly recognized regularities did not show a detection effect, and other regularities showed a detection effect but were forgotten in the recognition test, and the results were obtained again with the intact pairs of Experiment 3.

This manner of double dissociation of performance across tasks is classically taken as evidence for different processes in cognitive research (Chun, 1997; Gabrieli, Fleischman, Keane, Reminger, & Morrell, 1995) and defies the alternative explanation that different tasks will naturally have different sensitivities because of the starkly opposite results seen in the dependent variables of the compared tasks. If the tasks were merely displaying different levels of sensitivities for the same process, we would expect similar results for both tasks, albeit with different effect sizes. Instead we observe results that consistently demonstrate one pattern for one task and an opposite pattern for another task. The observed search, recognition, and detection effects cannot be explained by individual shapes nor happenstance groupings of the shapes, as these were randomized and counterbalanced across participants. Furthermore, in Experiment 3, we provided evidence that dissociable patterns of learning for different pairs (positive vs. negative second position RT effects) can be observed within the same detection task. The question then becomes: why is learning expressed differently depending on the task?

A logical answer is that there are multiple processes that underlie different aspects of visual statistical learning. Moreover, to account for the observation that any given regularity is only reflected in one task, these systems may compete with each other. Neuroscientific investigations of statistical learning are consistent with this interpretation. Specifically, statistical learning is supported by at least two memory systems in the brain, the hippocampus and the striatum (Durrant et al., 2013; Schapiro et al., 2014, 2012; Turk-Browne et al., 2009, 2010). These systems have been shown to compete with each other during learning (Packard, 1999; Poldrack et al., 2001; but see Sadeh, Shohamy, Levy, Reggev, & Maril, 2011). The left inferior frontal cortex also supports statistical learning (Karuza et al., 2013; Turk-Browne et al., 2009), and it has been suggested that learning in frontal cortex differs from the striatum in terms of the speed of learning (Pasupathy & Miller, 2005). Different learning processes in the hippocampus, striatum, and frontal cortex may therefore occur at different rates and produce different kinds of behavioral effects (e.g., the hippocampus may underlie recognition judgments). Identifying other specific mechanisms that might underlie these processes will require future experimental and theoretical work. A first step could be to generalize existing computational models of statistical learning to account for multiple behavioral measures. Currently, these models account for either recognition (e.g., TRACX, French, Addyman, & Mareschal, 2011; PARSER, Perruchet & Vinter, 1998) or prediction (e.g., SRN, Cleeremans & McClelland, 1991; Elman, 1990), but not both.

An intriguing result from Experiment 2 is the difference in performance for regularities that were given "Familiar" versus "Remember" ratings. As discussed above, the dissociation seen in the detection task for familiar/remember pairs did not mirror the dissociation seen for learned/non-learned pairs as we had hypothesized it might. However, the fact that there is a visible difference between explicitly given "Familiar" and "Remember" ratings suggests that participants are able to effectively rank their implicit memories of the regularities and indicates a shade of grey between classic notions of implicit and explicit knowledge (Bertels, Franco, & Destrebecqz, 2012). This explicit sense of the richness of retrieval is intriguing because statistical learning is often thought to be an implicit process (Kim et al., 2009). Indeed, out of 134 participants, not a single participant reported consciously detecting any pattern to the shapes displayed in the experiment. Ultimately the familiar/remember aspect of this experiment failed to reveal a further dissociation of learning patterns across pairs but nevertheless, Experiment 2 provided compelling results regarding differences in processing between “Remembered” and “Familiar” pairs which warrants further study.

Experiment 3 provides evidence that the learning in both the detection and search tasks is associative. The results for the detection task as split by the search task show that when the second shape of a pair is replaced with a shape that it does not normally occur with, there is a slowing of RT (learned pairs) or a lack of facilitation (non-learned pairs). As discussed above, this different pattern of results for learned and non-learned pairs provides further evidence that the detection and search tasks are measuring two separate learning processes. This does not rule out the possibility that perceptual enhancement of the second shape also occurred (Barakat et al., 2013). Of note, RTs for mismatched second shapes were faster than for intact first shapes in the search task. Thus, a mix of associative and enhancement effects can jointly determine performance in statistical learning tasks.

In sum, the data presented here provide evidence that visual statistical learning might be composed of dissociable processes that can be revealed through different behavioral tasks. While it is possible that the different tasks used in the experiments reveal different aspects of a complex memory representation, the multiple-process model is consistent with neuroscience research showing that there are multiple brain systems that are sensitive to statistical regularities in the environment (Schapiro & Turk-Browne, 2015). Together, these findings challenge a common assumption that different operational methods of measuring statistical learning are interchangeable in terms of their interpretation. We caution against treating different measures of statistical learning as equivalent, since this not only discards useful variance in the data, but also gives the false impression that statistical learning is a single process rather than a multifaceted collection of processes. Our findings are useful in that they provide a foundation for future research in statistical learning that should more routinely use multiple tasks and seek to clarify dissociations of learning and the brain structures that underlie these dissociated processes.

References

Aslin, R. N., Saffran, J. R., & Newport, E. L. (1998). Computation of conditional probability statistics by 8-month-old infants. *Psychological Science*, *9*(4), 321–324.

Baker, C. I., Olson, C. R., & Behrmann, M. (2004). Role of Attention and Perceptual Grouping in Visual Statistical Learning. *Psychological Science*, *15*(7), 460–466.

Barakat, B. K., Seitz, A. R., & Shams, L. (2013). The effect of statistical learning on internal stimulus representations: Predictable items are enhanced even when not predicted. *Cognition*, *129*(2), 205–211. http://doi.org/10.1016/j.cognition.2013.07.003

Bertels, J., Franco, A., & Destrebecqz, A. (2012). How implicit is visual statistical learning? *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *38*(5), 1425–1431. http://doi.org/10.1037/a0027210

Campbell, K. L., Healey, M. K., Lee, M. M. S., Zimerman, S., & Hasher, L. (2012). Age Differences in Visual Statistical Learning. *Psychology and Aging*, *27*(3), 650–656. http://doi.org/10.1037/a0026780.Age

Chalk, M., Seitz, A. R., & Seriès, P. (2010). Rapidly learned stimulus expectations alter perception of motion. *Journal of Vision*, *10*(8), 1–18. http://doi.org/10.1167/10.8.2

Chun, M. M. (1997). Types and tokens in visual processing: A double dissociation between the attentional blink and repetition blindness. *Journal of Experimental Psychology: Human Perception and Performance*, *23*(3), 738–755. http://doi.org/10.1037/0096-1523.23.3.738

Cleeremans, A., & McClelland, J. L. (1991). Learning the structure of event sequences. *Journal of Experimental Psychology. General*, *120*(3), 235–253. http://doi.org/10.1037/0096-3445.120.3.235

Conway, C. M., & Christiansen, M. H. (2005). Modality-constrained statistical learning of tactile, visual, and auditory sequences. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *31*(1), 24–39.

Durrant, S. J., Cairney, S. A., & Lewis, P. A. (2013). Overnight consolidation aids the transfer of statistical knowledge from the medial temporal lobe to the striatum. *Cerebral Cortex*, *23*(10), 2467–2478. http://doi.org/10.1093/cercor/bhs244

Durrant, S. J., Taylor, C., Cairney, S. A., & Lewis, P. A. (2011). Sleep-dependent consolidation of statistical learning. *Neuropsychologia*, *49*(5), 1322–1331. http://doi.org/10.1016/j.neuropsychologia.2011.02.015

Elman, J. L. (1990). Finding structure in time. *Cognitive Science*, *14*(2), 179–211. http://doi.org/10.1207/s15516709cog1402_1

Fiser, J., & Aslin, R. N. (2001). Unsupervised statistical learning of higher-order spatial structures from visual scenes. *Psychological Science*, *12*(6), 499–504.

Fiser, J., & Aslin, R. N. (2002). Statistical learning of higher-order temporal structure from visual shape sequences. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *28*(3), 458–467.

Fiser, J., & Aslin, R. N. (2005). Encoding multielement scenes: Statistical learning of visual feature hierarchies. *Journal of Experimental Psychology: General*, *134*(4), 521–537.

Fletcher, P., Büchel, C., Josephs, O., Friston, K., & Dolan, R. (1999). Learning-related neuronal responses in prefrontal cortex studied with functional neuroimaging. *Cerebral Cortex*, *9*(2), 168–178.

French, R. M., Addyman, C., & Mareschal, D. (2011). TRACX: A recognition-based connectionist framework for sequence segmentation and chunk extraction. *Psychological Review*, *118*(4), 614–636. http://doi.org/10.1037/a0025255

Frost, R., Siegelman, N., Narkiss, A., & Afek, L. (2013). What predicts successful literacy acquisition in a second language? *Psychological Science*, *24*(7), 1243–1252. http://doi.org/10.1177/0956797612472207

Gabrieli, J. D. E., Fleischman, D. A., Keane, M. M., Reminger, S. L., & Morrell, F. (1995). Double dissociation between memory systems underlying explicit and implicit memory in the human brain. *Psychological Science*, *6*(2), 76–82.

Hunt, R., & Aslin, R. (2001). Statistical learning in a serial reaction time task: Access to separable statistical cues by individual learners. *Journal of Experimental Psychology: General*, *130*(4), 658–680.

Ingram, K. M., Mickes, L., & Wixted, J. T. (2012). Recollection can be weak and familiarity can be strong. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *38*(2), 325–339.

Karuza, E. A., Newport, E. L., Aslin, R. N., Starling, S. J., Tivarus, M. E., & Bavelier, D. (2013). The neural correlates of statistical learning in a word segmentation task: An fMRI study. *Brain and Language*, *127*(1), 46–54. http://doi.org/10.1016/j.bandl.2012.11.007

Kim, R., Seitz, A., Feenstra, H., & Shams, L. (2009). Testing assumptions of statistical learning: Is it long-term and implicit? *Neuroscience Letters*, *461*(2), 145–149. http://doi.org/10.1016/j.neulet.2009.06.030

Kirkham, N. Z., Slemmer, J. A., & Johnson, S. P. (2002). Visual statistical learning in infancy: Evidence for a domain general learning mechanism. *Cognition*, *83*(2), B35–B42.

Le Dantec, C. C., Melton, E. E., & Seitz, A. R. (2012). A triple dissociation between learning of target , distractors , and spatial contexts. *Journal of Vision*, *12*(2), 1–12. http://doi.org/10.1167/12.2.5.Introduction

Lieberman, M. D., Chang, G. Y., Chiao, J., Bookheimer, S. Y., & Knowlton, B. J. (2004). An event-related fMRI study of artificial grammar learning in a balanced chunk strength design. *Journal of Cognitive Neuroscience*, *16*(3), 427–438. http://doi.org/10.1162/089892904322926764

Loftus, G. R., & Masson, M. E. J. (1994). Using confidence intervals in within-subject designs. *Psychonomic Bulletin & Review*, *1*(4), 476–490.

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.

Packard, M. G. (1999). Glutamate infused posttraining into the hippocampus or caudate-putamen differentially strengthens place and response learning. *Proceedings of the National Academy of Sciences*, *96*(22), 12881–12886.

Pasupathy, A., & Miller, E. K. (2005). Different time courses of learning-related activity in the prefrontal cortex and striatum. *Nature*, *433*(7028), 873–876. http://doi.org/10.1038/nature03287

Perruchet, P., & Pacton, S. (2006). Implicit learning and statistical learning: One phenomenon, two approaches. *Trends in Cognitive Sciences*, *10*(5), 233–8. http://doi.org/10.1016/j.tics.2006.03.006

Perruchet, P., & Vinter, A. (1998). PARSER: A model for word segmentation. *Journal of Memory and Language*, *39*(2), 246–263. http://doi.org/10.1006/jmla.1998.2576

Poldrack, R. A., Clark, J., Paré-Blagoev, E. J., Shohamy, D., Creso Moyano, J., Myers, C., & Gluck, M. A. (2001). Interactive memory systems in the human brain. *Nature*, *414*(6863), 546–550. http://doi.org/10.1038/35107080 process. (2015). Retrieved August 09, 2015, from http://www.merriam-webster.com/dictionary/process.

Sadeh, T., Shohamy, D., Levy, D. R., Reggev, N., & Maril, A. (2011). Cooperation between the hippocampus and the striatum during episodic encoding. *Journal of Cognitive Neuroscience*, *23*(7), 1597–1608.

Saffran, J. R., Aslin, R. N., & Newport, E. L. (1996). Statistical learning by 8-month-old infants. *Science*, *274*(5294), 1926–1928.

Saffran, J. R., Johnson, E., Aslin, R. N., & Newport, E. L. (1999). Statistical learning of tone sequences by human infants and adults. *Cognition*, *70*(1), 27–52.

Saffran, J. R., Newport, E. L., Aslin, R. N., Tunick, R. A., & Barrueco, S. (1997). Incidental language learning: Listening (and learning) out of the corner of your ear. *Psychological Science*, *8*(2), 101–105.

Saffran, J. R., & Thiessen, E. (2003). Pattern induction by infant language learners. *Developmental Psychology*, *39*(3), 484–494.

Schapiro, A. C., Gregory, E., Landau, B., McCloskey, M., & Turk-Browne, N. B. (2014). The necessity of the medial temporal lobe for statistical learning. *Journal of Cognitive Neuroscience*, *26*(8), 1736–1747. http://doi.org/doi:10.1162/jocn_a_00578

Schapiro, A. C., Kustner, L. V, & Turk-Browne, N. B. (2012). Shaping of object representations in the human medial temporal lobe based on temporal regularities. *Current Biology*, *22*(17), 1622–1627. http://doi.org/10.1016/j.cub.2012.06.056

Schapiro, A. C., & Turk-Browne, N. B. (2015). Statistical learning. In A. W. Toga & R. A. Poldrack (Eds.), *Brain Mapping: An Encyclopedic Reference* (pp. 501–506). Academic Press.

Seger, C., Prabhakaran, V., Poldrack, R. A., & Gabrieli, J. (2000). Neural activity differs between explicit and implicit learning of artificial grammar strings: An fMRI study. *Psychobiology*, *28*(3), 283–292.

Toro, J. M., Sinnett, S., & Soto-Faraco, S. (2005). Speech segmentation by statistical learning depends on attention. *Cognition*, *97*(2), B25–B34.

Turk-Browne, N. B., Isola, P. J., Scholl, B., & Treat, T. A. (2008). Multidimensional visual statistical learning. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *34*(2), 399–407.

Turk-Browne, N. B., Jungé, J. A., & Scholl, B. J. (2005). The automaticity of visual statistical learning. *Journal of Experimental Psychology: General*, *134*(4), 552–564.

Turk-Browne, N. B., & Scholl, B. (2009). Flexible visual statistical learning: transfer across space and time. *Journal of Experimental Psychology: Human Perception and Performance*, *35*(1), 195–202.

Turk-Browne, N. B., Scholl, B. J., Chun, M. M., & Johnson, M. K. (2009). Neural evidence of statistical learning: Efficient detection of visual regularities without awareness. *Journal of Cognitive Neuroscience*, *21*(10), 1934–1945.

Turk-Browne, N. B., Scholl, B., Johnson, M. K., & Chun, M. M. (2010). Implicit perceptual anticipation triggered by statistical learning. *Journal of Neuroscience*, *30*(33), 11177–11187.

Wixted, J. T. (2007). Dual-process theory and signal-detection theory of recognition memory. *Psychological Review*, *114*(1), 152–176.

Yang, C. D. (2004). Universal Grammar, statistics or both? *Trends in Cognitive Sciences*, *8*(10), 451–456.

Yang, J., & Li, P. (2012). Brain networks of explicit and implicit learning. *PloS One*, *7*(8), e42993. http://doi.org/10.1371/journal.pone.0042993

Yonelinas, A. P. (1994). Receiver-operating characteristics in recognition memory: evidence for a dual-process model. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *20*(6), 1341–1354.

Zhao, J., Al-Aidroos, N., & Turk-Browne, N. B. (2013). Attention is spontaneously biased toward regularities. *Psychological Science*, *24*(5), 667–677. http://doi.org/10.1177/0956797612460407

Zhao, J., Ngo, N., McKendrick, R., & Turk-Browne, N. B. (2011). Mutual interference between statistical summary perception and statistical learning. *Psychological Science*, *22*(9), 1212–1219. http://doi.org/10.1177/0956797611419304

Chapter 1 Supplemental Data

Reliability of learned and non-learned classifications

The pairs which were classified as learned and non-learned in the search task of Experiment 1 were classified by averaging the RTs of a pair's particular first-position shape across all six blocks of the search task and comparing that to the average RT of that pair's second-position shape across all six blocks of the search task. Each shape was tested once in each block. Although each trial of a block only included a single target, and thus no within-trial comparison of a pair's first- and second-position shapes is possible, it is still possible to compare the RTs of each pair's two shapes within a block. (This assumes that a subject's RT will be relatively stable over the block and that the randomized position of the target shape within the trial presentation will not drastically affect the RT.) By counting the number of instances in which a pair's second shape had a faster RT than its first shape on a block-by-block basis, we can obtain a crude measure of reliability of the learned vs. non-learned classifications. We would expect when comparing pairs classified as learned to pairs classified as non-learned that the learned pairs would comprise a higher number of blocks in which the second shape has a lower RT than the first shape. Figures S1A and S1B show the distribution of within-block item comparisons in which the RT for the second-position shape is lower than the RT for the first-position shape for the 106 pairs classified as learned and for the 79 pairs classified as non-learned in Experiment 1, respectively. It is possible for a given pair to have a second-position shape with a lower RT than its first-position shape up to six times - once in each block of the search task. The ordinate of both figures corresponds to the total count within each bin of the histograms.

The mean number of blocks with a faster second-position RT than first-position RT for the learned pairs is 3.80 (Fig. S1A, dashed green line; SD = 1.046) and for the non-learned pairs is 2.18 (Fig. S1B, dashed green line; SD = 1.059); an independent-samples t test reveals a highly significant difference between these two means ($t(183)=10.39$, $p<0.001$, Cohen's $d = 1.54$).

Statistical analyses

Given that subjects differed in the number of "learned" and "non-learned" pairs in the search task, we employed a modified 2x2 (position: first/second X learning status: learned/non-learned) factorial ANOVA approach to analyze these data, which included subtracting each participant's mean RT (across all shapes) from the RT for each shape. This method is statistically equivalent to a repeated-measures design (removing between-subject variance but retaining within-subject comparisons) while also permitting unequal cell counts (and was verified on balanced datasets). This approach was not an attempt to increase statistical power but rather was a direct method designed to address unequal cell counts, which themselves were an expected result of the coding procedure used. Analyzing data containing unequal cell counts is unadvisable (and sometimes impossible) with traditional repeated-measures designs and obtaining equal cell sizes in these experiments could only occur if each participant had the exact same number of pairs classified as learned and non-learned, regardless of how many total pairs were used.

Overall detection task results

Prior to splitting the pairs based on the post-test of each experiment, the detection task generally showed an overall pattern of lower RTs for second compared to first positions. However, the reliability of this effect was variable across experiments.

Experiment 1 (Figure S2) displayed a non-significant decrease in RT for second vs. first positions (666.7 vs. 674.5 ms, respectively; $t(36)=1.08$, $p=0.29$, Cohen's $d=0.18$), and a non-significant increase in accuracy for second vs. first positions (85.6 vs. 84.8%, respectively; $t(36)=0.69$, $p=0.50$, Cohen's $d=0.12$).

Experiment 2 (Figure S3) showed a trend for a decrease in RT for second vs. first positions (596.3 vs. 603.6 ms, respectively; $t(40)=1.70$, $p=0.097$, Cohen's $d=0.26$), however also a significant decrease in accuracy for second vs. first positions (88.3 vs. 90.7%, respectively; $t(40)=2.71$, $p=0.0098$, Cohen's $d=0.43$); this may represent a speed accuracy trade-off.

Experiment 3 (Figure S4) displayed a significant decrease in RT for second vs. first positions in the intact condition (550.0 vs. 557.2 ms, respectively; $t(55)=2.05$, $p=0.046$, Cohen's $d=0.27$) and a non-significant increase in accuracy for second vs. first positions in the intact condition (88.7 vs. 88.3%, respectively; $t(55)=0.44$, $p=0.66$, Cohen's $d=0.071$). There was no significant difference between second vs. first positions in the foil condition for RT (561.0 vs. 560.7, respectively; $t(55)=0.076$, $p=0.94$, Cohen's $d=0.012$) or accuracy (89.4 vs. 89.7%; $t(55)=0.34$, $p=0.73$, Cohen's $d=0.058$). Mismatched second shapes displayed a small but significant increase in accuracy compared to intact first shapes (89.9

vs. 88.3%, respectively; *t*(55)=2.35, *p*=0.023, Cohen's *d*=0.32), but no significant difference in RT (559.1 vs. 557.2 ms, respectively; *t*(55)=0.46, *p*=0.64, Cohen's *d*=0.064).

Results using the full triplet structure

Although we do not believe that the full triplet structure was learned in our experiments, it is nevertheless informative to perform the analyses for Experiments 1 and 2 using the full triplet structures of the experiments. Figure S5 shows the search task results for Experiment 1, in which there is an expected monotonic decrease in RT across item position (535ms vs. 520ms vs. 502ms, respectively; $F(2,72)=9.42$, $p=0.0002$, $\eta^2=0.021$). In order to classify triplets as “learned” or “non-learned”, a metric similar to that used with pairs was applied, in which a triplet was classified as “learned” if it showed a monotonic decrease in RT across item position (i.e., item 1 RT > item 2 RT > item 3 RT) and “non-learned” if the triplet did not meet this standard. Although this rule is similar to the rule used for pairs, it results in different assignments to triplets than would have been made via a decision based on the first two items of that triplet. This can be seen in Figure S6, which shows accuracy and RT for the detection task of Experiment 1 for triplets as defined by whether they were learned or not in the search task. Although the trend is similar to the patterns seen from analyzing pairs, due to the different categorizations there is not as clear of a separation between the items classified as learned and non-learned in accuracy (interaction $F(2,549)=0.71$, $p=0.49$, $\eta^2=0.0026$) or RT (interaction $F(2,549)=2.86$, $p=0.058$, $\eta^2=0.01$).

Experiment 2 utilized a recognition task to measure learning after the detection task and, as reported in the main text, 139 triplets were correctly identified and 66 triplets were not correctly identified. These classifications of the triplets are the same as the classifications for the pairs reported in the main text since the recognition judgment was made using triplets and does not change whether we analyze the full triplet or just the first two items of that triplet in the detection task. The results for the full triplets in the detection task, as split by whether they were classified as learned or non-learned based on their identification in the recognition task, and split by whether they were judged as "Familiar" or "Remember" (see Experiment 2 Methods in main text), can be seen in Figure S7. Patterns similar to those seen in the pair analyses emerge, with a significant interaction for RT (interaction $F(4,606)=2.56$, $p=0.038$, $\eta^2=0.016$) but not for accuracy (interaction $F(4,606)=1.31$, $p=0.26$, $\eta^2=0.0084$). Collapsing the Familiar and Remember judgments (as in Figure 7 of the main text) reveals similar effects, with a significant interaction for RT (interaction $F(2,609)=4.74$, $p=0.009$, $\eta^2=0.015$) but not for accuracy (interaction $F(2,609)=1.7$, $p=0.18$, $\eta^2=0.0055$).

Figures

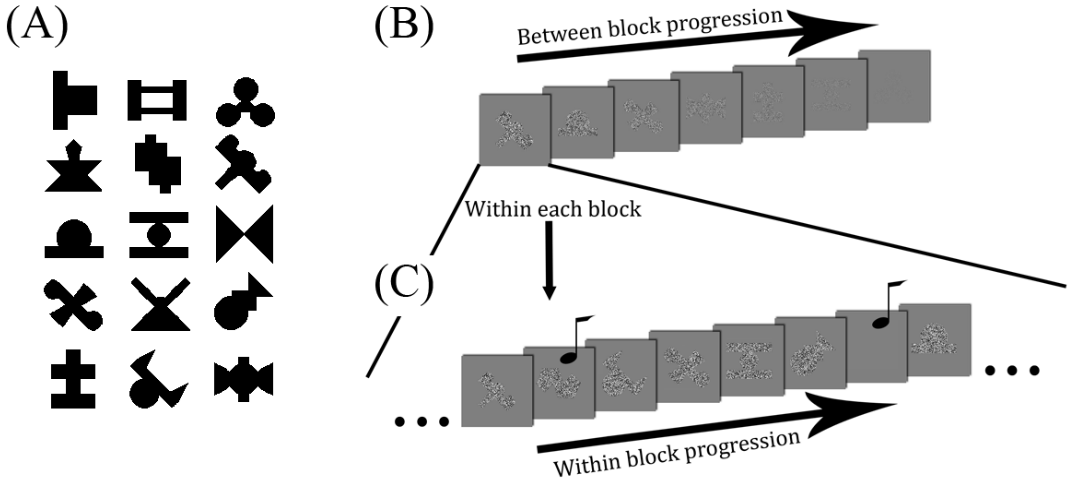

Figure 1 - (A) 15 shapes used in Experiment 1, shown here grouped into five example triplets. (B) Example of block progression and of stimuli at different contrasts. (C) Example of progression within a single block. Stimuli appear onscreen sequentially and musical notes indicate the occurrence of the periodic tone, which instructs participants to respond whether a shape was or was not onscreen.

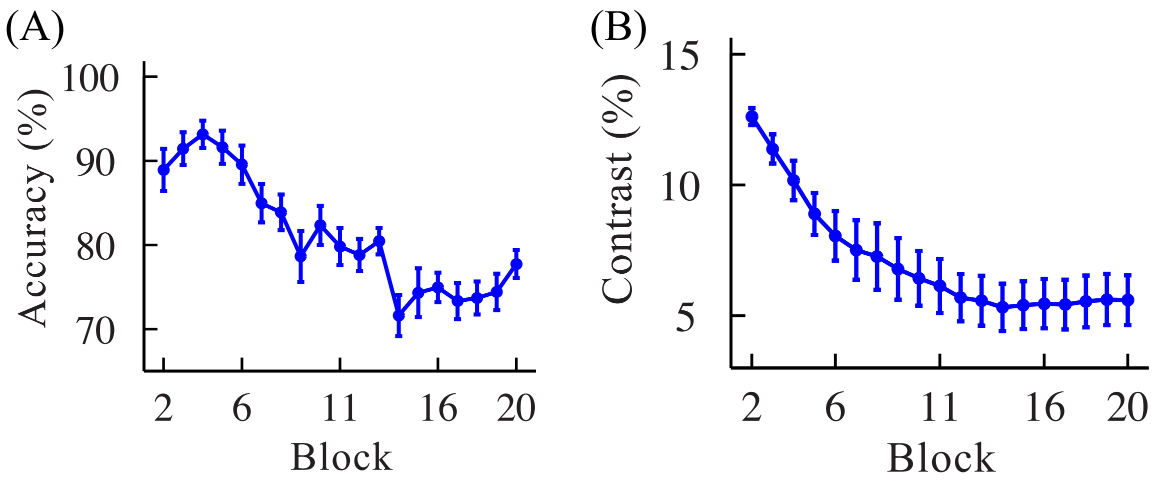

Figure 2 - (A) Mean accuracy as a function of block number. (B) Contrast levels at each block, averaged over the 37 participants of Experiment 1. The ordinate displays the proportion contrast, above or below the background. The first block was a practice block and was not analyzed. Error bars in both figures represent between-subjects standard error of the mean (SEM).

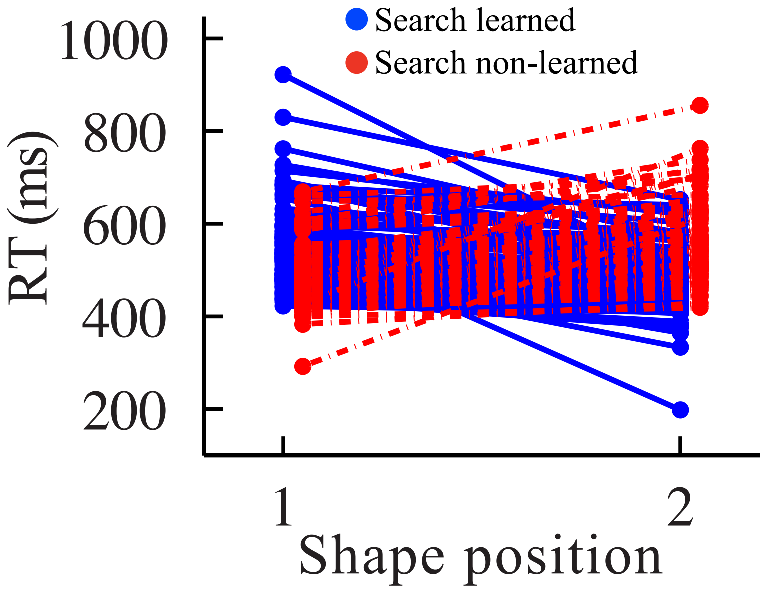

Figure 3 – Mean RTs of each pair across participants for the search task of Experiment 1. "Search learned" were pairs showing learning in the search task in terms of a faster RT for the second vs. first shape (102 pairs, solid blue lines, negative slope). "Search non-learned" were pairs not showing learning (78 pairs, dashed red lines, flat or positive slope). N = 36 participants (1 participant, comprising 5 pairs, omitted from figure for clarity, due to RTs greater than 1000ms).

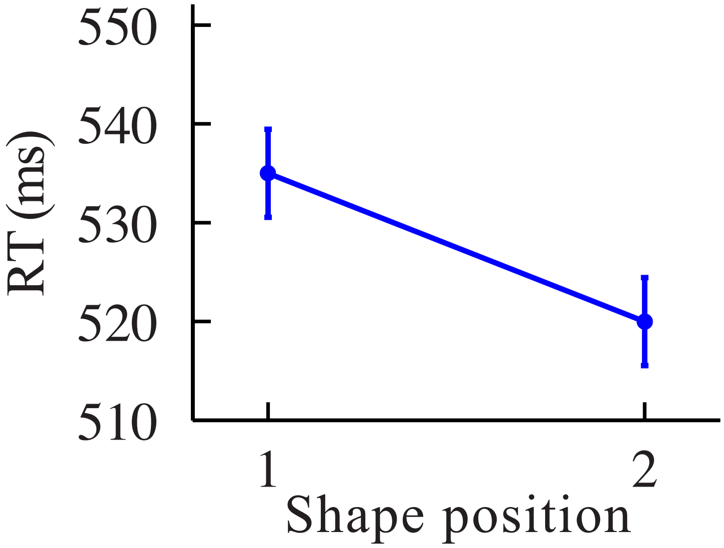

Figure 4 – Mean RT in the search task of Experiment 1. Error bars reflect +/- 1 within-subjects SEM (Loftus & Masson, 1994). N = 37.

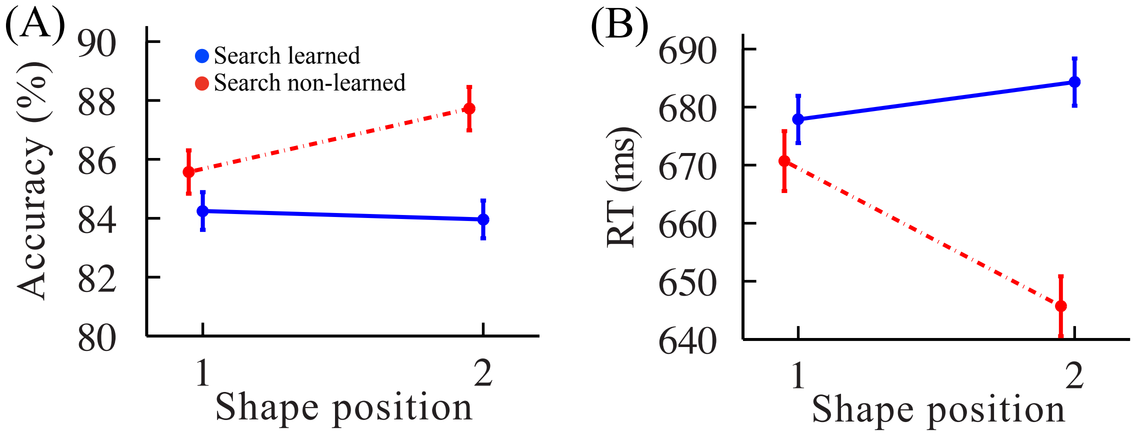

Figure 5 - Detection task results in Experiment 1 split by the search task, in terms of (A) accuracy and (B) RT. "Search learned" were pairs that demonstrated learning in the subsequent search task (solid blue lines). "Search non-learned" were pairs that did not demonstrate learning in the subsequent search task (dashed red lines). Error bars reflect +/- 1 within-subject SEM. N = 37. (N of pairs in blue curves = 106; N of pairs in red curves = 79.)

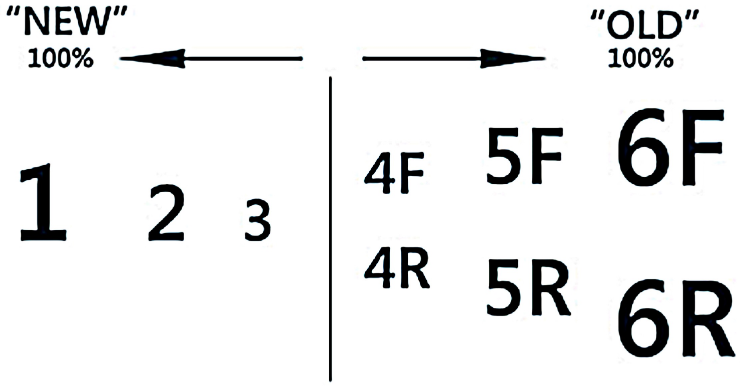

Figure 6 - Response scale used during the recognition task. "F" stands for "Familiar" and "R" stands for "Remember". Size of numbers and letters corresponds to confidence levels, with 1 and 6 being the most confident in a "New" or "Old" response, respectively.

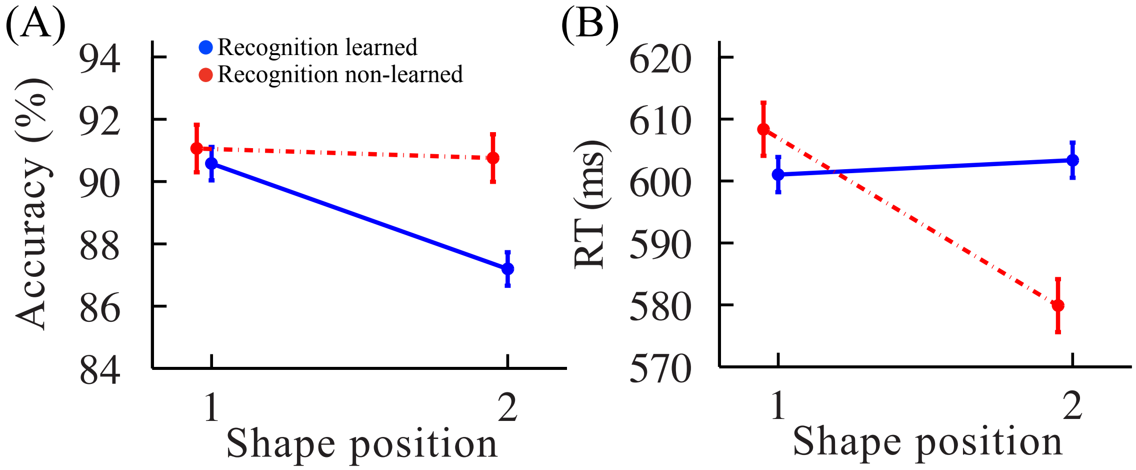

Figure 7 - Detection task results in Experiment 2 split by the recognition task, in terms of (A) accuracy and (B) RT. "Recognition learned" were pairs correctly identified in the subsequent recognition task (solid blue lines). "Recognition non-learned" were pairs not correctly identified in the subsequent recognition task (dashed red lines). Error bars reflect +/- 1 within-subject SEM. N = 41. (N of pairs in blue curves = 139; N of pairs in red curves = 66.)

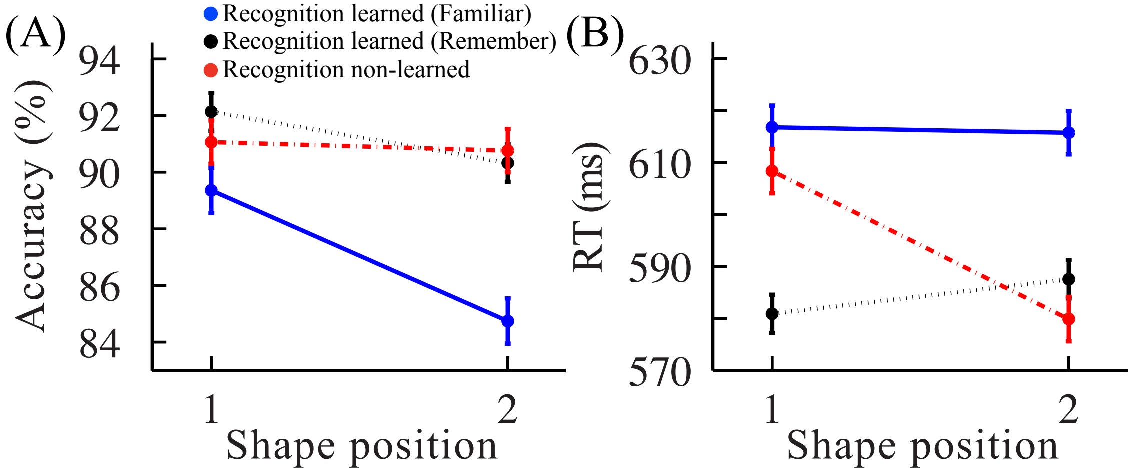

Figure 8 - Detection task results in Experiment 2 split by the Familiar/Remember ratings in the recognition task, in terms of (A) accuracy and (B) RT. "Recognition learned (Familiar)" were pairs correctly identified in the subsequent recognition task and given a "Familiar" rating (solid blue lines). "Recognition learned (Remember)" were pairs correctly identified in the subsequent recognition task and given a "Remember" rating (dotted black lines). "Recognition non-learned" were pairs not correctly identified in the subsequent recognition task (dashed red lines). Error bars reflect +/- 1 within-subject SEM. N = 41. (N of pairs in blue curves = 78; N of pairs in black curves = 61; N of pairs in red curves = 66.)

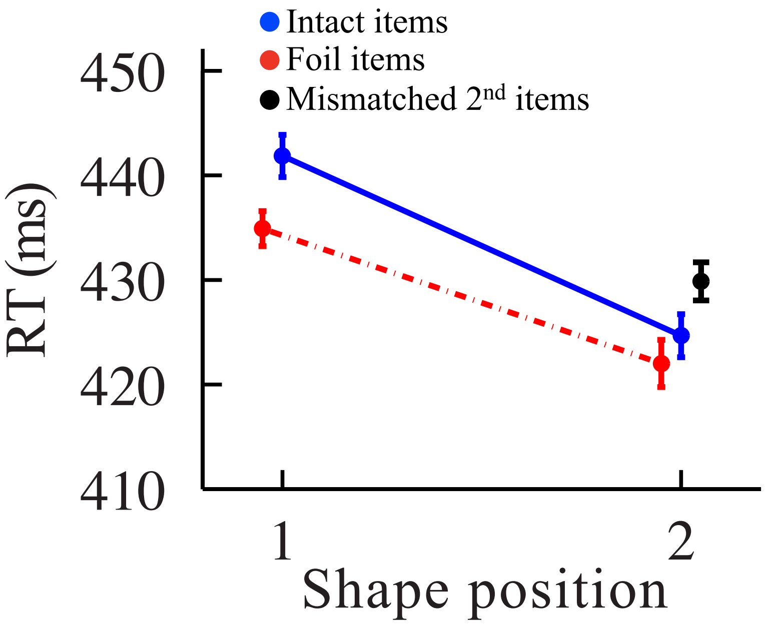

Figure 9 - RTs in the search task of Experiment 3. "Intact items" were shapes from conditions in which the pairs were presented intact (solid blue line). "Foil items" were shapes from conditions in which pairs were presented with either the first or second shape replaced with a foil unseen in the first ten blocks of exposure (dashed red line). Note that the foil items were not matched as the intact items were; the dashed line is only to demonstrate the difference between the two position RTs. "Mismatched 2nd items" were shapes from the condition in which the second shape of a pair was replaced with the second shape of another pair (black point). Error bars reflect +/- 1 within-subject SEM. N = 56.

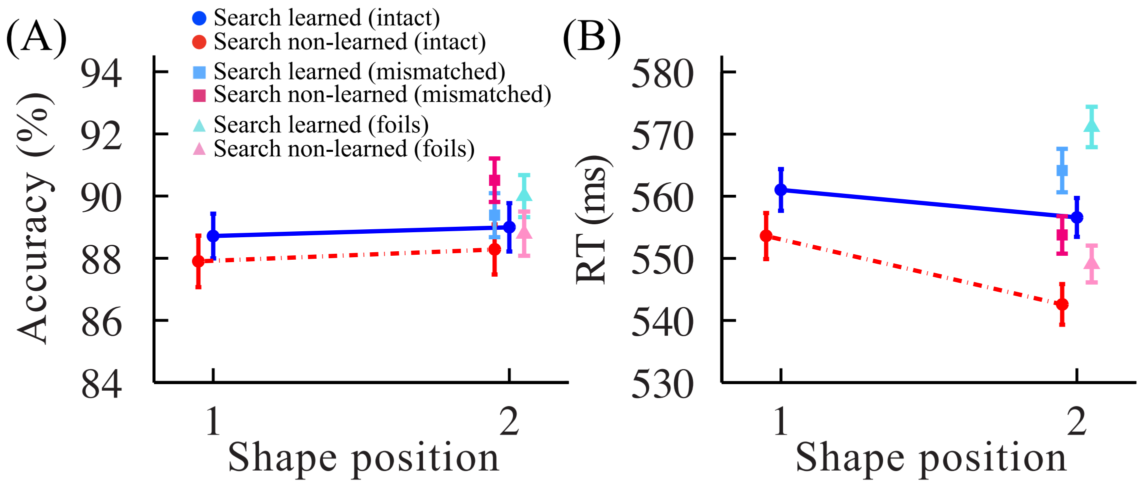

Figure 10 - Detection task results for intact, foil, and mismatched conditions in Experiment 3 split by the search task, in terms of (A) accuracy and (B) RT. "Search learned" circles were intact pairs that showed evidence of learning in the subsequent search task. "Search non-learned" circles were intact pairs that did not show learning in the subsequent search task. "Search learned" triangles were foils following an intact first shape that showed learning in the subsequent search task. "Search non-learned" triangles were foils following an intact first shape that did not show learning in the subsequent search task. "Search learned" squares were mismatched second shapes following an intact first shape that showed learning in the subsequent search task. "Search non-learned" squares were mismatched second shapes following an intact first shape that did not show learning in the subsequent search task. Error bars reflect +/- 1 within-subject SEM. N = 56. (N of blue pairs in each condition = 179; N of red pairs in each condition = 157.)

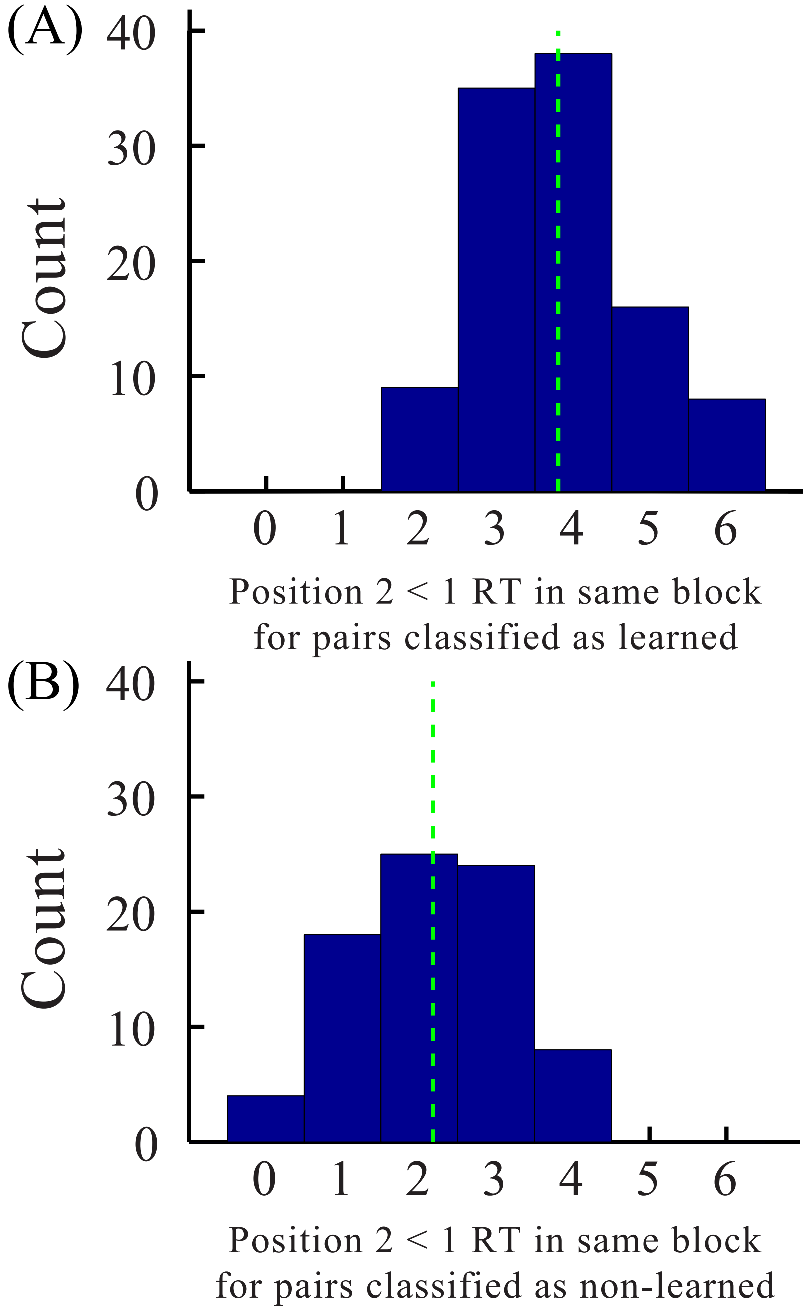

Figure S1 - Histograms displaying the number of times the RT to a second-position shape of a pair was lower than the RT to a first-position shape within the same block of the search task of Experiment 1 for (A) each of the 106 learned pairs and (B) each of the 79 non-learned pairs. The dashed green line on each figure represents the mean of the distribution, (A) 3.80 and (B) 2.18.

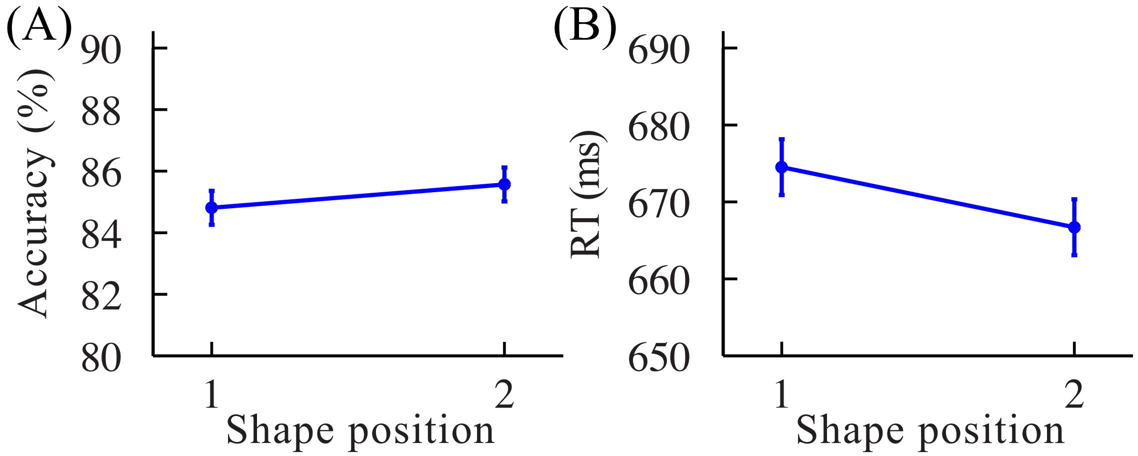

Figure S2 - Detection task results in Experiment 1, in terms of (A) accuracy and (B) RT. Error bars reflect +/- 1 within-subject SEM (Loftus & Masson, 1994). N = 37.

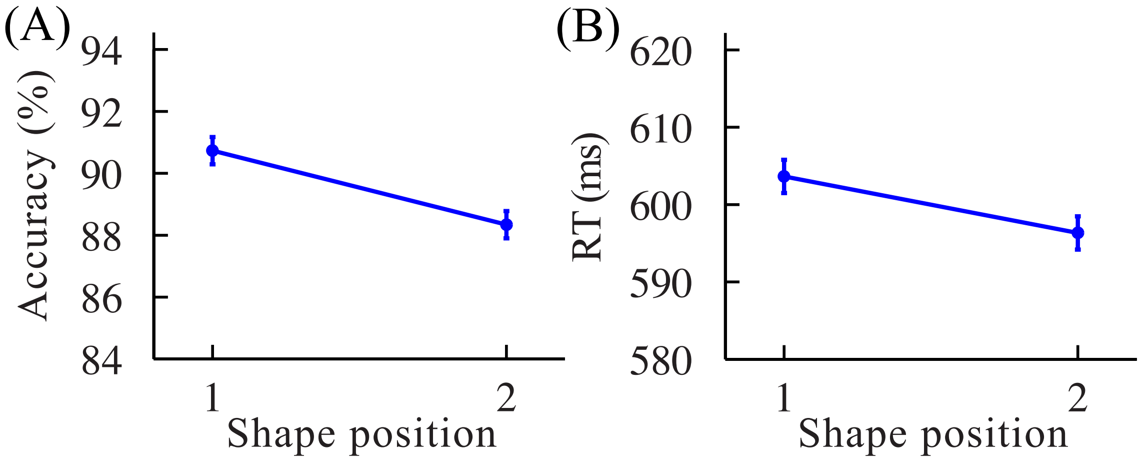

Figure S3 - Detection task results in Experiment 2, in terms of (A) accuracy and (B) RT. Error bars reflect +/- 1 within-subject SEM. N = 41.

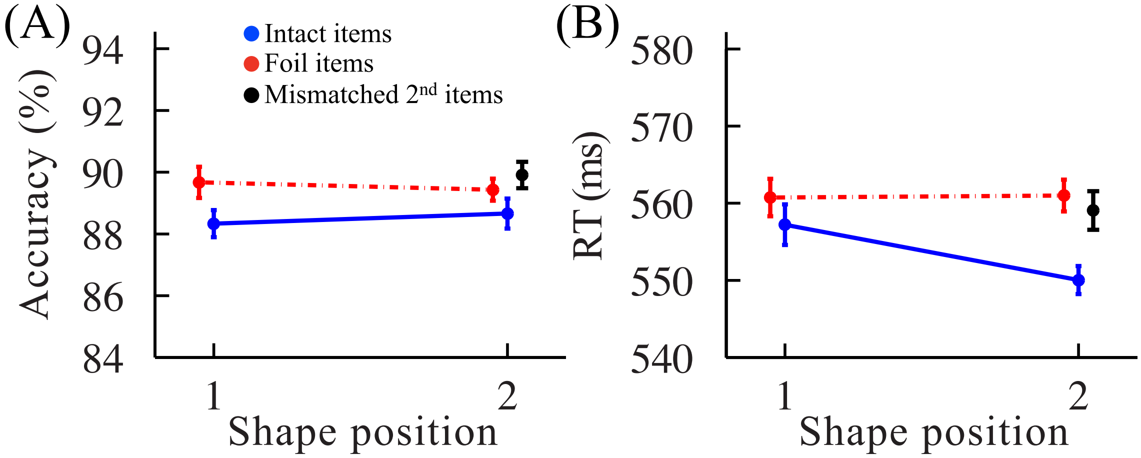

Figure S4 - Detection task results in Experiment 3. "Intact items" were items presented in their associated pairs (solid blue line). "Foil items" were items presented with either the first or second item replaced with a foil unseen in the first ten blocks of exposure (dashed red line). "Mismatched 2nd items" were items in which the second item of a pair was replaced with the second item of another pair (black point). Error bars reflect +/- 1 within-subject SEM. N = 56.

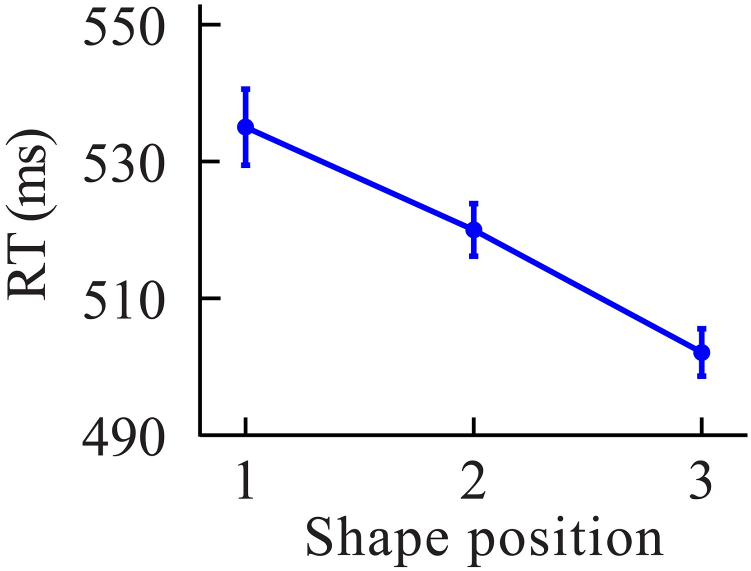

Figure S5 - Mean RT for the full triplet structure in the search task of Experiment 1. Error bars reflect +/- 1 within-subject SEM. N = 37.

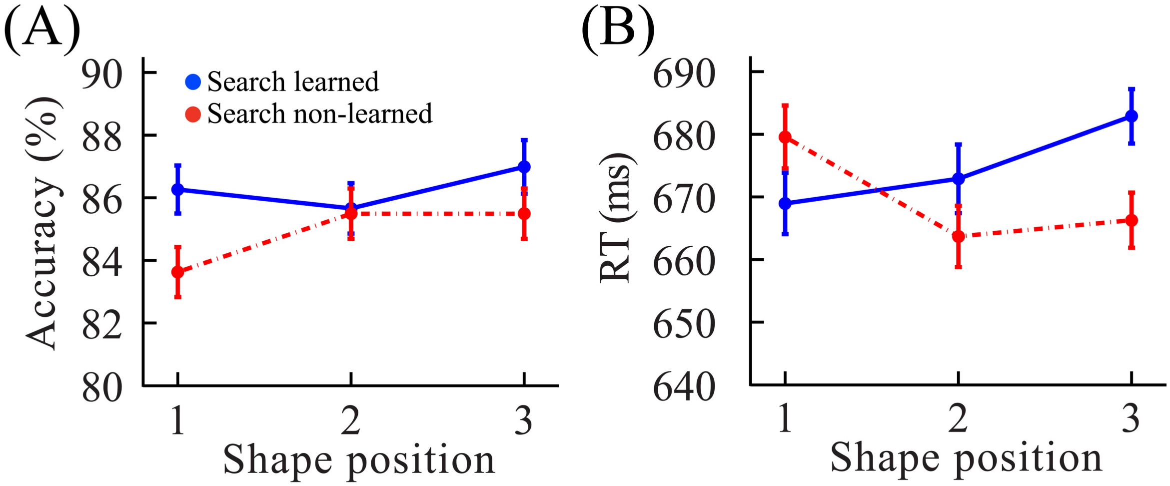

Figure S6 - Detection task results for the full triplet structure in Experiment 1 split by the search task, in terms of (A) accuracy and (B) RT. "Search learned" were triplets that demonstrated learning in the subsequent search task (solid blue lines). "Search non-learned" were triplets that did not demonstrate learning in the subsequent search task (dashed red lines). Error bars reflect +/- 1 within-subject SEM. N = 37. (N of triplets in blue curves = 83; N of triplets in red curves = 102.)

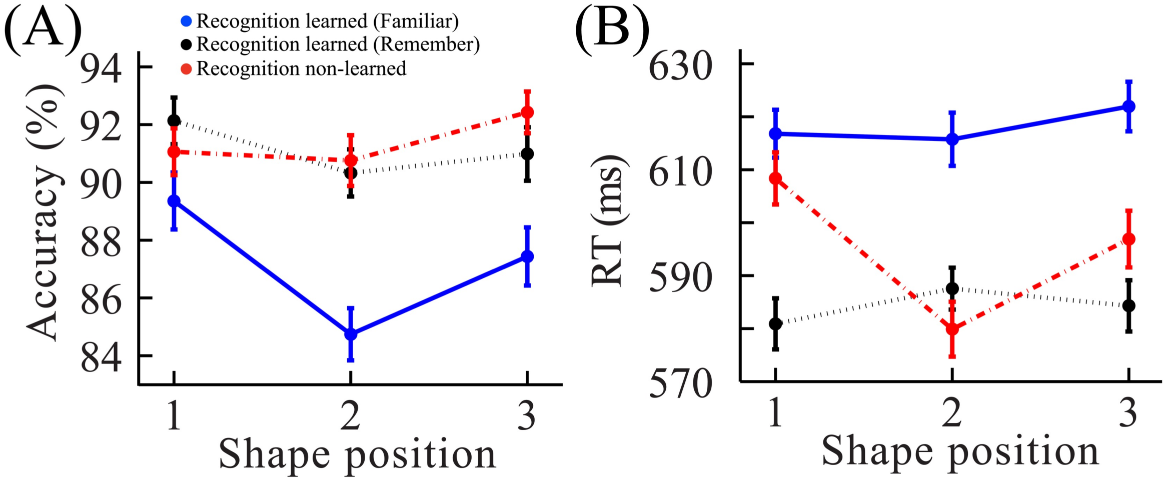

Figure S7 - Detection task results for the full triplet structure in Experiment 2 split by the Familiar/Remember ratings in the recognition task, in terms of (A) accuracy and (B) RT. "Recognition learned (Familiar)" were triplets correctly identified in the subsequent recognition task and given a "Familiar" rating (solid blue lines). "Recognition learned (Remember)" were triplets correctly identified in the subsequent recognition task and given a "Remember" rating (dotted black lines). "Recognition non-learned" were triplets not correctly identified in the subsequent recognition task (dashed red lines). Error bars reflect +/- 1 within-subject SEM. N = 41. (N of triplets in blue curves = 78; N of triplets in black curves = 61; N of triplets in red curves = 66.)

Tables of Means

Chapter 1 - Experiment 1	Shape 1	Shape 2	
Variable	*M*	*M*	*SD*
Search Task RT (ms)	535.0016	519.9835	27.0906
Search Learned RT (ms)	677.8779	684.3018	41.9448
Search Learned Accuracy (%)	84.2453	83.9623	6.5993
Search Non-learned RT (ms)	670.7070	645.7044	45.8544
Search Non-learned Accuracy (%)	85.5696	87.7215	6.5374

Table 1 – Means and within-subject standard deviations for the search task and the detection task as split by the search task in Experiment 1. Note that within-subject SD is calculated according to Loftus and Masson (1994) and involves subtracting a participant's overall mean RT from each condition's mean RT, thus resulting in the same within-subjects SD for each condition.

Chapter 1 - Experiment 2	Shape 1	Shape 2	
Variable	*M*	*M*	*SD*
Recog. Learned RT (ms)	601.0396	603.3661	33.4764
Recog. Learned Acc. (%)	90.5755	87.1942	6.3290
Recog. Non-learned RT (ms)	608.3596	579.8756	34.8195
Recog. Non-learned Acc. (%)	91.0606	90.7576	6.1998
Recog. Learned (Fam.) RT (ms)	616.7955	615.7430	36.8466
Recog. Learned (Fam.) Acc. (%)	89.3590	84.7436	7.0569
Recog. Learned (Rem.) RT (ms)	580.8928	587.5400	28.7532
Recog. Learned (Rem.) Acc. (%)	92.1311	90.3279	5.2048

Table 2 – Means and within-subject standard deviations for the detection task as split by the recognition task (Recog.) in Experiment 2 and as further split by Familiar (Fam.)/Remember (Rem.) ratings in the recognition task. Note that within-subjects SD is calculated according to Loftus and Masson (1994) and involves subtracting a participant's overall mean RT from each condition's mean RT, thus resulting in the same within-subjects SD for each condition.

Chapter 1 - Experiment 3	Shape 1	Shape 2	
Variable	*M*	*M*	*SD*
Search Task (Intact) RT (ms)	441.8604	424.6667	15.1232
Search Task (Foil) RT (ms)	434.9080	422.0179	16.8743
Search Task (Mismatched) RT (ms)	-	429.8590	13.6318
Detect. Learned (Intact) RT (ms)	561.0158	556.5837	44.9820
Detect. Learned (Intact) Acc. (%)	88.7151	88.9944	10.4170
Detect. Learned (Foil) RT (ms)	-	571.1587	43.5238
Detect. Learned (Foil) Acc. (%)	-	90.0000	9.0451
Detect. Learned (Mis.) RT (ms)	-	564.1364	46.8164
Detect. Learned (Mis.) Acc. (%)	-	89.3855	9.4754
Detect. Non-learn. (Intact) RT (ms)	553.5948	542.5806	46.4856
Detect. Non-learn. (Intact) Acc. (%)	87.8981	88.2802	10.4046
Detect. Non-learn. (Foil) RT (ms)	-	549.0857	37.0857
Detect. Non-learn. (Foil) Acc. (%)	-	88.7898	8.9181
Detect. Non-learn. (Mis.) RT (ms)	-	553.7758	37.7127
Detect. Non-learn. (Mis.) Acc. (%)	-	90.5096	8.7767

Table 3 – Means and within-subject standard deviations for the search task and the detection task as split by the search task in Experiment 3. The detection task split by the search task only included the second shapes of the intact and mismatched pairs. Note that within-subjects SD is calculated according to Loftus and Masson (1994) and involves subtracting a participant's overall mean RT from each condition's mean RT, thus resulting in the same within-subjects SD for each condition.

Chapter 1 - Supplemental Data

Variable	*M*	*SD*
Position 2 < 1 Learned RT	3.8019	1.0458
Position 2 < 1 Non-learned RT	2.1772	1.0593
Exp. 1 Detect. Task RT (ms)		
Shape 1	674.5226	22.0731
Shape 2	666.7086	22.0731
Exp. 1 Detect. Task Acc. (%)		
Shape 1	84.8108	3.3529
Shape 2	85.5676	3.3529
Exp. 2 Detect. Task RT (ms)		
Shape 1	603.6415	13.7694
Shape 2	596.3334	13.7694
Exp. 2 Detect. Task Acc. (%)		
Shape 1	90.7317	2.8215
Shape 2	88.3415	2.8215
Exp. 3 Detect. Task RT (ms)		
Shape 1 (Intact)	557.2170	19.6873
Shape 2 (Intact)	550.0484	19.6873
Shape 1 (Foil)	560.7402	18.1728
Shape 2 (Foil)	561.0014	18.1728
Shape 2 (Mismatched)	559.0566	18.7134
Exp. 3 Detect. Task Acc. (%)		
Shape 1 (Intact)	88.3333	3.6446
Shape 2 (Intact)	88.6607	3.6446
Shape 1 (Foil)	89.6726	3.7797
Shape 2 (Foil)	89.4345	2.6689
Shape 2 (Mismatched)	89.9107	3.2004
Exp. 1 Search Task Triplet RT (ms)		
Shape 1	535.0016	33.7906
Shape 2	519.9835	23.4039
Shape 3	502.0861	21.0593
Exp. 1 Detect. Task Triplet RT (ms)		
Shape 1 (Learned)	668.9590	44.6678
Shape 2 (Learned)	672.9014	49.9690
Shape 3 (Learned)	682.8752	39.5317
Exp. 1 Detect. Task Triplet Acc. (%)		
Shape 1 (Learned)	86.2651	6.9939
Shape 2 (Learned)	85.6626	7.3337
Shape 3 (Learned)	86.9880	7.7871
Exp. 1 Detect. Task Triplet RT (ms)		
Shape 1 (Non-learned)	679.5779	50.6901

Shape 2 (Non-learned)	663.6845	49.4496
Shape 3 (Non-learned)	666.2951	44.4885
Exp. 1 Detect. Task Triplet Acc. (%)		
Shape 1 (Non-learned)	83.6274	8.0554
Shape 2 (Non-learned)	85.4902	8.1072
Shape 3 (Non-learned)	85.4902	8.1072
Exp. 2 Detect. Task Triplet RT (ms)		
Shape 1 (Learned Familiar)	616.7955	39.8886
Shape 2 (Learned Familiar)	615.7430	44.4447
Shape 3 (Learned Familiar)	621.9238	41.2576
Exp. 2 Detect. Task Triplet Acc. (%)		
Shape 1 (Learned Familiar)	89.3590	8.7093
Shape 2 (Learned Familiar)	84.7436	7.9623
Shape 3 (Learned Familiar)	87.4359	8.9050
Exp. 2 Detect. Task Triplet RT (ms)		
Shape 1 (Learned Remember)	580.8928	37.6057
Shape 2 (Learned Remember)	587.5400	30.8788
Shape 3 (Learned Remember)	584.2880	37.7941
Exp. 2 Detect. Task Triplet Acc. (%)		
Shape 1 (Learned Remember)	92.1311	6.3053
Shape 2 (Learned Remember)	90.3279	6.3728
Shape 3 (Learned Remember)	90.9836	7.2374
Exp. 2 Detect. Task Triplet RT (ms)		
Shape 1 (Non-learned)	608.3596	39.9798
Shape 2 (Non-learned)	579.8756	42.1087
Shape 3 (Non-learned)	596.9038	43.5140
Exp. 2 Detect. Task Triplet Acc. (%)		
Shape 1 (Non-learned)	91.0606	6.5666
Shape 2 (Non-learned)	90.7576	7.1425
Shape 3 (Non-learned)	92.4242	5.8753

Table 4 – Means and within-subject standard deviations for the Supplemental data of Chapter 1, listed in order of discussion within the Supplemental data section. Note that with the exception of the first two variables, all SD is within-subjects SD, which is calculated according to Loftus and Masson (1994) and involves subtracting a participant's overall mean RT from each condition's mean RT. For situations in which there are only two conditions this results in the same within-subjects SD for each condition.

Chapter 2

This chapter has previously been published as

Alpha-Band EEG Activity in Perceptual Learning

Brett C. Bays[1], Kristina M. Visscher[2], Christophe C. Le Dantec[1], Aaron R. Seitz[1]

[1]University of California, Riverside

[2]University of Alabama at Birmingham

Journal of Vision (2015) 15(10):7, 1-12

Abstract

In studies of perceptual learning (PL), subjects are typically highly trained across many sessions to achieve perceptual benefits on the stimuli in those tasks. There is currently significant debate regarding what sources of brain plasticity underlie these PL based learning improvements. Here we investigate the hypothesis that PL, among other mechanisms, leads to task automaticity, especially in the presence of the trained stimuli. To investigate this hypothesis, we trained participants for 8 sessions to find an oriented target in a field of near-oriented distractors and examined alpha-band activity, which modulates with attention to visual stimuli, as a possible measure of automaticity. Alpha-band activity was acquired via EEG, before and after training, as participants performed the task with trained and untrained stimuli. Results show that participants underwent significant learning in this task (as assessed by thresholds, accuracy and reaction time improvements) and that alpha power increased during the pre-stimulus period and then underwent greater desynchronization at the time of stimulus presentation following training. However, these changes in alpha-band activity were not specific to the trained stimuli with similar patterns of post-training alpha power for trained and untrained stimuli. These data are consistent with the view that participants were more efficient at focusing resources at the time of stimulus presentation and are consistent with a greater automaticity of task performance. These findings have implications for PL, as transfer effects from trained to untrained stimuli may partially depend on differential effort of the individual at the time of stimulus processing.

Introduction

Perceptual learning (PL) is defined as improvement in performance on perceptual tasks after training or experience with stimuli related to those tasks. PL is typically thought to be an implicit process and has been shown to occur in numerous modalities and in a wide variety of animal models, including non-primates, non-human primates, and humans (for reviews see, Fahle, 2005; Ghose, 2004; Gilbert, Sigman, & Crist, 2001; Sagi, 2011; Sasaki, Náñez, & Watanabe, 2012). In the visual modality, PL is often investigated with simple visual features, e.g., orientation (Dobres & Seitz, 2010; Schoups, Vogels, Qian, & Orban, 2001; Yang & Maunsell, 2004), line or dot offset (Fahle, Edelman, & Poggio, 1995; Hung & Seitz, 2014), and motion (Seitz & Watanabe, 2005; Zohary, Celebrini, Britten, & Newsome, 1994), although more complex visual stimuli, such as human faces, have also been successfully used to study PL (Hussain, Sekuler, & Bennett, 2011).

In PL paradigms, behavioral improvements are often task-specific and stimulus-specific. For example, if a key parameter of the stimulus, such as orientation, is changed, then observed behavioral improvements often disappear (Fahle, 2005). This specificity led many early researchers to hypothesize that PL is a result of feed-forward changes occurring in early visual areas (De Valois, 1977; Fiorentini & Berardi, 1980; Ramachandran & Braddick, 1973). Subsequently, neuronal changes in response to PL were reported in early visual areas that are specific to trained features (Bao, Yang, Rios, He, & Engel, 2010; Gilbert, Li, & Piech, 2009; Gilbert et al., 2001; Hua et al., 2010) providing further evidence for feed-forward models of PL. However, under certain training conditions, behavioral improvements do generalize to untrained stimuli (Ahissar & Hochstein, 2004; Deveau, Ozer, & Seitz, 2014; Hung & Seitz, 2014; Xiao et al., 2008; Zhang et al., 2010). These observations have led to an important and ongoing debate as to whether representation or readout changes are responsible for different observations of PL (Ahissar & Hochstein, 2004; Byers & Serences, 2012; Dosher & Lu, 1998; Fahle, 2005; Hung & Seitz, 2014; Jeter, Dosher, Liu, & Lu, 2010; Petrov, Dosher, & Lu, 2005; Pilly, Grossberg, & Seitz, 2010; Xiao et al., 2008; Zhang et al., 2010).

An additional mechanism that may explain at least some component of transfer in PL is the extent to which participants are able to focus resources during task performance after training. This idea of task focus is often not well defined and typically described with terms such as attentiveness, alertness, vigilance, etc., and each have nuanced meanings that sometimes depend on the subfield and can be overlapping. Here we use the terms *attention* to refer to up and down regulation of task resources (Posner & Petersen, 1990) and *automaticity* to describe the extent to which attention can be regulated with minimal executive control.

The concept of automaticity has been studied for decades yet remains relatively difficult to define. For example, Posner and Snyder (1975) define automatic processes as those which do not rely on conscious attention, Jacoby (1991) defines automaticity as processing that “occurs as a passive consequence of stimulation, is not necessarily accompanied by awareness, and requires neither intention nor processing capacity,” while Logan (1992) argues that automaticity is “processing that involves a different way of attending.” To address changes of task-processing after PL, here we offer an operational definition of automaticity: when a task is more automatic, it can be performed with more efficient use of resources and less attention is required to perform the task to maintain, or achieve superior, task performance. This definition is not meant to be authoritative but is one that fits into many of these theories of attentional and automatic processes. While automaticity has been described conceptually, there is a question of how best to measure it. A difficulty is that behavioral measures of automaticity have the potential to disrupt the flow of the learned task. For this reason we chose to measure a possible correlate of automaticity, namely alpha-band EEG activity.

The alpha bandwidth found within the electroencephalogram (EEG) refers to the set of frequencies ranging approximately from 8-12 Hz. This bandwidth was first observed and studied by Hans Berger (Berger, 1929), who noted that the amplitude of activity in these frequencies increased significantly when human subjects sat quietly with their eyes closed. A large body of evidence points towards thalamo-cortico connections as the source of alpha oscillations (for a review see Hughes & Crunelli, 2005) although evidence also exists for intracortical sources (Bollimunta, Chen, Schroeder, & Ding, 2008; Jones, Pritchett, Stufflebeam, Hämäläinen, & Moore, 2007; Lopes da Silva, van Lierop, Schrijer, & Storm van Leeuwen, 1973; Ronnqvist, McAllister, Woodhall, Stanford, & Hall, 2013; Silva, Amitai, & Connors, 1991). Alpha power is most prominent in occipital channels of the EEG but can also be found across other areas of the scalp (e.g., Rolandic alpha rhythms found over sensory-motor areas). These alpha oscillations have been shown to vary significantly based on a participant's cognitive state (Berger, 1929; Klimesch, 2012), and level of alpha power during a range of tasks can predict performance (Hanslmayr, Gross, Klimesch, & Shapiro, 2011; Payne & Sekuler, 2014).

Importantly for the current study, alpha power is generally found to be reduced with greater effort and attention to visual tasks (Bollimunta et al., 2008; Ergenoglu et al., 2004; Hanslmayr et al., 2007; Nenert, Viswanathan, Dubuc, & Visscher, 2012; Snyder & Foxe, 2010; Vaden, Hutcheson, McCollum, Kentros, & Visscher, 2012). For example, Hanslmayr et al. (2007) found that participants with lower overall alpha power better discriminated brief visual stimuli, Snyder and Foxe (2010) found that alpha power modulates depending on which features of visual stimuli were being attended, and Chaumon and Busch (2014) found that occipital alpha power before high-contrast visual detection trials correlated negatively with performance. Results such as these provide evidence for the "inhibition" hypothesis of alpha oscillations, which states that strong alpha power reflects top-down inhibition on processes which are not being used for a task, whereas alpha power is suppressed for processes which are needed for a task (Klimesch, Sauseng, & Hanslmayr, 2007; Sigala, Haufe, Roy, Dinse, & Ritter, 2014). While the link between alpha power and automaticity is not fully established, alpha power is modulated by precisely the elements that define the automaticity of the task: Less attention is required of automatic tasks, and less attention leads to increases in alpha power (Jensen & Mazaheri, 2010). Other task conditions can modulate alpha power --for example holding items in working memory can increase alpha power (Jensen, Gelfand, Kounios, & Lisman, 2002), though it has been argued that this effect is in fact driven by decreased attention to anticipated visual distraction (Bonnefond & Jensen, 2012). However, when stimulus parameters and task demands are otherwise held constant, most current interpretations show changes in alpha power during a visual task as reflecting changes in the level of attention being directed to a stimulus (Foxe & Snyder, 2011; Jensen & Mazaheri, 2010; Jensen, Spaak, & Zumer, 2014; Lange, Keil, Schnitzler, van Dijk, & Weisz, 2014; Palva & Palva, 2011). Thus, for the purposes of this paper, we chose to examine how alpha power is modulated following perceptual learning.

In the present study, we examine how psychophysical and electrophysiological measures change as participants gain proficiency in a visual search task. We find that there are indeed substantial changes in how alpha band activity is regulated after learning (with higher alpha in the pre-stimulus period followed by greater alpha desynchronization during stimulus processing) and suggest that these may provide a basis for understanding aspects of stimulus transfer after PL.

Methods

Participants

Eight undergraduates at the University of California, Riverside (age range 19-25 years) were included in this study. Inclusion required completion of all experimental procedures without technical errors, such as improperly affixed electrodes, or excessive muscular noise in the EEG. Participants were paid $10 an hour for their participation, gave written informed consent as approved by the Human Research Review Board, and had normal or corrected-to-normal vision.

Display Apparatus

An Apple Mac Mini (Apple, Inc., Cupertino, CA, USA) running OSX 10.5.6 controlled the experiment. The stimuli were displayed on a 24” wide Sony Trinitron (Sony Corp., Tokyo, Japan) CRT monitor with a resolution of 1600x1200 pixels and a refresh rate of 100 Hz. Participants sat 50-55” from the screen with their heads restrained by a chinrest. The range in distance is due to individual differences in posture since a chinrest was used without a forehead restraint. An EyeLink 1000 eyetracking system (SR Research, Ltd., Mississauga, ON, Canada) was used with custom software to ensure that stimuli were only displayed while participants fixated on the center of the screen. Stimuli were created and controlled by custom code written in Matlab (The Mathworks, Inc., Natick, MA, USA), using the Psychophysics Toolbox (Brainard, 1997; Kleiner, Brainard, & Pelli, 2007). Mediating the connection between the monitor, the computer, and the EEG system was a Datapixx processor (Vpixx Technologies, Inc., Saint-Bruno, QC, Canada) which enables a 16-bit DAC, allowing for a 256-fold increase in the display’s possible contrast values, and which provides monitor-refresh-locked stimulus presentations for accurate timing of stimuli and response triggers.

PL Training

The PL training took place over eight days and began one day after the pre-test (Figure 11). On each day, participants performed a visual search task for approximately one hour (Figure 12). The stimuli in the task comprised white or black lines (0.1ºx1º; 95 cd/m^2 and 5.5 cd/m^2, respectively) that were presented on a gray background (40 cd/m^2).

On each trial, participants first fixated on a centrally presented red dot for 1100-2000ms (determined pseudorandomly). The trial only proceeded if the participant maintained fixation for this period of time. After fixation, a search display was presented for 100ms, followed by a blank gray response screen that was presented for up to 2000ms during which the participant made a response, and a further 500ms intertrial interval (ITI).

The participant's task in each trial was to find a target line within a set of distractor lines in the search display and report with a keypress ("1" for white and "2" for black) during the response period whether the line was white or black. The target line was defined by its orientation, which could be either 45º or 135º (counterbalanced across participants), and was randomly assigned its color for each trial. The orientations of the distractors were determined by a staircase wherein the distractor lines were offset from the target line by a number of degrees between 0-90º, which we refer to as θ. After every 24 trials, θ was adjusted according to the participant's performance such that if the average performance for the previous 24 trials was above 80% correct then θ was decreased, making the task more difficult, and if the average performance was lower than 70% correct then θ was increased, making the task easier (Le Dantec, Melton, & Seitz, 2012). Each training session took place on a separate day, consisted of 1200 trials, and lasted approximately one hour. The 1200 trials of each session were split into eight blocks with a short participant-controlled break between each block. In addition, on the first day of the experiment there was a familiarization session in which participants were instructed on the task and ran 20 practice trials with visual feedback.

Pre- and Post-Testing

One day before training and one day after training, pre- and post-test sessions were conducted. These sessions were similar to the training sessions with three main differences. First, EEG recordings were collected during these test sessions. Second, the target line could either be of the trained orientation or untrained orientation, run in separate, interleaved blocks so that the participants knew which orientation to search for in each block of trials. Third, instead of a staircase determining θ, the offset of the distractor lines was set to 30º for all pre-test trials and 15º for all post-test trials. This was done to avoid stimulus-driven differences in processing between orientations while keeping stimuli close to threshold. An examination of the average beginning and ending θ thresholds in the training sessions (Figure 14, in Results below) confirm that 30º and 15º were very near the obtained average thresholds.

Each session consisted of 1200 trials, lasted approximately 1.5 hours (plus additional time for EEG set-up), and was split into eight blocks with a 30 second break between each block and a 3-minute break half-way through the session in which participants were required to get up and stretch. Each of the eight blocks consisted of 150 trials and each block alternated between containing targets of a trained orientation or targets of an untrained orientation, for a total of 600 trials in each condition.

Electroencephalography (EEG)

EEG was recorded using 128-active Ag/AgCl electrodes (ActiveTwo system, BioSemi, Inc., Amsterdam, Netherlands) at a rate of 1024 Hz. All electrodes were mounted in an elastic ActiveTwo cap according to the BioSemi layout and labeled according to the

10/20 system (Oostenveld & Praamstra, 2001; Figure 13A). Given that alpha power is most prominent in occipital channels, and that we were analyzing a visual task, a bilateral selection of nine occipital and parietal electrodes was analyzed, corresponding approximately to sites Oz, O1, O2, PO7, PO8, PO9, PO10, P3, and P4 (Figure 13A, highlighted regions). The selection of electrode sites to analyze was based on post hoc analyses of where the greatest overall areas of alpha power occurred in the recorded EEGs. Horizontal (HEOG) and vertical (VEOG) electrooculograms were recorded, using additional electrodes affixed with adhesive disks at, respectively, the outer right and left canthi (HEOG) and below the right and left eye (VEOG). Conductive gel was applied to maintain the contact between the electrodes and the scalp (Signa Gel, Parker Laboratories, Inc., Fairfield, NJ, USA).

After recording, EEG data were initially processed using EMSE Suite 5.4 (Source Signal Imaging, Inc., San Diego, CA, USA). The data were first referenced to the average of all active electrodes (Keil et al., 2014) and filtered using zero phase-shift Butterworth high- and low-pass filters with half-amplitude cutoffs of 0.01 Hz and 100 Hz, respectively. Ocular artifacts were corrected using a proprietary algorithm of the EMSE Suite which is designed to remove eyeblink noise without removing the underlying signal (Pflieger, 2001).

After processing using EMSE Suite software, time-frequency analysis was conducted using Matlab and the FieldTrip toolbox (Oostenveld, Fries, Maris, & Schoffelen, 2011). The data were segmented into six-second periods centered on each stimulus presentation and convolved with a Morlet wavelet. The frequencies of interest extracted were 2-20Hz and each wavelet had a width of seven cycles.

In order to prevent individual differences in raw alpha power (which can vary dramatically between individuals) from driving the results, all alpha power values were normalized to a [0-1] scale before being analyzed. For each subject, the minimum and maximum alpha power value was calculated. The minimum value was then subtracted from all alpha values and the result divided by the difference between the maximum and minimum values (i.e., the range). This transformed each subject's alpha values such that the minimum value became 0 and the maximum value became 1, with all other values falling within the [0-1] range.

EEG data were analyzed primarily by comparing pre-test alpha power vs. post-test alpha power. Within the pre- and post-tests, two time periods of interest were defined – a *pre-stimulus period,* 1000ms preceding the stimulus onset in each trial for each participant, and the stimulus processing period, 250-500ms following the stimulus onset in each trial for each participant (Figure 13B). These two periods were defined post hoc based on the length of pre-stimulus fixation and on the average timing of alpha desynchronization ("desynchronization", in this usage, describing a decrease in overall alpha power following stimulus presentation). Statistical tests to determine differences between the pre-test and post-test values within these periods were performed by calculating the mean power during the period of interest in the pre- and post-tests for each participant and conducting either repeated measures factorial ANOVA or paired-samples t tests between those mean values, depending on the analysis of interest.

Results

Behavioral Results

Behavioral results, in the form of orientation thresholds, response accuracy, and reaction times (RTs), all demonstrate classical evidence of PL. Orientation thresholds (θ) decreased as a function of training (Figure 14; effect of day: $F(7,56)=5.88$, $p=0.000038$, $\eta^2=0.42$) and a planned t test between θ on the first and last day of training (mean of 28.44° and 11.96°, respectively) revealed a significant learning effect ($t(14)=5.59$, $p=0.000067$, Cohen's $d=2.98$). Accuracy improved overall as a function of training from the pre-test to the post-test (Figure 15A; main effect of test session: $F(1,7)=11.02$, $p=0.013$, $\eta^2=0.18$), however this was largely due to the greater increase in accuracy for trained targets as compared to untrained targets (Target X Session interaction: $F(1,7)=76.37$, $p=0.0001$, $\eta^2=0.17$). Similarly, reaction times show an overall decrease in latency as a function of training from the pre-test to the post-test (Figure 15B; main effect of test session: $F(1,7)=10.78$, $p=0.013$, $\eta^2=0.13$), and also showed a significant interaction between trained/untrained targets and testing session, where the trained targets showed a greater decrease in RT than the untrained targets (Target X Session interaction: $F(1,7)=13.29$, $p=0.0082$, $\eta^2=0.024$). These data show that learning is, at least in part, specific to the trained orientation.

EEG Data

To evaluate how alpha changed with PL, we analyzed alpha power across all trials of the pre-test vs. the post-test. Our first observation is that during the pre-stimulus period (1000ms prior to stimulus onset; see Figure 13B) there is significantly more alpha power in the post-test than in the pre-test ($t(7)=3.97$, $p=0.0054$, Cohen's $d=1.40$; mean normalized alpha power values of 0.67 and 0.39, respectively; Figure 16A). Topographic maps for the pre-stimulus periods in the pre-test and post-test can be seen in Figure 16B. Lighter regions represent more alpha power and darker regions represent less alpha power.

Once the stimulus appears there is a notable reduction of alpha (often referred to as alpha desynchronization) with a greater desynchronization of alpha in the post-test compared to in the pre-test. (Note here there are actually two phases of alpha desynchronization - one occurring around 500ms before stimulus onset that corresponds with the onset of the fixation period and another at 0ms when the stimulus array appeared. We refer to the post-stimulus desynchronization in subsequent usage.) Clarifying this effect, we examined whether the extent of alpha desynchronization (1000ms pre-stimulus period minus stimulus processing period - 250-500ms) significantly differed between the pre-/post-test. Here a 2 (Test session) X 2 (Trial period) ANOVA showed a significant Session X Period interaction ($F(1,7)=13.36$, $p=0.0081$, $\eta^2=0.044$), signifying that the amount of alpha desynchronization at the time of stimulus processing was greater after PL. Notably, alpha was also slightly, but significantly, greater during the stimulus processing period (250-500ms after stimulus onset; see Figure 13B) in the post-test than in the pre-test ($t(7)=2.53$, $p=0.039$, Cohen's $d=0.90$; mean normalized alpha power values of 0.13

and 0.066, respectively). Topographic maps for the stimulus processing periods of the pre-test and post-test can be seen in Figure 16B.

Together, these results are consistent with the view that subjects learn to allocate their attentional resources more effectively after training, exerting fewer attentional resources during the pre-stimulus period, as indicated by the greater pre-stimulus period alpha power, and then appropriately allocating attention at the time of stimulus onset, as indicated by the strong alpha desynchronization. Further, the finding that alpha power was greater after training during the stimulus processing period is consistent with our view of automaticity, that after training participants could perform a more difficult task with less focus.

A key question regards the extent to which changes in alpha power between the pre-test and the post-test reflect the specificity of the perceptual learning. To test this, we compared alpha power between trials with trained vs. untrained targets in the post-test (Figure 17). Within the pre-stimulus period there is a notable lack of difference between the trained and untrained conditions ($t(7)=0.23$, $p=0.82$, Cohen's $d=0.083$; mean normalized alpha power values of 0.62 and 0.63, respectively) without a significant change in alpha desynchronization ($F(1,7)=1.22$, $p=0.31$, $\eta^2=0.00077$. However, there was a trend for slightly greater alpha power in the trained compared to untrained condition in the stimulus processing period ($t(7)=1.93$, $p=0.095$, Cohen's $d=0.68$; mean normalized alpha power values of 0.11 and 0.086, respectively). Of note, while there are apparent differences in alpha between the trained and untrained conditions growing in the 500-1000 time period, these are during the response period and are likely related to the different reaction times observed between these conditions. As a whole, these results suggest that the observed changes in alpha with learning are largely independent of the specificity found in the behavioral results.

While it is clear that changes in alpha EEG activity occurred between the pre- and post-testing sessions, an important question is whether these are correlated with task performance. An examination of the correlation between alpha power and individual trials could potentially provide additional insight into these results. To this effect, the alpha power in the pre-stimulus period, the stimulus processing period and the level of alpha desynchronization were calculated for each trial and then correlated with reaction times and accuracy. In no case, whether in individual participants or combined across participants, did we find an $r^2>.05$, or any correlation with a $p < 0.05$. Likewise we also examined whether there were correlations with changes in training-related alpha power (pre-stimulus, desynchronization and stimulus processing) and changes in reaction time or threshold and again found no significant correlations. We further address these correlational analyses in the discussion.

Discussion

Here we examined alpha power in EEG recordings and its relationship to PL. Behavioral results (Figures 14, 15) show that PL occurred over the training period with improved orientation discrimination thresholds and superior accuracy and lower response latencies for the trained compared to the untrained target orientations. After training, EEG alpha power during the pre-stimulus period increased, and desynchronization during the stimulus-processing period also increased. However, while the change in alpha power with PL was dramatic and strongly significant, these changes did not appear to reflect a stimulus-specific component of learning in this task. We suggest that these results are consistent with the hypothesis of an increase of automaticity with learning, and that this increase is at least partially stimulus independent.

Changes in alpha power have been shown to reflect modulations in the level of attention to a visual stimulus (for example, Bollimunta et al., 2008; Ergenoglu et al., 2004; Hanslmayr et al., 2007; Nenert et al., 2012; Snyder & Foxe, 2010; Vaden et al., 2012). It is debatable whether these attentional modulations are driven by active suppression of visual inputs (Kelly, Lalor, Reilly, & Foxe, 2006), processes such as vigilance (Klimesch, 1999), or some combination. Regardless, changes in alpha power relate to attentional modulations of visual stimuli and help regulate transfer of information during visual processing (Romei, Gross, & Thut, 2010; Thut, Nietzel, Brandt, & Pascual-Leone, 2006). The extensive previous literature examining modulations of occipital alpha power thus suggests that alpha power can be interpreted in the context of attention to vision and automaticity, as defined in the Introduction.

Our strongest results were that training resulted in more alpha power during the pre-stimulus period and larger alpha desychronization after stimulus onset. The increase in desynchronization after training fits in well with the inhibition theory of alpha (Klimesch et al., 2007; Payne & Sekuler, 2014; Sigala et al., 2014) – after training, fewer resources are needed for the overall task during the pre-stimulus period but as soon as resources are needed to perform the most demanding portion of the task, alpha levels are lowered, thereby releasing the resources from inhibition. Because participants achieve superior task performance despite apparently allocating fewer attentional resources to the task, this result suggests that the task became more automatic after training, though the results cannot be conclusively linked to automaticity. While other models can be considered to explain the EEG data, for example, boredom with the task following training, such models are less consistent with the larger alpha desychronization observed. This observation seems most consistent with a more efficient deployment of resources following training.

While it is natural to assume that changes in alpha should be related to task performance, there are a number of reasons to expect that direct correlations may not be in evidence. First off, there were only 8 participants and numerous factors (differences in wakefulness, use of caffeine or other drugs, differences in impedance between the sessions, etc.) could impact how individual magnitudes of change of alpha may not be linearly related to changes in performance levels, especially across sessions. There are also possible cognitive explanations that could have given rise to a lack of correlations. For example, if participants actively regulate (whether implicitly or explicitly) task related resources then changes in alpha power with training would reflect how much alpha power the system can tolerate during task performance. This would mean that accuracy, reaction time, or threshold would be kept relatively constant while alpha fluctuates, leading to no expected correlation. A lack of correlations of alpha power with performance and learning may be consistent with a subject's being able to regulate the amount of alpha that can be "tolerated" based upon their skill at the task. Further research will be required to substantiate this postulate, but in any event the lack of correlations found between alpha power and performance is not evidence for or against our interpretation.

We found that participants showed both increased pre-stimulus alpha power and increased stimulus processing period desynchronization after training. The pattern of our results supports a model where automaticity leads to efficient allocation of attentional resources through, as noted above, keeping the level of resource use relatively low until the moment when it is needed, at which time there is strong alpha desynchronization. Of course, there are other possible sets of results that would have been consistent with changing allocation of resources. For example, suppose the finding had been that after training, pre-stimulus power and post-stimulus desynchronization were weaker than before training, instead of stronger as we actually found. The level of post-stimulus desynchronization has been thought to reflect the recruitment of attentional resources to process a stimulus (Van Winsum, Sergeant, & Geuze, 1984). Thus, weaker desynchronization after training would have indicated that subjects could perform the task while recruiting fewer visual cortical resources on a trial-by-trial basis, consistent with greater task automaticity. However, the structure of this hypothetical automaticity is of a different kind than what we observed. We did *not* find that there were fewer resources used on a trial by trial manner during stimulus presentation (as measured by desynchronization or power during the stimulus processing period). Instead we found stronger alpha power during the pre-stimulus period in the post-test than the pre-test even though the task required more precision of orientation processing in the post-test than in the pre-test. These data are consistent with a model of automaticity in which, following training, subjects could perform the task using fewer visual cortical resources to prepare for trials, while the trial-to-trial resource use was unchanged.

However, there is also the possibility the changes in alpha are epiphenomenal and are unrelated to perceptual learning. The issue of causality is one that is difficult to address, and in fact, even if significant correlations with behavior had been found then this still would be insufficient to prove that changes in alpha were causal or even directly related to perceptual learning. While we thus realize that some aspects of the current results are preliminary, in that the causal relations between changes in alpha and perceptual learning are not determined, they do raise important issues about the relationship of alpha power to perceptual learning that have not previously been raised in the literature. The benefit of using neural measures like EEG is that we can use them in this way to help us better understand the temporal profile of processes associated with constructs like automaticity. Given the current debate in the field about the myriad mechanisms involved in perceptual learning, we believe that the data reported help provide additional understanding of what changes in the brain occur after extensive training, although readers may come to different conclusions than we do. Further research will be required to gain more understanding of how changes in alpha and the regulation of alpha may be related to components of behavioral changes found in perceptual learning.

An interesting question is to what extent changes in alpha may also represent specific components of PL. For example, one may expect for the trained orientation that participants would be even more automatic in their deployment of resources (especially given that trained and untrained orientations were given in separate blocks). Consistent with this, we did find a trend for stronger alpha power during the stimulus processing period for trained stimuli, though the magnitude of this effect is small compared to the pre- vs. post-test changes in alpha that were observed. The different reaction times of these trained vs. untrained conditions may also contribute to this effect. Furthermore other aspects of perceptual learning may also explain some aspects of the transfer of the alpha effect to untrained orientations. Comparison of the accuracy and RT performance for untrained stimuli in pre-test vs. post-test shows that, despite the fact that θ changed from 30 degrees in the pre-test to 15 degrees in the post-test, accuracy and RT were maintained. This substantial amount of non-specific learning could reflect learning of other aspects of the stimulus array such as the characeristics of the background elements (Le Dantec et al., 2012), specific locations of training (Le Dantec & Seitz, 2012) or other factors related to the task. These and other factors may also be related to changes in alpha power and future research will be required to more fully describe how different compents of learning contribute to the changes in alpha power observed here.

As a whole, our results enrich the current discussion in the literature regarding the mechanisms that underlie PL. Instead of the classic view that PL is a unitary process reflecting changes in processing in low-level perceptual areas (Fahle, 2004; Fiorentini & Berardi, 1980; Gilbert et al., 2001) the field is increasingly recognizing that PL involves plasticity in myriad brain processes related to the trained task and stimuli (Watanabe & Sasaki, 2015). For example PL has been observed in both early (Schoups et al., 2001) and late processing stages (Law & Gold, 2008) and can be at least partially explained by changes in decision processes (Dosher, Jeter, Liu, & Lu, 2013). In fact small changes in training procedures can give rise to substantial changes in the behavioral characteristics of PL and likely the underlying distribution of learning across the brain (Hung & Seitz, 2014). Our results add to this literature and are consistent with models of PL which posit that attention is a contributing factor (Byers & Serences, 2012) and suggest that a component of transfer found in studies of PL may depend on an individual's brain state at the time of stimulus processing. While more research will be required to clarify the links between alpha EEG, automaticity and PL, the present results suggest that alpha EEG is a useful window into an individual's level of attention during task performance and may help us better understand what is learned during PL.

References

Ahissar, M., & Hochstein, S. (2004). The reverse hierarchy theory of visual perceptual learning. *Trends in Cognitive Sciences*, *8*(10), 457–64. doi:10.1016/j.tics.2004.08.011

Bao, M., Yang, L., Rios, C., He, B., & Engel, S. A. (2010). Perceptual learning increases the strength of the earliest signals in visual cortex. *Journal of Neuroscience*, *30*(45), 15080–15084.

Berger, H. (1929). Über das elektrenkephalogramm des menschen. *Archiv Für Psychiatrie*, *87*(1), 527–570.

Bollimunta, A., Chen, Y., Schroeder, C. E., & Ding, M. (2008). Neuronal mechanisms of cortical alpha oscillations in awake-behaving macaques. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *28*(40), 9976–9988. doi:10.1523/JNEUROSCI.2699-08.2008

Bonnefond, M., & Jensen, O. (2012). Alpha oscillations serve to protect working memory maintenance against anticipated distracters. *Current Biology*, *22*(20), 1969–1974. doi:10.1016/j.cub.2012.08.029

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*, 433–436.

Byers, A., & Serences, J. T. (2012). Exploring the relationship between perceptual learning and top-down attentional control. *Vision Research*, *74*, 30–39. doi:10.1016/j.visres.2012.07.008

Chaumon, M., & Busch, N. (2014). Prestimulus Neural Oscillations Inhibit Visual Perception via Modulation of Response Gain. *Journal of Cognitive Neuroscience*, *26*(11), 2514–2529. doi:10.1162/jocn_a_00653

De Valois, K. (1977). Spatial frequency adaptation can enhance contrast sensitivity. *Vision Research*, *17*(9), 1057–1065.

Deveau, J., Ozer, D. J., & Seitz, A. R. (2014). Improved vision and on-field performance in baseball through perceptual learning. *Current Biology*, *24*(4), R146–R147. doi:10.1016/j.cub.2014.01.004

Dobres, J., & Seitz, A. (2010). Perceptual learning of oriented gratings as revealed by classification images. *Journal of Vision*, *10*(13), 8–11. doi:10.1167/10.13.8.Introduction

Dosher, B. A., Jeter, P., Liu, J., & Lu, Z.-L. (2013). An integrated reweighting theory of perceptual learning. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(33), 13678–13683. doi:10.1073/pnas.1312552110

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 of the United States of America*, *95*(23), 13988–13993.

Ergenoglu, T., Demiralp, T., Bayraktaroglu, Z., Ergen, M., Beydagi, H., & Uresin, Y. (2004). Alpha rhythm of the EEG modulates visual detection performance in humans. *Cognitive Brain Research*, *20*(3), 376–383. doi:10.1016/j.cogbrainres.2004.03.009

Fahle, M. (2004). Perceptual learning: a case for early selection. *Journal of Vision*, *4*(10), 879–890. doi:10.1167/4.10.4

Fahle, M. (2005). Perceptual learning: specificity versus generalization. *Current Opinion in Neurobiology*, *15*(2), 154–160. doi:10.1016/j.conb.2005.03.010

Fahle, M., Edelman, S., & Poggio, T. (1995). Fast perceptual learning in hyperacuity. *Vision Research*, *35*(21), 3003–3013.

Fiorentini, A., & Berardi, N. (1980). Perceptual learning specific for orientation and spatial frequency. *Nature*, *287*(5777), 43–44.

Foxe, J. J., & Snyder, A. C. (2011). The role of alpha-band brain oscillations as a sensory suppression mechanism during selective attention. *Frontiers in Psychology*, *2*(154), 1–13. doi:10.3389/fpsyg.2011.00154

Ghose, G. M. (2004). Learning in mammalian sensory cortex. *Current Opinion in Neurobiology*, *14*(4), 513–8. doi:10.1016/j.conb.2004.07.003

Gilbert, C. D., Li, W., & Piech, V. (2009). Perceptual learning and adult cortical plasticity. *Journal of Physiology*, *587*(12), 2743–2751.

Gilbert, C. D., Sigman, M., & Crist, R. E. (2001). The Neural Basis of Perceptual Learning. *Neuron*, *31*(5), 681–697.

Hanslmayr, S., Aslan, A., Staudigl, T., Klimesch, W., Herrmann, C. S., & Bäuml, K.-H. (2007). Prestimulus oscillations predict visual perception performance between and within subjects. *NeuroImage*, *37*(4), 1465–1473. doi:10.1016/j.neuroimage.2007.07.011

Hanslmayr, S., Gross, J., Klimesch, W., & Shapiro, K. L. (2011). The role of alpha oscillations in temporal attention. *Brain Research Reviews*, *67*(1-2), 331–343. doi:10.1016/j.brainresrev.2011.04.002

Hua, T., Bao, P., Huang, C.-B., Wang, Z., Xu, J., Zhou, Y., & Lu, Z.-L. (2010). Perceptual Learning Improves Contrast Sensitivity of V1 Neurons in Cats. *Current Biology*, *20*, 887–894.

Hughes, S. W., & Crunelli, V. (2005). Thalamic mechanisms of EEG alpha rhythms and their pathological implications. *The Neuroscientist : A Review Journal Bringing Neurobiology, Neurology and Psychiatry*, *11*(4), 357–372. doi:10.1177/1073858405277450

Hung, S.-C., & Seitz, A. R. (2014). Prolonged training at threshold promotes robust retinotopic specificity in perceptual learning. *The Journal of Neuroscience*, *34*(25), 8423–8431. doi:10.1523/JNEUROSCI.0745-14.2014

Hussain, Z., Sekuler, A. B., & Bennett, P. J. (2011). Superior identification of familiar visual patterns a year after learning. *Psychological Science*, *22*(6), 724–730. doi:10.1177/0956797611409591

Jacoby, L. L. (1991). A process dissociation framework: Separating automatic from intentional uses of memory. *Journal of Memory and Language*, *30*, 513–541.

Jensen, O., Gelfand, J., Kounios, J., & Lisman, J. E. (2002). Oscillations in the alpha band (9-12 Hz) increase with memory load during retention in a short-term memory task. *Cerebral Cortex*, *12*(8), 877–882. doi:10.1093/cercor/12.8.877

Jensen, O., & Mazaheri, A. (2010). Shaping functional architecture by oscillatory alpha activity: gating by inhibition. *Frontiers in Human Neuroscience*, *4*(186), 1–8. doi:10.3389/fnhum.2010.00186

Jensen, O., Spaak, E., & Zumer, J. M. (2014). Human brain oscillations : from physiological mechanisms to analysis and cognition. In S. Supek & C. J. Aine (Eds.), *Magnetoencephalography. From Signals to Dynamic Cortical Networks* (pp. 359–404). Springer Berlin.

Jeter, P. E., Dosher, B. A., Liu, S.-H., & Lu, Z.-L. (2010). Specificity of perceptual learning increases with increased training. *Vision Research*, *50*(19), 1928–1940. doi:10.1016/j.visres.2010.06.016

Jones, S. R., Pritchett, D. L., Stufflebeam, S. M., Hämäläinen, M., & Moore, C. I. (2007). Neural correlates of tactile detection: a combined magnetoencephalography and biophysically based computational modeling study. *The Journal of Neuroscience*, *27*(40), 10751–10764. doi:10.1523/JNEUROSCI.0482-07.2007

Keil, A., Debener, S., Gratton, G., Junghöfer, M., Kappenman, E. S., Luck, S. J., … Yee, C. M. (2014). Committee report: publication guidelines and recommendations for studies using electroencephalography and magnetoencephalography. *Psychophysiology*, *51*(1), 1–21. doi:10.1111/psyp.12147

Kelly, S. P., Lalor, E. C., Reilly, R. B., & Foxe, J. J. (2006). Increases in alpha oscillatory power reflect an active retinotopic mechanism for distracter suppression during sustained visuospatial attention. *Journal of Neurophysiology*, *95*(6), 3844–3851. doi:10.1152/jn.01234.2005

Kleiner, M., Brainard, D. H., & Pelli, D. G. (2007). What's new in Psychtoolbox-3? *Perception*, *36*(ECVP Abstract Supplement).

Klimesch, W. (1999). EEG alpha and theta oscillations reflect cognitive and memory performance: a review and analysis. *Brain Research Reviews*, *29*(2-3), 169–195.

Klimesch, W. (2012). Alpha-band oscillations, attention, and controlled access to stored information. *Trends in Cognitive Sciences*, *16*(12), 606–617. doi:10.1016/j.tics.2012.10.007

Klimesch, W., Sauseng, P., & Hanslmayr, S. (2007). EEG alpha oscillations: the inhibition-timing hypothesis. *Brain Research Reviews*, *53*(1), 63–88. doi:10.1016/j.brainresrev.2006.06.003

Lange, J., Keil, J., Schnitzler, A., van Dijk, H., & Weisz, N. (2014). The role of alpha oscillations for illusory perception. *Behavioural Brain Research*, *271*, 294–301. doi:10.1016/j.bbr.2014.06.015

Law, C.-T., & Gold, J. I. (2008). Neural correlates of perceptual learning in a sensory-motor, but not a sensory, cortical area. *Nature Neuroscience*, *11*(4), 505–513. doi:10.1038/nn2070

Le Dantec, C. C., Melton, E. E., & Seitz, A. R. (2012). A triple dissociation between learning of target , distractors , and spatial contexts. *Journal of Vision*, *12*(2), 1–12. doi:10.1167/12.2.5.Introduction

Le Dantec, C. C., & Seitz, A. R. (2012). High resolution, high capacity, spatial specificity in perceptual learning. *Frontiers in Psychology*, *3*(222), 1–7. doi:10.3389/fpsyg.2012.00222

Logan, G. D. (1992). Attention and preattention in theories of automaticity. *American Journal of Psychology*, *105*(2), 317–339.

Lopes da Silva, F. H., van Lierop, T. H. M. T., Schrijer, C. F., & Storm van Leeuwen, W. (1973). Organization of thalamic and cortical alpha rhythms: spectra and coherences. *Electroencephalography and Clinical Neurophysiology*, *35*, 627–639.

Nenert, R., Viswanathan, S., Dubuc, D. M., & Visscher, K. M. (2012). Modulations of ongoing alpha oscillations predict successful short-term visual memory encoding. *Frontiers in Human Neuroscience*, *6*(May), 1–11. doi:10.3389/fnhum.2012.00127

Oostenveld, R., Fries, P., Maris, E., & Schoffelen, J.-M. (2011). FieldTrip: Open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. *Computational Intelligence and Neuroscience*, *2011*(156869), 1–9. doi:10.1155/2011/156869

Oostenveld, R., & Praamstra, P. (2001). The five percent electrode system for high-resolution EEG and ERP measurements. *Clinical Neurophysiology : Official Journal of the International Federation of Clinical Neurophysiology*, *112*(4), 713–719.

Palva, S., & Palva, J. M. (2011). Functional roles of alpha-band phase synchronization in local and large-scale cortical networks. *Frontiers in Psychology*, *2*(204), 1–15. doi:10.3389/fpsyg.2011.00204

Payne, L., & Sekuler, R. (2014). The Importance of Ignoring: Alpha oscillations protect selectivity. *Current Directions in Psychological Science*, *23*(3), 171–177. doi:10.1177/0963721414529145

Petrov, A. A., Dosher, B. A., & Lu, Z.-L. (2005). The dynamics of perceptual learning: an incremental reweighting model. *Psychological Review*, *112*(4), 715–743. doi:10.1037/0033-295X.112.4.715

Pflieger, M. (2001). Theory of a spatial filter for removing ocular artifacts with preservation of EEG. *EMSE Workshop*, 7–8.

Pilly, P. K., Grossberg, S., & Seitz, A. R. (2010). Low-level sonsory plasticity during task-irrelevant perceptual learning: Evidence from conventional and double training procedures. *Vision Research*, *50*, 424–432.

Posner, M. I., & Petersen, S. E. (1990). The attention system of the human brain. *Annual Review of Neuroscience*, *13*, 25–42. doi:10.1146/annurev.ne.13.030190.000325

Posner, M. I., & Snyder, C. R. R. (1975). Attention and cognitive control. In R. L. Solso (Ed.), *Information processing and cognition: The Loyola symposium* (pp. 55–85). Hillsdale, NJ: Erlbaum.

Ramachandran, V. S., & Braddick, O. (1973). Orientation-specific learning in stereopsis. *Perception*, *2*(3), 371–376.

Romei, V., Gross, J., & Thut, G. (2010). On the role of prestimulus alpha rhythms over occipito-parietal areas in visual input regulation: correlation or causation? *The Journal of Neuroscience*, *30*(25), 8692–8697. doi:10.1523/JNEUROSCI.0160-10.2010

Ronnqvist, K. C., McAllister, C. J., Woodhall, G. L., Stanford, I. M., & Hall, S. D. (2013). A multimodal perspective on the composition of cortical oscillations. *Frontiers in Human Neuroscience*, *7*(April), 132. doi:10.3389/fnhum.2013.00132

Sagi, D. (2011). Perceptual learning in Vision Research. *Vision Research*, *51*(13), 1552–1566. doi:10.1016/j.visres.2010.10.019

Sasaki, Y., Náñez, J., & Watanabe, T. (2012). Recent progress in perceptual learning research. *Wiley Interdisciplinary Reviews: Cognitive Science*, *3*(3), 293–299. doi:10.1002/wcs.1175.Recent

Schoups, A., Vogels, R., Qian, N., & Orban, G. (2001). Practising orientation identification improves orientation coding in V1 neurons. *Nature*, *412*(6842), 549–553.

Seitz, A., & Watanabe, T. (2005). A unified model for perceptual learning. *Trends in Cognitive Sciences*, *9*(7), 329–334.

Sigala, R., Haufe, S., Roy, D., Dinse, H. R., & Ritter, P. (2014). The role of alpha-rhythm states in perceptual learning: insights from experiments and computational models. *Frontiers in Computational Neuroscience*, *8*(36), 1–19. doi:10.3389/fncom.2014.00036

Silva, L., Amitai, Y., & Connors, B. (1991). Intrinsic oscillations of neocortex generated by layer 5 pyramidal neurons. *Science*, *251*(4992), 432–435.

Snyder, A. C., & Foxe, J. J. (2010). Anticipatory attentional suppression of visual features indexed by oscillatory alpha-band power increases: a high-density electrical mapping study. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *30*(11), 4024–4032. doi:10.1523/JNEUROSCI.5684-09.2010

Thut, G., Nietzel, A., Brandt, S. a, & Pascual-Leone, A. (2006). Alpha-band electroencephalographic activity over occipital cortex indexes visuospatial attention bias and predicts visual target detection. *The Journal of Neuroscience*, *26*(37), 9494–9502. doi:10.1523/JNEUROSCI.0875-06.2006

Vaden, R. J., Hutcheson, N. L., McCollum, L. a, Kentros, J., & Visscher, K. M. (2012). Older adults, unlike younger adults, do not modulate alpha power to suppress irrelevant information. *NeuroImage*, *63*(3), 1127–1133. doi:10.1016/j.neuroimage.2012.07.050

Van Winsum, W., Sergeant, J., & Geuze, R. (1984). The functional significance of event-related desynchronization of alpha rhythm in attentional and activating tasks. *Electroencephalography and Clinical Neurophysiology*, *58*(6), 519–524. doi:10.1016/0013-4694(84)90042-7

Watanabe, T., & Sasaki, Y. (2015). Perceptual learning: Toward a comprehensive theory. *Annual Review of Psychology*, *66*, 197–221. doi:10.1146/annurev-psych-010814-015214

Xiao, L.-Q., Zhang, J.-Y., Wang, R., Klein, S. a, Levi, D. M., & Yu, C. (2008). Complete transfer of perceptual learning across retinal locations enabled by double training. *Current Biology : CB*, *18*(24), 1922–1926. doi:10.1016/j.cub.2008.10.030

Yang, T., & Maunsell, J. H. R. (2004). The effect of perceptual learning on neuronal responses in monkey visual area V4. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *24*(7), 1617–1626. doi:10.1523/JNEUROSCI.4442-03.2004

Zhang, J.-Y., Zhang, G.-L., Xiao, L.-Q., Klein, S. a, Levi, D. M., & Yu, C. (2010). Rule-based learning explains visual perceptual learning and its specificity and transfer. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *30*(37), 12323–12328. doi:10.1523/JNEUROSCI.0704-10.2010

Zohary, E., Celebrini, S., Britten, K. H., & Newsome, W. T. (1994). Neuronal plasticity that underlies improvement in perceptual performance. *Science (New York, N.Y.)*, *263*(5151), 1289–1292.

Figures

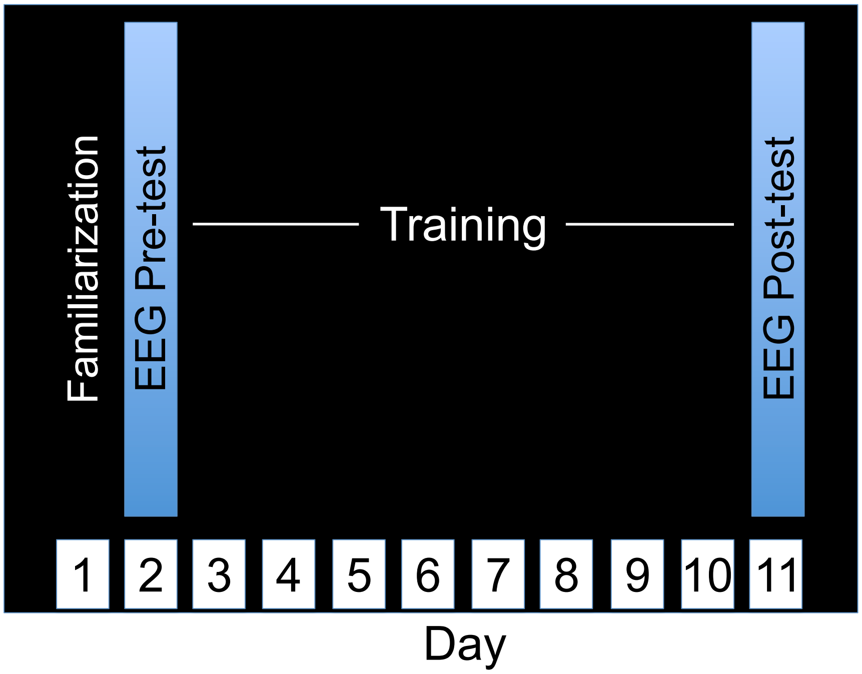

Figure 11 – Schedule of the experimental sessions. Day 1 consisted of a familiarization session, Day 2 consisted of the pre-test, Days 3-10 consisted of the training sessions, and Day 11 consisted of the post-test.

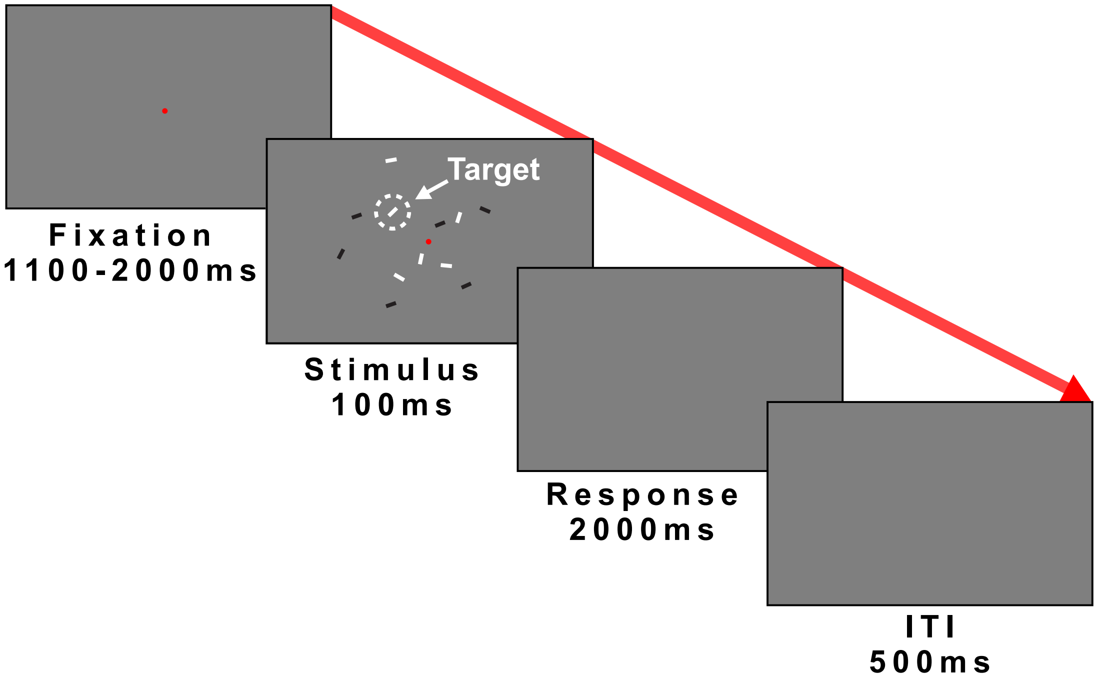

Figure 12 – Diagram of a single trial. After a fixation period the stimulus array appeared for 100ms. (The target is marked for illustrative purposes here but was distinguishable only by its orientation during actual presentations.) This was followed by a blank screen while the response was made and a 500ms intertrial interval after the response.

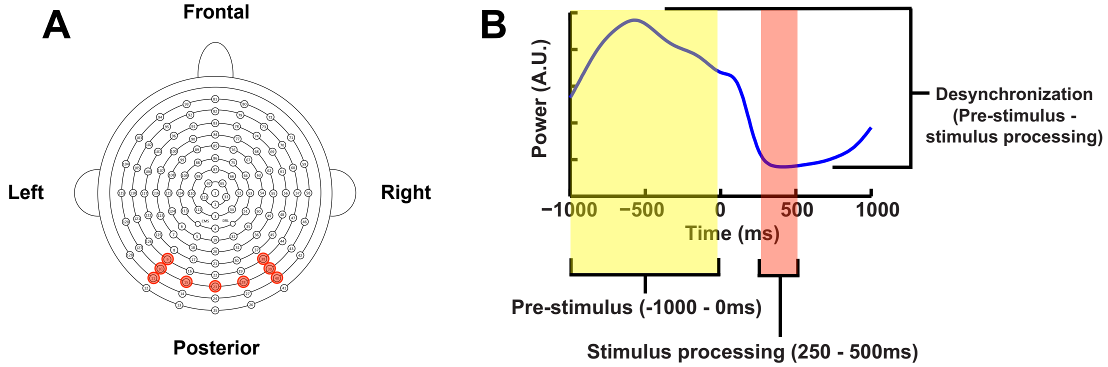

Figure 13 – (A) Overhead view of the 128 electrode placement using the BioSemi ActiveTwo system. Red highlighted regions denote electrodes used in the alpha power analyses, corresponding approximately to sites Oz, O1, O2, PO7, PO8, PO9, PO10, P3, and P4. (B) Diagram of the pre-stimulus period (yellow shaded region), the stimulus processing period (red shaded region), and desynchronization (the difference between the mean pre-stimulus period and mean stimulus processing period) used in the alpha power analyses. The pre-stimulus period consists of the 1000ms before the stimulus onset (0ms). The stimulus processing period consists of the 250-500ms after the stimulus onset.

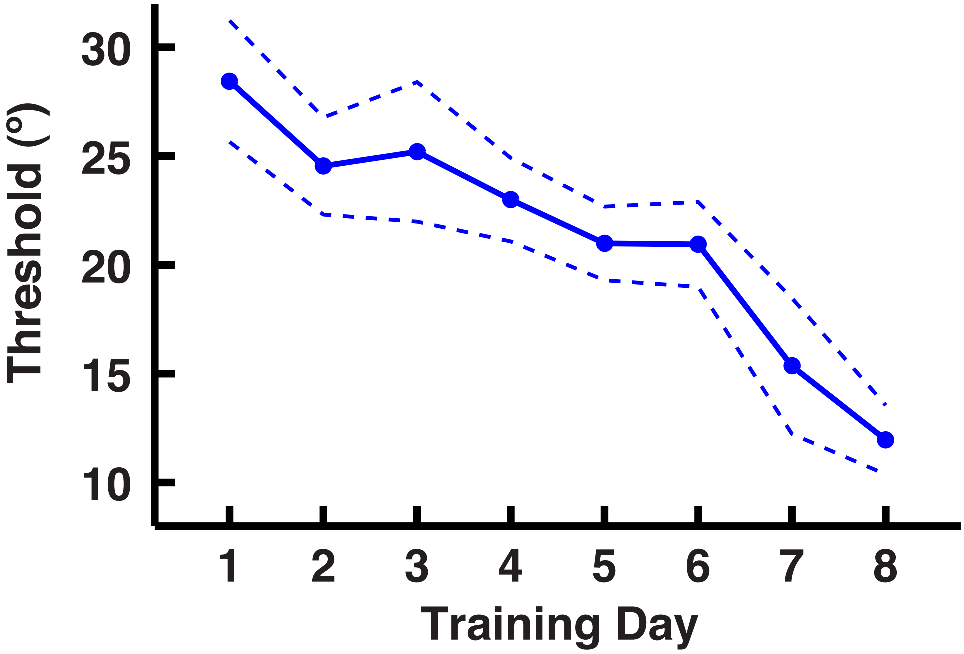

Figure 14 – Orientation offset (θ) threshold as a function of training day. Dashed lines denote +/- 1 SEM.

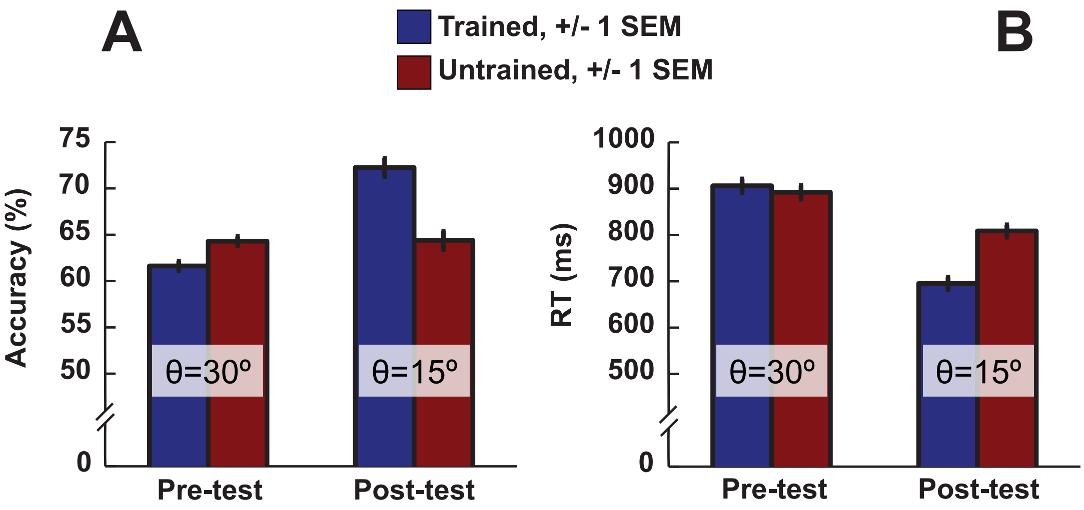

Figure 15 – Accuracy (A) and reaction times (B) for trained targets (blue bars) and untrained targets (red bars) during the pre-test and post-test. Error bars denote +/- 1 SEM. θ denotes the orientation offset, in degrees, between the target and the distractors in the pre- and post-test.

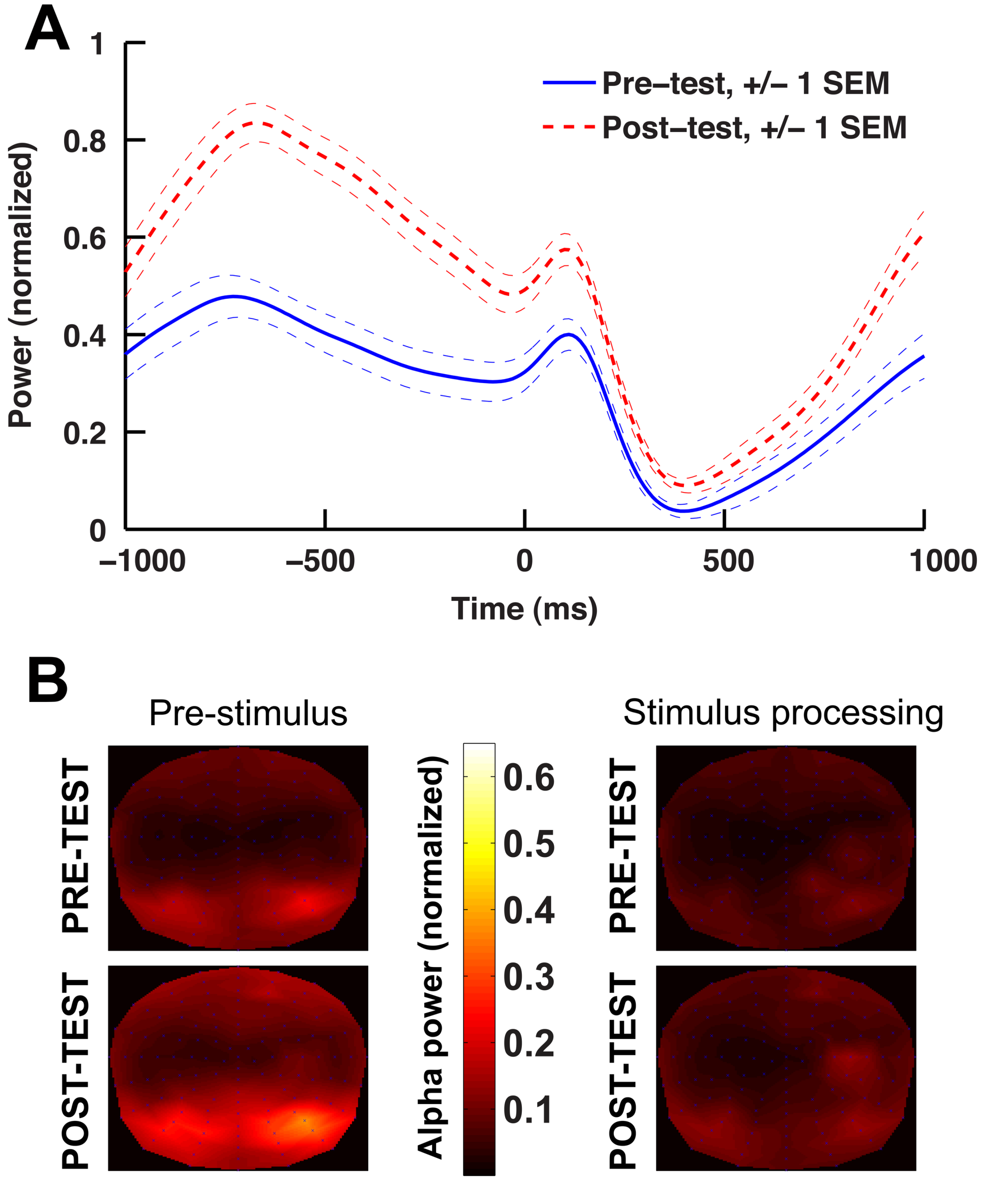

Figure 16 – (A) Peristimulus period of normalized alpha power as a function of pre-test (thick solid blue line) and post-test (thick dashed red line) with all trial conditions contributing. Thin dashed lines denote +/- 1 SEM. (B) Scalp distributions showing normalized alpha power during the pre-stimulus period (-1000ms – 0ms) as a function of pre-test and post-test (left side) and normalized alpha power during the stimulus processing period (250ms – 500ms) as a function of pre-test and post-test (right side). Lighter regions denote more relative alpha power, darker regions denote less relative alpha power. Nose is up, left on left.

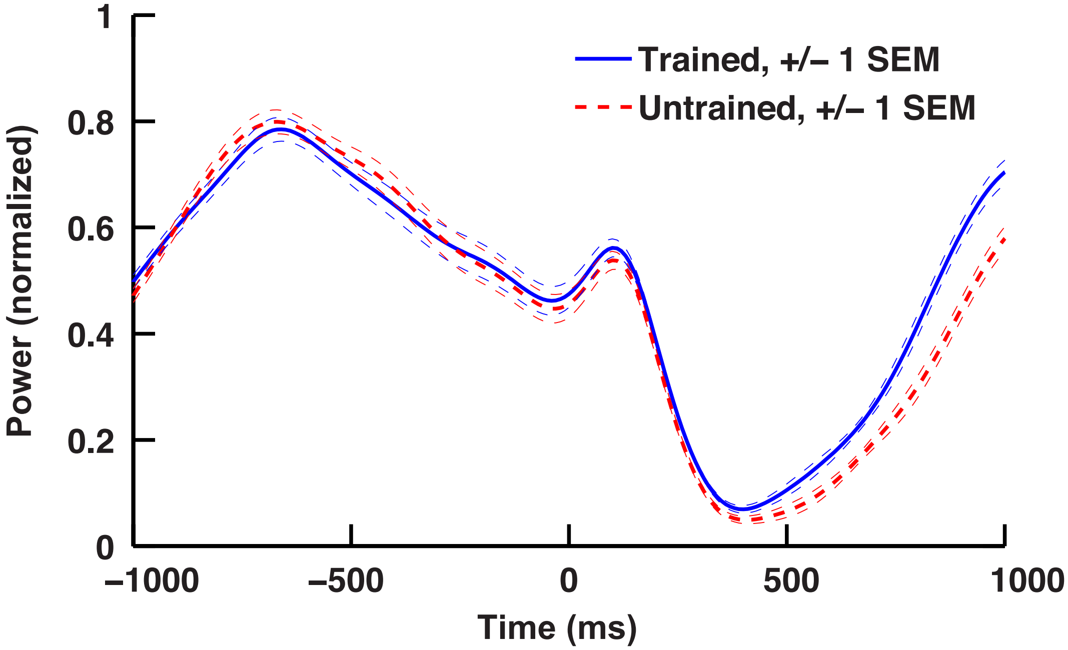

Figure 17 - Peristimulus period of normalized alpha power as a function of trained targets (thick solid blue line) and untrained targets (thick dashed red line) within the post-test only. Thin dashed lines denote +/- 1 SEM. The pre-stimulus period is -1000ms – 0ms and the stimulus processing period is 250ms – 500ms.

Table of Means

Chapter 2 - All

Variable	*M*	*SD*
Orientation Offset Threshold (deg.)		
Day 1	28.4414	7.8831
Day 2	24.5411	6.3218
Day 3	25.1930	9.0739
Day 4	22.9928	5.4176
Day 5	20.9841	4.7902
Day 6	20.9403	5.5054
Day 7	15.3559	8.8280
Day 8	11.9638	4.4865
Pre-test RT (ms)		
Trained	906.1055	41.7535
Untrained	892.1720	37.6136
Pre-test Accuracy (%)		
Trained	61.6267	1.4175
Untrained	64.3044	2.8019
Post-test RT (ms)		
Trained	695.3097	41.7535
Untrained	808.5520	37.6136
Post-test Accuracy (%)		
Trained	72.2555	1.4175
Untrained	64.3967	2.8019
Pre-test Alpha Power (Normalized)		
Pre-stimulus Period (Overall)	0.3864	0.1860
Stim. Processing Period (Overall)	0.0662	0.0752
Post-test Alpha Power (Normalized)		
Pre-stimulus Period (Overall)	0.6748	0.1126
Pre-stimulus Period (Trained)	0.6253	0.0910
Pre-stimulus Period (Untrained)	0.6342	0.1355
Stim. Processing Period (Overall)	0.1315	0.1030
Stim. Processing Period (Trained)	0.1107	0.1054
Stim. Processing Period (Untrained)	0.0854	0.0955

Table 5 – Means and within-subject standard deviations for analyses in Chapter 2, listed in order of discussion. SD is within-subjects SD, calculated according to Loftus and Masson (1994).

Chapter 3

A novel paradigm to examine how perceptual learning, statistical learning, and multisensory integration jointly contribute to perceptual performance

Abstract

It is well established that our visual perceptions are jointly determined by visual input, expectations of the world, and informative inputs to other sensory modalities. Numerous studies examine different aspects of this equation. For example, studies of perceptual learning (PL), statistical learning (SL), and multisensory integration (MI) detail, respectively, improvements in perceptual processing after repeated exposure to certain stimuli, learning of relationships between stimuli after repeated exposure, and interactions between modalities that lead to improved processing of multisensory objects. Researchers typically design paradigms that investigate one of these phenomena independently and discuss the results in terms of mechanisms for that phenomenon alone. However, it is unclear the extent to which these cognitive processes share common mechanisms and how their interactions impact perception. To investigate this, we designed a novel paradigm through which to understand how PL, SL, and MI jointly influence perception and tested it with two sets of experiments. Across all experiments, participants performed a discrimination task on audio-visual stimuli that appeared in different locations according to controlled spatio-temporal statistics. Behavioral data show some learning for position and statistical probability, and auditory benefits on trials. Electroencephalographic (EEG) data hints at an SL alpha power relationship and at a general increase in alpha power over all trials. Paradigms such as this have important implications for a wide variety of fields as the results can help elucidate underlying mechanisms driving different types of perceptual processes and also demonstrate where these different processes may intersect.

Introduction

It is well established that our visual perceptions are jointly determined by visual input, expectations of the world, and informative inputs to other sensory modalities. Numerous studies examine different aspects of this equation. For example, studies of perceptual learning (PL), statistical learning (SL), and multisensory integration (MI) detail, respectively, improvements in perceptual processing after repeated exposure to certain stimuli, learning of relationships between stimuli after repeated exposure, and interactions between modalities that lead to improved processing of multisensory objects (for reviews see, Koelewijn, Bronkhorst, & Theeuwes, 2010; Sagi, 2011; Sasaki, Náñez, & Watanabe, 2012; Seitz & Dinse, 2007; Shimojo & Shams, 2001; Stein & Stanford, 2008; Turk-Browne, 2012; Watanabe & Sasaki, 2015). Researchers typically design paradigms that investigate one of these phenomena independently and discuss the results in terms of mechanisms for that phenomenon alone. However, it is unclear the extent to which cognitive processes responsible for these three types of learning share common mechanisms and how their interactions impact perception.

PL is typically thought to be an implicit process and has been shown to occur in numerous modalities and in a wide variety of animal models, including non-primates, non-human primates, and humans (Fahle, 2005; Ghose, 2004). In the visual modality, PL is often investigated with simple visual features, e.g., orientation (Dobres & Seitz, 2010; Schoups, Vogels, Qian, & Orban, 2001; Yang & Maunsell, 2004), line or dot offset (Fahle, Edelman, & Poggio, 1995; Hung & Seitz, 2014), and contrast (Adini, Sagi, & Tsodyks, 2002; Hua et al., 2010; Yu, Klein, & Levi, 2004), although more complex visual stimuli, such as human faces, have also been successfully used to study PL (Hussain, Sekuler, & Bennett, 2011). PL is thought to underlie our visual system's ability to adapt and improve, and although perceptual improvements are often specific to the task, stimuli, and other parameters used during training, PL has also been shown to transfer to untrained stimuli (Ahissar & Hochstein, 2004; Hung & Seitz, 2014; Xiao et al., 2008; Zhang et al., 2010). PL has even been shown to transfer to situations outside of the laboratory, such as visual improvements and performance improvements for baseball players after undergoing PL training (Deveau, Ozer, & Seitz, 2014).

SL is another implicit process which, similar to PL, has also been shown to occur in a variety of paradigms, modalities, and in both human and non-human primates (Conway & Christiansen, 2006; Fiser & Aslin, 2001; Hauser, Newport, & Aslin, 2001; Saffran, Aslin, & Newport, 1996; Turk-Browne, Isola, Scholl, & Treat, 2008). Instead of measuring perceptual improvements in the processing of simple stimuli as is done in PL studies, SL studies typically measure learned associations between stimuli which have been organized probabilistically. Within the visual modality, these relationships might be visuo-temporal, where the temporal structure of observed sequences of shapes are learned (Bays, Turk-Browne, & Seitz, 2016; Fiser & Aslin, 2002; Zhao, Al-Aidroos, & Turk-Browne, 2013), or visuo-spatial, where the spatial structures of layouts of shapes are learned (Fiser & Aslin, 2001, 2005). The ability of the visual system to learn these relationships has been hypothesized to help bind features and objects (Turk-Browne et al., 2008), to define the scale of visual objects (Fiser & Aslin, 2001, 2005), to orient attention (Zhao et al., 2013), and to affect our perceptions of stimuli (Barakat, Seitz, & Shams, 2013; Chalk, Seitz, & Seriès, 2010).

MI has come to be understood as a historically underappreciated method of sensory processing and has increasingly been studied as an important part of everyday perception (Koelewijn et al., 2010; Shams & Seitz, 2008; Shimojo & Shams, 2001; Stein & Stanford, 2008). Perceptions in one modality are known to affect perceptions in another modality (Shams, Kamitani, & Shimojo, 2000) and integration of the auditory and visual modalities has been shown to be particularly important for visual learning (Kim, Seitz, & Shams, 2008; Raposo, Sheppard, Schrater, & Churchland, 2012; Seitz, Kim, & Shams, 2006; Shams & Seitz, 2008; Sheppard, Raposo, & Churchland, 2013). The neural substrates of MI are not as well-known as substrates for unisensory processing but there is abundant evidence for early, low level interactions between modalities (Powers, Hevey, & Wallace, 2012; Seitz et al., 2006; Shimojo & Shams, 2001) which suggests that MI is able to affect perception and sensory learning at an extremely basic level.

These three perceptual processes – PL, SL, and MI – are typically studied and discussed independently. However, there is evidence for interactions among them. Barakat, Seitz, and Shams (2013) found that SL was also accompanied by PL, as measured by an improved ability for participants performing a shape detection task to detect the second shape of a pair compared to the first shape of a pair, even though the detection task presented the shapes without their statistical context. SL has also been shown to interact with MI in a study by Seitz, Kim, van Wassenhove, and Shams (2007). Using visual pairs, auditory pairs, and audio-visual pairs, they showed that participants learned all three types of associations and that these unimodal and crossmodal learning experiences occurred independently of each other. Some of the same researchers have also shown interactions between PL and MI (Seitz et al., 2006). In this study, they found that multisensory PL training facilitated visual learning and also decreased the amount of time that the PL required in order to demonstrate reliable behavioral results. Further work has shown that audio-visual pairs can also improve auditory perceptions (von Kriegstein & Giraud, 2006) and that congruent multisensory stimuli provide more perceptual learning than incongruent stimuli (Kim et al., 2008; von Kriegstein & Giraud, 2006). Together, this body of research strongly suggests that sensory learning may be optimized by including multiple strategies, including PL, SL, and MI.

In addition to behavioral measures, electroencephalographic (EEG) measures can provide insight into the interactions between PL, SL, and MI. Previous work studying PL with EEG has used evoked potentials (Bao, Yang, Rios, He, & Engel, 2010; Woodman, 2010), pattern classification algorithms (Das, Giesbrecht, & Eckstein, 2010), and analyses of the alpha bandwidth, which occurs between 8-12Hz in the EEG power spectrum (Bays, Visscher, Le Dantec, & Seitz, 2015; Freyer, Becker, Dinse, & Ritter, 2013; Sigala, Haufe, Roy, Dinse, & Ritter, 2014). Alpha power analyses are of particular interest because of previous work showing they may be related to the amount of effort used during an experimental session (Bays et al., 2015). Romei, Gross, and Thut (2012) analyzed alpha power in a MI context and found that crossmodal phase synchronization served to influence the neural excitability in visual areas. While there exists SL research utilizing EEG (Abla, Katahira, & Okanoya, 2008; Abla & Okanoya, 2009), none have specifically looked at power modulation in the alpha bandwidth. However, based on the body of research showing alpha modulation in response to PL and for MI, one might reasonably expect SL to correlate with alpha power in an informative manner.

Here we present data from a novel paradigm designed to investigate how PL, SL, and MI jointly influence perception and tested the paradigm with two sets of experiments. Across all experiments, participants performed a discrimination task (PL) on audio-visual stimuli (MI) that appeared in different locations according to controlled spatio-temporal statistics (SL). Behavioral data show some learning for position and statistical probability, and auditory benefits in the form of speeded RT and higher accuracy. EEG data suggests an SL alpha power relationship, where more probable locations contain more alpha power during the trial. Paradigms such as this have important implications for a wide variety of fields as the results can help elucidate underlying mechanisms driving different types of learning and also demonstrate where these different types of learning may intersect.

Experiment 1

Experiment 1 took place over the course of two one-hour sessions that occurred on consecutive days. It was designed to analyze whether there are behavioral interactions between PL, SL, and MI, whether neural correlates of any effects can be found, and to gather initial results before conducting the nine-day version of the experiment (Experiment 2, below).

Methods

Participants

Fifteen undergraduates at the University of California, Riverside (age range 18-22 years, nine female) were included in this study. EEG was recorded from seven of these participants on the second day. Inclusion in data analyses for any participant required completion of both experimental sessions and procedures without technical errors, such as improperly affixed electrodes, or excessive muscular noise in the EEG. The seven participants from whom EEG was recorded were paid $10 an hour for their participation and the other eight participants received credit toward partial fulfillment of course requirements for an introductory psychology course. All participants gave written informed consent as approved by the Human Research Review Board and had normal or corrected-to-normal vision.

An additional fifteen undergraduates at the University of California, Riverside (age range 18-22 years, seven female) were included in a control study (see Control Study section below). Inclusion required completion of both experimental sessions and procedures without technical errors. Participants received credit toward partial fulfillment of course requirements for an introductory psychology course, gave written informed consent as approved by the Human Research Review Board, and had normal or corrected-to-normal vision.

Display Apparatus

An Apple Mac Mini (Apple, Inc., Cupertino, CA, USA) running OSX 10.5.6 controlled the experiment. The stimuli were displayed on a 48.26cm wide Sony Trinitron (Sony Corp., Tokyo, Japan) CRT monitor with a resolution of 1600x1200 pixels and a refresh rate of 100 Hz. Participants sat 67cm from the screen with their heads restrained by a chinrest. An EyeLink 1000 eyetracking system (SR Research, Ltd., Mississauga, ON, Canada) was used with custom software to ensure that stimuli were only displayed while participants fixated on the center of the screen. Stimuli were created and controlled by custom code written in Matlab (The Mathworks, Inc., Natick, MA, USA), using the Psychophysics Toolbox (Brainard, 1997; Kleiner, Brainard, & Pelli, 2007). Mediating the connection between the monitor, the computer, and the EEG system was a Datapixx processor (Vpixx Technologies, Inc., Saint-Bruno, QC, Canada) which enables a 16-bit DAC, allowing for a 256-fold increase in the display's possible contrast values, and which provides monitor-refresh-locked stimulus presentations for accurate timing of stimuli and response triggers. Responses were collected using a RESPONSEPixx button box (VPixx Technologies) that enables microsecond precision of response latency measurement.

Session Order

The experiment took place over two one-hour sessions that occurred on subsequent days. The first session was a combined PL/SL/MI training session and the second session was a post-training test session during which EEG was recorded from seven participants (see sections below).

PL/SL/MI Training

The combined PL/SL/MI training took place during the first session of the experiment. The session consisted of 1200 trials discriminating the orientation of a gabor grating. The trials were grouped into eight blocks and there was a thirty second break between each block. Each trial consisted of a 100ms presentation of a gabor grating at one of three locations, called the "trained locations" for that participant. These three locations were either 5º visual angle up and right of center, center, and 5º visual angle down and left of center, or they were 5º visual angle up and left of center, center, and 5º visual angle down and right of center. This resulted in one trained presentation position in the center of the visual field and two trained presentation positions in the periphery of the visual field for each participant. These two possible sets of trained locations were counterbalanced across participants. In all analyses, data from the peripheral locations are combined together and analyzed as a single peripheral location, and results are split by the central visual field presentations and the (combined) peripheral visual field presentations.

A customized Markov chain determined the location of each presentation. This was calculated beforehand to counterbalance presentations at the three locations and ensured that from each position, one of the other positions was 60% likely to host the next trial, one was 30% likely to host the next trial, and one was 10% likely to host the next trial (Figure 18). These probabilities were maintained for each participant across both sessions and are referred to as the "trained statistics" of the stimuli.

The gabor gratings were presented on a grey background for 100ms with a 1350-1450ms jittered ISI during which the participant responded as to whether the gabor was oriented towards the right or left (22.5º, 67.5º, 112.5º, or 157.5º) by pressing one of two buttons on the button box. The gabors were 3º visual angle in diameter, used a spatial frequency of 4 c/d, and were counterbalanced between four phase values (0º, 45º, 90º, or 135º) with a sigma of 0.5º. The contrast of the gabor gratings was controlled by the QUEST procedure (Watson & Pelli, 1983), a Bayesian algorithm for determining thresholds, implemented in Matlab using the Psychophysics Toolbox. Each location received its own threshold estimate.

Auditory stimuli were also presented concurrently with the visual stimuli 94% of the time. These stimuli were ramped pure tones at 500Hz, 310Hz, and 200Hz, creating high, middle, and low tones. They could be presented from either the left, right, or both left and right speakers, and were presented according to three conditions. The “correct tone” condition occurred on 82% of trials and paired a tone with the spatial location of the visual stimulus according to pitch and azimuth. For example, the correct tone for a gabor presented in the upper right position would be a high tone out of the right speaker, the correct tone for a centrally presented gabor would be a middle tone out of both speakers, and the correct tone for a lower left position gabor would be a low tone out of the left speaker. The “incorrect tone” condition occurred on 12% of the trials and involved playing a tone that was incorrectly matched according to pitch. These were balanced according to the two possible incorrect pitches that could be played on a trial. The “silent” condition occurred on 6% of the trials and involved no tone being played for that trial. The auditory stimuli were presented using speakers set up to the left and right of the computer monitor and covered with auditory-invisible black cloth.

Post-Training EEG

On the second session of the experiment, a post-training EEG session was conducted. This session was similar to the training session with four main differences. First, EEG recordings were collected during these test sessions for seven of the 15 participants. Second, there were 180 trials per block, or a total of 1440 trials in the session. Third, trials were balanced between having a sound or not having a sound, with no incorrect sound trials occurring. And fourth, each of the eight blocks utilized either trained or untrained positions and trained or untrained statistics. The trained positions consisted of the three locations the participant received during the training session and the untrained positions consisted of the two opposite corners of the screen plus the central location. For example, if a participant were trained on the upper left, center, and lower right locations, then the untrained locations would be the upper right, center, and lower left locations. The untrained statistics consisted of switching the 60% and 30% probabilities of the Markov chain controlling the next trial's location. Thus, if from the central location the trained statistics would normally go to the lower left position 60% of the time and the upper right position 30% of the time, a block using the untrained statistics would go to the upper right position 60% of the time and the lower left position 30% of the time from the central location. Each of the eight blocks used one of the four combinations of trained and untrained positions and statistics and the blocks were presented in the following order: 1)

Trained locations/Trained statistics; 2) Trained locations/Untrained statistics; 3) Untrained locations/Trained statistics; 4) Untrained locations/Untrained statistics; 5) Untrained locations/Trained statistics; 6) Untrained locations/Untrained statistics; 7) Trained locations/Trained statistics; 8) Trained locations/Untrained statistics.

Electroencephalography (EEG)

EEG was recorded using 64-active Ag/AgCl electrodes (ActiveTwo system, BioSemi, Inc., Amsterdam, Netherlands) at a rate of 1024 Hz. All electrodes were mounted in an elastic ActiveTwo cap according to the BioSemi layout and labeled according to the 10/20 system (Oostenveld & Praamstra, 2001). For alpha bandwidth analyses, a bilateral selection of nine occipital and parietal electrodes was analyzed, corresponding approximately to sites Oz, O1, O2, PO7, PO8, PO9, PO10, P3, and P4 (Figure 19, highlighted regions), given that alpha power is most prominent in occipital channels and that we were analyzing a visual task. Horizontal (HEOG) and vertical (VEOG) electrooculograms were recorded, using additional electrodes affixed with adhesive disks at, respectively, the outer right and left canthi (HEOG) and above and below the right and left eye (VEOG). Conductive gel was applied to maintain the contact between the electrodes and the scalp (Signa Gel, Parker Laboratories, Inc., Fairfield, NJ, USA).

After recording, EEG data were initially processed using EMSE Suite 5.4 (Source Signal Imaging, Inc., San Diego, CA, USA). The data were first referenced to the average of all active electrodes (Keil et al., 2014) and filtered using zero phase-shift Butterworth high- and low-pass filters with half-amplitude cutoffs of 0.01 Hz and 40 Hz, respectively.

Ocular artifacts were corrected using a proprietary algorithm of the EMSE Suite which is designed to remove eyeblink noise without removing the underlying signal (Pflieger, 2001).

After processing using EMSE Suite software, time-frequency analysis was conducted using Matlab and the FieldTrip toolbox (Oostenveld, Fries, Maris, & Schoffelen, 2011). The data were segmented into three-second periods centered on each stimulus presentation and convolved with a Morlet wavelet. The frequencies of interest extracted were 2-20Hz and each wavelet had a width of seven cycles.

In order to prevent individual differences in raw alpha power (which can vary dramatically between individuals) from driving the results, all alpha values were normalized to a [0-1] scale before being analyzed. For each subject, the minimum and maximum alpha value across the EEG session was calculated. The minimum value was then subtracted from all alpha values and the result divided by the difference between the maximum and minimum values (i.e., the range). This transformed each subject's alpha values such that the minimum value became 0 and the maximum value became 1, with all other values falling within the [0-1] range.

Control Study

In addition to the fifteen participants run under the conditions above, fifteen more participants were run in a control study to examine whether the adaptive contrast affected SL. The control study was identical to all parameters described for Experiment 1 except that the contrast of the stimuli was held constant at 100% and there were no EEG recordings on the second day. All other aspects of the methods were the same between the two experiments. None of the participants in the control study had previously partaken in any other version the experiment.

Results

Behavioral Results - PL

Standard measures of PL include decreases in threshold across training days and, depending on the paradigm used, greater effects for stimuli in trained positions versus stimuli in untrained positions. Because there was only one training session in this experimental design, we could not examine contrast thresholds across days. However, we could examine whether a single day of training was enough to produce a positional effect in the second session, where we predicted lower RTs and higher accuracy for stimuli in blocks using trained positions versus stimuli in blocks using untrained positions. These results can be seen in Figure 20, where the trials are also split up according to transition probability to examine whether there are any interactions with SL. The pattern of RT results (Figure 20A) is in the predicted direction for PL, with a lower average RT for trained positions (560.0ms) compared to untrained positions (577.1ms), although it does not reach statistical significance (2 (trained/untrained position x 3 (transition probability) repeated measures ANOVA, trained/untrained F(1,14)=2.80, p=0.12, transition probability F(2,28)=0.92, p=0.41, interaction F(2,28)=0.53, p=0.60). The average accuracy (Figure 20B) between the trained position blocks (84.73%) and untrained position blocks (85.15%) did not show any statistically significant differences (2 (trained/untrained position x 3 (transition probability) repeated measures ANOVA, trained/untrained F(1,14)=0.028, p=0.87, transition probability F(2,28)=0.12, p=0.89, interaction F(2,28)=1.56, p=0.23), which implies there was no speed-accuracy trade-off with the lower RTs in the trained position blocks. There was no interaction between trained positions and transition probabilities for either RT or accuracy (see preceding ANOVA results).

Behavioral Results - SL

SL typically occurs on a timescale of minutes and when RT is the dependent measure a predicted effect would be a lower response latency for higher probability transitions compared to lower probability transitions. Thus, we predicted to see effects in the second half of the training session, with a pattern of lowest RTs for trials at 60% likely positions, higher RTs for trials at 30% likely positions, and highest RTs for trials at 10% likely positions. This was examined in the training session in two ways – calculating the average RT over the second half of the session for each transition probability (after learning is assumed to have occurred); and by subtracting the average RT from the first half of the training session from the second half of the training session for each corresponding set of trials, i.e., by calculating the difference between the second half and the first half of the training session. This second method has the advantage of controlling for baseline differences between the trial types. Note that the pattern of RT effects for the difference between the second half and the first half would be the opposite of the raw RT effect. After learning has occurred then higher probability transitions should have a lower RT than lower probability transitions, which means the difference when subtracting the first half (a baseline measure) from the second half of the session should be smaller, or more negative, for higher probability transitions and larger for lower probability transitions.

Results from both methods can be seen in Figure 21. The average RT for each trial type in the second half of the training session (Figure 21A) does not demonstrate the predicted pattern (peripheral location means for 60%, 30%, and 10% trials, respectively: 637.4ms, 635.5ms, 638.7ms; central location means for 60%, 30%, and 10% trials, respectively: 634.9ms, 643.9ms, 631.5ms), nor do differences between the trial types approach statistical significance at either location (peripheral location repeated measure ANOVA F(2,28)=0.13, p=0.88, partial η^2=0.0093; central location repeated measure ANOVA F(2,28)=1.49, p=0.24, partial η^2=0.096).

However, the RT differences between the second half of the session and the first half of the session (Figure 21B) reveal a trend in the predicted direction for centrally presented trials and also a slowing for 10% trials in the peripheral locations. In the central location, there is an overall slowing of RTs compared to the first half of the session but 60% trials slow the least (20.16ms), followed by 30% trials (32.38ms), and the most slowing occurring for 10% trials (39.14ms). This effect trends on significance when analyzed with a repeated measures ANOVA (F(2,28)=2.71, p=0.084, partial η^2=0.16) and the difference between the 60% mean and the 10% mean reaches significance when analyzed with a post hoc Bonferroni corrected t test (t(14)=2.80, p=0.043, Cohen's d=0.64). The RT differences in the peripheral locations did not reach significance, either with a repeated measures ANOVA (F(2,28)=1.95, p=0.16, partial η^2=0.12) or with post hoc Bonferroni corrected t tests (all p>0.2). The pattern of means, however, demonstrates more slowing for the 10% trials (5.92ms) than the 60% trials (-9.71ms) or the 30% trials (-10.73ms).

We also examined whether there were RT and accuracy differences related to the transition probabilities in the post-training session by looking at blocks that used trained statistical structures versus blocks that used untrained statistical structures (Figure 22). Here there was no effect for whether trained or untrained statistics were used, nor for the transition probability, in either RTs or in accuracy, as measured by a 3 (transition probability) x 2 (trained/untrained statistics block) repeated measures ANOVA for RT and for accuracy (RT: transition probability F(2,28)=0.22, p=0.81, trained/untrained F(1,14)=0.42, p=0.52, interaction F(2,28)=0.62, p=0.54; Accuracy: transition probability F(2,28)=0.11, p=0.90, trained/untrained F(1,14)=0.43, p=0.52, interaction F(2,28)=0.16, p=0.85).

Behavioral Results - MI

MI typically manifests as an improvement for trials which contain multisensory stimuli as compared to unisensory trials. A predicted result here would be increased efficiency for trials with both auditory and visual stimuli as compared to trials with only visual stimuli. This effect is clearly seen in Figure 23, which shows trials in the second session in which auditory tones occurred compared to trials in which no tone occurred, split by transition probability to examine whether there are any interactions with SL. The average RT for trials with auditory stimuli (558.8ms) was significantly lower than the average RT for trials without auditory stimuli (578.2ms), and the average accuracy for trials with auditory stimuli (88.85%) was higher than the average accuracy for trials without auditory stimuli (80.98%), with no interaction between sound and SL (2 (sound) x 3 (transition probability) repeated measures ANOVA, RT: sound F(1,14)=6.44, p=0.024, transition probability F(2,28)=0.53, p=0.59, interaction F(2,28)=0.36, p=0.70; Accuracy: sound F(1,14)=34.73, p=0.000039, transition probability F(2,28)=0.12, p=0.89, interaction F(2,28)=0.44, p=0.65).

EEG Data

As described in the Methods section, EEG data was analyzed by looking for differences in alpha power. Following Bays et al. (2015), a period of time from 250ms after the stimulus presentation to 500ms after the stimulus presentation was averaged over for each condition and compared. We predicted that if SL were correlated with alpha power then there would be more alpha power during 60% trials, less in 30% trials, and the least in 10% trials. These results can be seen in Figure 24. Although there is a weak pattern for the mean of the normalized alpha power of 60% trials (.1682) to be higher than that of 30% trials (.1642), which are higher than that of 10% trials (.1592), a repeated measures ANOVA revealed no significant differences between the three trial types (F(2,12)=0.02, p=0.98).

Control Study SL Results

As described in the Methods section, a control study was conducted to investigate whether the adaptive contrast reduced SL. This experiment was identical in all respects except that the stimuli were always presented at full contrast and there were no EEG recordings on the second day. Analyses of the second half of the first session were carried out as described above, with similar predictions. Figure 25 shows the results of these analyses. The raw RT means from the second half of the session (Figure 25A) generally follow the predicted pattern of faster 60% trials (peripheral mean 552.1ms, central mean 549.9ms), followed by slower 30% trials (peripheral mean 556.0ms, central mean 552.9ms), and slower 10% trials (peripheral mean 557.6ms, central mean 563.0ms), but none of these differences reach statistical significance (Peripheral repeated measure ANOVA F(2,28)=0.32, p=0.72; Central repeated measure ANOVA F(2,28)=1.60, p=0.22). However, the RT difference between the second half and the first half of the session (Figure 25B) shows highly significant results in the predicted pattern. Trials with a 60% transition probability showed the most negative mean difference (peripheral -27.9ms, central +34.6ms), followed by higher 30% trial differences (peripheral -15.9ms, central +44.1ms), and highest 10% trial differences (peripheral +4.6ms, central +56.5ms) and both sets of means were significantly different (Peripheral repeated measures ANOVA F(2,28)=11.12, p=0.00028, partial η^2=0.44; central repeated measure ANOVA F(2,28)=3.51, p=0.044, partial η^2=0.20). The implications of obtaining a clear SL result in the non-adaptive version of the experiment and not in the adaptive version of the experiment are expanded upon in the Results section.

Experiment 2

Experiment 2 took place over the course of nine one-hour sessions. It was designed to analyze whether there are behavioral interactions between PL, SL, and MI using a novel training paradigm; whether neural correlates of any effects can be found; and whether the PL training can transfer to untrained visual acuity tasks.

Methods

Participants

Six undergraduates at the University of California, Riverside (age range 18-26 years, four female) were included in this study. Inclusion required completion of all experimental sessions and procedures without technical errors, such as improperly affixed electrodes, or excessive muscular noise in the EEG. Participants were paid $10 an hour for their participation, gave written informed consent as approved by the Human Research Review Board, and had normal or corrected-to-normal vision.

Display Apparatus

All equipment was identical to that used in Experiment 1.

Session Order

The experiment took place over a total of nine sessions (Figure 26), each lasting one hour and taking place on a different day. Subsequent sessions did not necessarily take place on subsequent days but each participant was required to complete the nine sessions within fourteen days of beginning. The first and last sessions were visual assessments (see section below), the second and penultimate sessions were EEG pre- and post-training (see section below), and the middle five sessions were combined PL/SL/MI training (see section below).

Visual Assessments

The first and last session consisted of three visual assessments – a Landolt C test, a cutoff spatial frequency test, and an MN Read test. The Landolt C test consisted of discriminating the orientation of a briefly presented letter C on a computer screen. There were five possible presentation locations – centrally, 5º visual angle up and to the right of center, 5º up and to the left of center, 5º down and to the right of center, and 5º down and to the left of center. Each trial presented a white letter C in the Sloan font on a grey background for 100ms with a 1900ms ISI during which the participant responded as to whether the C was oriented at 0º, 90º, 180º, or 270º, but pressing one of four buttons on the button box. The orientation was counterbalanced across trials and there were 40 trials at each of the five locations, for a total of 200 trials. The font size of the letter at each position was controlled by a 3 down 1 up staircase in order to determine the participant's threshold and each position initiated with a font size of 20. A trial could only initiate if the participant maintained fixation on a dot in the center of the screen and every 10 trials there was a three second break in which the participants could rest their eyes.

The cutoff spatial frequency test consisted of discriminating the orientation of a briefly presented gabor grating on a computer screen. There were five possible presentation locations – centrally, 5º visual angle up and to the right of center, 5º up and to the left of center, 5º down and to the right of center, and 5º down and to the left of center. Each trial presented a gabor grating on a grey background for 100ms with a 1350-1450ms jittered ISI during which the participant responded as to whether the gabor was oriented towards the right or left (22.5º, 67.5º, 112.5º, or 157.5º) but pressing one of two buttons on the button box. The gabors were 3º visual angle in diameter, counterbalanced between four phase values (0º, 45º, 90º, or 135º), were presented at 50% contrast, and used a sigma of 0.5º. The orientation was counterbalanced across trials and there were 40 trials at each of the five locations, for a total of 200 trials. The spatial frequency of the gabors at each position was controlled by a 3 down 1 up staircase in order to determine the participant's threshold and each position initiated with spatial frequency of 6 c/d. A trial could only initiate if the participant maintained fixation on a dot in the center of the screen and every 10 trials there was a three second break in which the participants could rest their eyes. Similar to Experiment 1, peripheral locations were combined for analyses of the Landolt C test and the cutoff spatial frequency test.

The MN Read test (Precision Vision, La Salle, IL, USA) is an acuity test requiring the participant to read sentences of different font sizes from a printed chart. Three measurements were obtained from this test – "reading acuity", which is a measure of the smallest print size the participant was able to accurately read, "maximum reading speed", which is a measure of the fastest the participant can read at any font size, and "critical print size", which is a measure of the smallest print size the participant was able to read close to their maximum reading speed. Reading acuity and critical print size are measured in “logMAR” units, where a smaller value indicates a smaller print size, and maximum reading speed is measured in words per minute. Participants placed their heads on a chin rest while performing this test, the chart was displayed 40cm from the participants’ head, and it used black text on a white background.

PL/SL/MI Training

The combined PL/SL/MI training took place during the third through seventh sessions of the experiment. Each session was identical to the training session described in Experiment 1 with the exception of the spatial frequency of the gabor stimuli. Instead of a single spatial frequency, three spatial frequencies were used – 1 c/d, referred to as “low” spatial frequency, 4 c/d, referred to as “peak” spatial frequency, and the maximum spatial frequency value determined for the participant by the first visual assessment session, referred to as the “cutoff” spatial frequency. Each of these spatial frequency presentations were counterbalanced for position, transition probability, auditory tone, and orientation. There was a separate QUEST contrast threshold estimate for each combination of position and spatial frequency, resulting in nine contrast threshold estimates.

Pre- and Post-Training EEG

On the second and eighth sessions of the experiment, i.e., the session before the training sessions began and the session after the training sessions ended, pre- and post-training EEG sessions were conducted. These sessions are identical to the second session described in Experiment 1, including the use of a single spatial frequency – 4 c/d, or the "peak" spatial frequency – in all trials (for further discussion on using the peak spatial frequency see the Discussion section). EEG was recorded from all participants in Experiment 2 during these sessions.

Electroencephalography (EEG)

EEG recordings, processing, and analyses were conducted in an identical way to those described in Experiment 1 with one exception – when normalizing alpha power values to a [0-1] scale, the minimum and maximum alpha values for each participant were determined from across both of that participant's EEG recording sessions instead of from a single session.

Results

Behavioral Results – PL

As described in Experiment 1, standard measures of PL include decreases in threshold across training days and greater effects for stimuli in trained positions versus stimuli in untrained positions. The final QUEST estimates for contrast threshold across training days can be seen in Figure 27, split by visual field location and spatial frequency and plotted in logarithmic units. Unfortunately decreases in threshold across training days were not statistically significant. There is a trend for the cutoff spatial frequency stimuli to decrease in the central location (Means across training days in logarithmic units: -0.84, -0.92, -1.02, -0.90, -1.03; repeated measures ANOVA F(4,20)=2.42, p=0.082, partial η^2=0.32) but no other threshold curves approached statistically significant differences (p values from repeated measures ANOVA range from p=0.12 to p=0.74). However, when fit with linear functions, all threshold curves displayed negative slopes and Pearson's r correlations between the contrast values and the training day (essentially measuring the goodness of fit of the points to a linear function) were all negative, ranging from r=-0.43 to r=-0.70, although none of the correlation values were statistically significant either.

The effect of training on presentation positions can be seen in Figure 28, where the results are split by training session, trained or untrained trials, and, in order to examine SL interactions, transition probability. Although no effects reached statistical significance, there is a pattern that corresponds to lower RTs for trained positions after training has occurred compared to untrained positions (Figure 28B), which is in line with the predicted PL effect. A 2 (trained/untrained position) x 3 (transition probability) x 2 (pre-/post-training session) repeated measures ANOVA did not show a significant interaction for position x session (F(1,5)=1.37, p=0.29) but a 2 (trained/untrained position) x 3 (transition probability) repeated measures ANOVA on the post-training session RT revealed a trend for lower average trained position RT (478.0ms) compared to average untrained position RT (491.0ms; main effect of position F(1,5)=4.727, p=0.082, partial η^2=0.22). There were no significant or trending results pertaining to the accuracy data, which also implies there was no speed-accuracy trade-off for the lower trained position RTs after training.

The visual assessment sessions before and after training were designed to investigate whether our training paradigm could transfer visual improvements to untrained tasks. If transfer occurred then we predicted to see improvements in the Landolt C task such that font size was reduced, in the cutoff spatial frequency task such that spatial frequency was increased, and in the MN Read test such that reading acuity and critical print size were decreased (which in logMAR units indicates smaller print sizes) and maximum reading speed was increased. There was a trend in the peripheral Landolt C data (Figure 29) in the predicted direction, where pre-training average font size (16.88) was larger than the post-training average font size (14.43; t(5)=2.52, p=0.053, Cohen's d=0.86). However, there was also a trend opposite the predicted direction in the central Landolt C data, where pre-training average font size (5.50) was smaller than the post-training average font size (6.00; t(5)=2.09, p=0.091, Cohen's d=0.91).

The cutoff spatial frequency data (Figure 30) show effects in the predicted direction for both locations, although only the peripheral location reached statistical significance. In the peripheral location, the average post-training cutoff spatial frequency (8.96 c/d) was significantly higher than the pre-training cutoff frequency (7.63 c/d; t(5)=5.69, p=0.0023, Cohen's d=1.88), and in the central location the average post-training cutoff spatial frequency (18.37 c/d) was higher than the pre-training cutoff frequency (16.93 c/d) but this difference did not reach statistical significance (t(5)=1.01, p=0.36, Cohen's d=0.42).

The MN Read data (Figure 31) did not reveal any evidence of transfer. There were no significant differences in reading acuity (pre-training mean: 0.015 logMAR; post-training mean: 0.0033 logMAR; t(5)=0.44, p=0.68, Cohen's d=0.14), critical print size (pre-training mean: 0.17 logMAR; post-training mean: 0.17 logMAR; t(5)<0.001, p>0.99, Cohen's d=0.00), or maximum reading speed (pre-training mean: 260.67 wpm; post-training mean: 246.67 wpm; t(5)=0.47, p=0.66, Cohen's d=0.30). It is worth noting that the MN Read task is the task most different from the training, both in dependent variable and in method of administration, and thus the lack of transfer observed in this task is not entirely surprising.

Behavioral Results – SL

As described in Experiment 1, a typical SL effect is a lower response latency for higher probability transitions compared to lower probability transitions after learning has occurred. Thus, we predicted to see effects in the second half of the training sessions, with a pattern of lowest RTs for trials at 60% likely positions, higher RTs for trials at 30% likely positions, and highest RTs for trials at 10% likely positions. This was examined separately for peripheral and central trials in each of the five training sessions (Figure 32). In addition, we examined RT in the first block of each EEG session, pre- and post-training, for comparison, although these sessions used different stimulus parameter and had lower overall RT. Unfortunately, in the peripheral location we did not observe the predicted SL effect in any of the training sessions, nor did we find an interaction between session and SL (mean 60% RT across sessions: 531.5ms; mean 30% RT across sessions: 529.6ms; mean 10% RT across sessions: 528.3ms; 3 (transition probability) x 5 (training session) repeated measures ANOVA main effect of transition probability $F(2,10)=0.52$, $p=0.61$; main effect of session $F(4,20)=0.195$, $p=0.94$; interaction $F(8,40)=0.61$, $p=0.76$). In the central location however, there was a significant main effect for transition probability ($F(2,10)=5.72$, $p=0.022$, partial $\eta^2=0.60$), where the mean of the 10% trials (539.3ms) was greater than the mean of the 60% trials (529.7ms) or the 30% trials (526.5ms). There was a large drop in mean 10% trial RT during the third training session, but the interaction between session day and transition probability was not statistically significant (F(8,40)=1.63, p=0.15) and this was likely random variation. SL was also examined across sessions by subtracting the first half mean RT from the second half mean RT, but as opposed to Experiment 1 this did not reveal any meaningful patterns and no F statistics on the data were significant or trending.

In the pre- and post-training EEG sessions, trials with trained statistics were compared to trials using untrained statistics (Figure 33) with a 2 (trained/untrained statistics) x 3 (transition probability) x 2 (session) repeated measures ANOVA. There was a trending interaction between transition probability and session (F(2,10)=3.37, p=0.076, partial η^2=0.50) which indicates that the differences between the different transition probabilities was different pre-training compared to post-training. However, the pattern of this interaction was not aligned with predicted SL effects – 10% trials showed the largest decrease in RT after training (mean pre-training: 496.2ms; mean post-training: 480.0ms; difference of -16.2ms), followed by 60% trials (mean pre-training: 484.8ms; mean post-training: 472.6ms; difference of -12.2ms), and then 30% trials (mean pre-training: 482.4ms; mean post-training: 482.0ms; difference of -0.4ms). No other SL effects were significant or trended on significance.

Behavioral Results – MI

Comparable to Experiment 1, there was an MI effect in Experiment 2 demonstrating increased response efficiency on trials with sound compared to trials without sound (Figure 34). A 2 (sound/no sound) x 3 (transition probability) x 2 (session) repeated measures

ANOVA revealed a significant main effect for sound, where there was lower mean RT for trials with sound (471.2ms) compared to trials without sound (495.7ms; F(1,5)=7.27, p=0.043, partial η^s=0.61) and higher accuracy for trials with sound (91.25%) compared to trials without sound (87.38%; F(1,5)=8.14, p=0.036, partial η^s=0.61). An interaction between sound and session would indicate that MI had changed as a result of training and while there was no significant interaction between sound and session for RT, (F(1,5)=0.60, p=0.47), the accuracy data showed a pattern of greater differences between sound and no sound trials after training (5.35%) compared to the differences seen before training (2.40%) that trended on significance (F(1,5)=4.84, p=0.079, partial η^2=0.5). There were no significant interactions between sound and SL.

EEG Data

As in Experiment 1, we predicted that SL effects would appear as differences in alpha power for different transition probabilities, such that higher transition probability trials would contain more alpha power after the stimulus appears compared to lower transition probability trials. EEG data was thus analyzed by looking for differences in alpha power averaged over the period of time 250ms-500ms after the stimulus appeared onscreen, named here the "post-stimulus interval", an analysis based on methods in Bays et al. (2015). Figure 35 displays these data split by transition probability and session. A 3 (transition probability) x 2 (session) repeated measures ANOVA using the mean alpha power from the post-stimulus interval did not reveal any statistically significant main effects or interactions (main effect of probability: F(2,10)=0.82, p=0.47; main effect of session: F(1,5)=0.12, p=0.74; interaction F(2,10)=0.42, p=0.67). There was a pattern for the 30% trials to contain more alpha power during this interval in the post-training session (.30) than in the pre-training session (.21) but this difference was not significant, nor would it be compatible with our predictions for only the 30% trials to show a difference in this interval.

We also examined whether there was a general PL effect for task learning by following Bays et al. (2015) and looking at alpha for all visible trials before and after training (Figure 36). Statistics were performed by averaging alpha power over the 600ms before the stimulus was shown (the "pre-stimulus interval") and over the period of time 250ms-500ms after the stimulus appeared (the "post-stimulus interval"). Although there was a pattern of more alpha power in the pre-stimulus interval post-training (.53) compared to pre-training (.42) as seen in Bays et al. (2015), the difference did not reach statistical significance (t(5)=0.76, p=0.48, Cohen's d=0.31). There was no significant difference in the post-stimulus interval post-training (.29) compared to pre-training (.23; t(5)=0.41, p=0.70, Cohen's d=0.17), which agrees with the previous results of Bays et al. (2015) but does not provide evidence for those results.

Discussion

In a series of experiments, we used a novel training paradigm to examine PL, SL, and MI; interactions between them; how alpha power informs the results; and whether learning transferred outside of the trained task. We found some evidence for PL, some evidence for SL, strong evidence for MI, some transfer to untrained tasks, and a large amount of results that did not reach statistical significance.

Evidence of PL was not as strong as expected although some results did suggest that PL occurred. RT for stimuli at trained positions was lower than at untrained positions in Experiment 1 and the same pattern appeared after training in Experiment 2. Given that there was only one day of training in Experiment 1, it is possible that this result of PL appears sooner than other PL results such as decreased thresholds. In Experiment 2, contrast thresholds did decrease for each spatial frequency and location across training days but not to the point of statistical significance. One possible explanation for this is improper estimation of contrast by the QUEST procedure. QUEST is a Bayesian method for estimating thresholds based on priors about the test population that are fed to the procedure as free parameters. If the priors that we chose to use did not accurately reflect parameters of our test population then QUEST may have reached incorrect estimations of their contrast thresholds on each day. Another possible explanation is that there were divided attentional effects resulting from the complex nature of the training paradigm. PL studies typically use stimuli and tasks that serve the sole purpose of producing PL effects. Training typically occurs in a single location with stimuli that vary on a single dimension. In our experiments, however, we use a paradigm that serves multiple purposes and contains multiple interacting parameters, including contrast, location, transition probabilities, and sound. There is little previous evidence to inform us as to how participants might react to a paradigm such as this and thus attentional effects, or roving effects, may play a very large role in the results. A third plausible explanation is that the results contained a large amount of variance due to our sample size. Although our sample sizes (N=15 in Experiment 1, N=15 in the control study of Experiment 1, N=6 in Experiment 2) are typical for PL studies, if the underlying effects we are analyzing are not large, then our sample sizes may not have been sufficient to capture the effect. Our use of the peak spatial frequency in the pre-training and post-training EEG sessions may have also obscured some PL effects. One might reasonably expect that the cutoff spatial frequency would demonstrate more PL effects due to the nature of there being more room for perceptual improvement for those stimuli. Thus in future versions of this experiment, using the cutoff spatial frequency for pre- and post-training sessions may reveal additional aspects of PL.

Transfer to untrained tasks was seen in the Landolt C test and the cutoff spatial frequency test, but not the MN Read test, of Experiment 2. In both the Landolt C results and the cutoff spatial frequency results there were improvements in the periphery, demonstrating that some visual acuity improved as a result of the training paradigm. The transfer of PL to untrained tasks is becoming well documented (Deveau, Lovcik, & Seitz, 2014; Deveau, Ozer, & Seitz, 2014; Hung & Seitz, 2014) and our data provide more evidence for PL transfer. It is also worth noting that our use of QUEST produced a much higher ratio of difficult trials (near threshold) than if we had used multiple short staircases. A high ratio of difficult trials has been linked to greater location specificity in PL (Hung & Seitz, 2014) and it is possible that if we adjusted the number of trials at threshold that we might find more transfer.

Evidence of SL was produced in both experiments, most notably in the control study of Experiment 1 that used a non-adaptive contrast, although predicted patterns of results were also seen in the RT differences of the adaptive version of Experiment 1 and in greater overall RTs for 10% trials in the second half of the training sessions in Experiment 2. In both studies the separation of 10% trials was more clear than the separation of 60% and 30% trials, suggesting that the strongest effect of the statistical structure was that participants learned that stimuli shouldn't appear in the same location twice (which is where all 10% presentations appeared). A number of factors may have affected learning of the statistical structure. Most SL studies are conducted using stimuli that are easy to see and presented centrally in the visual field. In fact we are aware of only one other study that has examined SL at threshold contrast levels (Bays et al., 2016). In that study, the researchers did not find strong RT results either. They did, however, find multiple patterns of RT after splitting the data up according to a post-learning test. The present paradigm did not lend itself to a similar analysis but it is well worth considering whether individual differences and multiple underlying processes may be obscuring SL effects in our data. Attention may also play a role in our SL effects. Although SL studies are often conducted with passive exposure or with cover tasks, attention is known to affect SL (Turk-Browne, Jungé, & Scholl, 2005) and also to be affected by SL (Zhao et al., 2013). If PL is drawing attention away from the statistical regularities then they may not be learned as well as they would otherwise, and if the statistical regularities are drawing attention away from the PL aspect of the study, then that might explain the smaller than expected PL effects. With respect to the greater effect for 10% trials compared to 60% or 30% trials, it may be possible that the difference between 60% trials and 30% trials in the Markov chain we constructed to control the location transitions was too subtle. However, this is belied by numerous studies of SL and of artificial grammar learning which have used transitional probabilities at least as complex as ours (Chalk et al., 2010; Cleeremans & McClelland, 1991; Hunt & Aslin, 2001; Lieberman, Chang, Chiao, Bookheimer, & Knowlton, 2004; Reber, 1967; Seger, Prabhakaran, Poldrack, & Gabrieli, 2000). Further research will be required to determine the factors affecting SL in this paradigm.

Analyses of alpha power did not reveal any statistically significant results but did show patterns consistent with SL and with previous PL research. Alpha power has been used as a proxy for attentional resources (Bays et al., 2015; Freyer et al., 2013; Sigala et al., 2014) and thus unexpected stimuli were predicted to reduce alpha to a greater extent than expected stimuli. Alpha power in Experiment 1 followed this prediction with a pattern of higher alpha power for higher probability trial positions, although the fact that these differences begin before the stimulus onset is problematic. This could be explained by temporal spreading that occurs when converting the time domain EEG signal to the time-frequency domain, or it could be that the pattern seen here is simply random variation and not reliable. In Experiment 2 there is additional evidence for SL when examining the pattern of alpha power for trial types in the post-training session (Figure 35D). Although not significant, there is less alpha power for 10% trial types after stimulus onset, which is in accordance with our predictions and the attentional resources explanation. This result also provides more evidence that the 10% probabilities were learned better than the 60% or 30% probabilities.

The alpha results also suggested that overall task learning that was not specific to any trial type may have occurred, as evidenced by a pattern of higher alpha power after training compared to before training. This pattern replicates the results of Bays et al. (2015) and could mean that participants are able to perform the task in this experimental paradigm with fewer attentional resources after training than they were able to before training. There are several possible reasons why the comparable results in the present study did not reach statistical significance as they did in Bays et al. (2015). The use of auditory stimuli in the present study may have reduced alpha in both sessions due to the alerting nature of the tones. Alpha power is also known to modulate depending on which features of visual stimuli are being attended (Snyder & Foxe, 2010) and so variance may have arisen from different participants focusing on different aspects of the visual stimuli in the present study.

MI was most clearly seen in significantly decreased RT and increased accuracy for multisensory trials compared to visual-only trials in both experiments. Although this result may not be surprising, it demonstrates that participants were able to use information from both modalities and that this began early on in training, as evidenced by the visibility of the effect in the pre-training session of Experiment 2. The lack of further MI interactions with SL or PL could be due to a variety of issues, most notably the lack of many significant unisensory results for the visual stimuli. As it is unclear how strongly PL or SL occurred, it is also unclear as to whether MI interactions with them failed because of a lack of integration or because of a lack of learning in either of the individual modalities.

In sum, our training paradigm showed PL effects, SL effects, multisensory effects, and some transfer to untrained tasks, which, while all promising, were not as strong as predicted. The complexity of the experiments leaves many possible explanations for the lack of results, including attentional effects, within-session fatigue, lack of power due to low cohort sizes, and inability of participants to learn the statistical sequences. Future designs investigating the interactions of PL, SL, and MI, might benefit from simplifying the experimental design and investigating pieces of this paradigm individually in order to reduce variance before combining them further.

References

Abla, D., Katahira, K., & Okanoya, K. (2008). On-line assessment of statistical learning by event-related potentials. *Journal of Cognitive Neuroscience*, *20*(6), 952–64. http://doi.org/10.1162/jocn.2008.20058

Abla, D., & Okanoya, K. (2009). Visual statistical learning of shape sequences: An ERP study. *Neuroscience Research*, *64*(2), 185–90. http://doi.org/10.1016/j.neures.2009.02.013

Adini, Y., Sagi, D., & Tsodyks, M. (2002). Context-enabled learning in the human visual system. *Nature*, *415*(6873), 790–793. http://doi.org/10.1038/415790a

Ahissar, M., & Hochstein, S. (2004). The reverse hierarchy theory of visual perceptual learning. *Trends in Cognitive Sciences*, *8*(10), 457–64. http://doi.org/10.1016/j.tics.2004.08.011

Bao, M., Yang, L., Rios, C., He, B., & Engel, S. A. (2010). Perceptual learning increases the strength of the earliest signals in visual cortex. *Journal of Neuroscience*, *30*(45), 15080–15084.

Barakat, B. K., Seitz, A. R., & Shams, L. (2013). The effect of statistical learning on internal stimulus representations: Predictable items are enhanced even when not predicted. *Cognition*, *129*(2), 205–211. http://doi.org/10.1016/j.cognition.2013.07.003

Bays, B. C., Turk-Browne, N. B., & Seitz, A. R. (2016). Dissociable behavioural outcomes of visual statistical learning. *Visual Cognition*, *6285*(February), 1–26. http://doi.org/10.1080/13506285.2016.1139647

Bays, B. C., Visscher, K. M., Le Dantec, C. C., & Seitz, A. R. (2015). Alpha-band EEG activity in perceptual learning. *Journal of Vision*, *15*(10), 1–12. http://doi.org/10.1167/15.10.7.doi

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*, 433–436.

Chalk, M., Seitz, A. R., & Seriès, P. (2010). Rapidly learned stimulus expectations alter perception of motion. *Journal of Vision*, *10*(8), 1–18. http://doi.org/10.1167/10.8.2

Cleeremans, A., & McClelland, J. L. (1991). Learning the structure of event sequences. *Journal of Experimental Psychology. General*, *120*(3), 235–253. http://doi.org/10.1037/0096-3445.120.3.235

Conway, C. M., & Christiansen, M. H. (2006). Statistical learning within and between modalities. *Psychological Science*, *17*(10), 905–912.

Das, K., Giesbrecht, B., & Eckstein, M. P. (2010). Predicting variations of perceptual performance across individuals from neural activity using pattern classifiers. *NeuroImage*, *51*(4), 1425–1437. http://doi.org/10.1016/j.neuroimage.2010.03.030

Deveau, J., Lovcik, G., & Seitz, A. R. (2014). Broad-based visual benefits from training with an integrated perceptual-learning video game. *Vision Research*, *99*, 134–140. http://doi.org/10.1016/j.visres.2013.12.015

Deveau, J., Ozer, D. J., & Seitz, A. R. (2014). Improved vision and on-field performance in baseball through perceptual learning. *Current Biology*, *24*(4), R146–R147. http://doi.org/10.1016/j.cub.2014.01.004

Dobres, J., & Seitz, A. R. (2010). Perceptual learning of oriented gratings as revealed by classification images. *Journal of Vision*, *10*(13), 8–11. http://doi.org/10.1167/10.13.8.Introduction

Fahle, M. (2005). Perceptual learning: specificity versus generalization. *Current Opinion in Neurobiology*, *15*(2), 154–160. http://doi.org/10.1016/j.conb.2005.03.010

Fahle, M., Edelman, S., & Poggio, T. (1995). Fast perceptual learning in hyperacuity. *Vision Research*, *35*(21), 3003–3013.

Fiser, J., & Aslin, R. N. (2001). Unsupervised statistical learning of higher-order spatial structures from visual scenes. *Psychological Science*, *12*(6), 499–504.

Fiser, J., & Aslin, R. N. (2002). Statistical learning of higher-order temporal structure from visual shape sequences. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *28*(3), 458–467.

Fiser, J., & Aslin, R. N. (2005). Encoding multielement scenes: Statistical learning of visual feature hierarchies. *Journal of Experimental Psychology: General*, *134*(4), 521–537.

Freyer, F., Becker, R., Dinse, H. R., & Ritter, P. (2013). State-dependent perceptual learning. *The Journal of Neuroscience*, *33*(7), 2900–2907. http://doi.org/10.1523/JNEUROSCI.4039-12.2013

Ghose, G. M. (2004). Learning in mammalian sensory cortex. *Current Opinion in Neurobiology*, *14*(4), 513–8. http://doi.org/10.1016/j.conb.2004.07.003

Hauser, M. D., Newport, E. L., & Aslin, R. N. (2001). Segmentation of the speech stream in a non-human primate: Statistical learning in cotton-top tamarins. *Cognition*, *78*(3), B53–B64.

Hua, T., Bao, P., Huang, C.-B., Wang, Z., Xu, J., Zhou, Y., & Lu, Z.-L. (2010). Perceptual Learning Improves Contrast Sensitivity of V1 Neurons in Cats. *Current Biology*, *20*, 887–894.

Hung, S.-C., & Seitz, A. R. (2014). Prolonged training at threshold promotes robust retinotopic specificity in perceptual learning. *The Journal of Neuroscience*, *34*(25), 8423–8431. http://doi.org/10.1523/JNEUROSCI.0745-14.2014

Hunt, R., & Aslin, R. (2001). Statistical learning in a serial reaction time task: Access to separable statistical cues by individual learners. *Journal of Experimental Psychology: General*, *130*(4), 658–680.

Hussain, Z., Sekuler, A. B., & Bennett, P. J. (2011). Superior identification of familiar visual patterns a year after learning. *Psychological Science*, *22*(6), 724–730. http://doi.org/10.1177/0956797611409591

Keil, A., Debener, S., Gratton, G., Junghöfer, M., Kappenman, E. S., Luck, S. J., … Yee, C. M. (2014). Committee report: publication guidelines and recommendations for studies using electroencephalography and magnetoencephalography. *Psychophysiology*, *51*(1), 1–21. http://doi.org/10.1111/psyp.12147

Kim, R., Seitz, A., & Shams, L. (2008). Benefits of Stimulus Congruency for Multisensory Facilitation of Visual Learning. *PloS One*, *3*(1), e1532.

Kleiner, M., Brainard, D. H., & Pelli, D. G. (2007). What's new in Psychtoolbox-3? *Perception*, *36*(ECVP Abstract Supplement).

Koelewijn, T., Bronkhorst, A., & Theeuwes, J. (2010). Attention and the multiple stages of multisensory integration: A review of audiovisual studies. *Acta Psychologica*, *134*(3), 372–384. http://doi.org/10.1016/j.actpsy.2010.03.010

Lieberman, M. D., Chang, G. Y., Chiao, J., Bookheimer, S. Y., & Knowlton, B. J. (2004). An event-related fMRI study of artificial grammar learning in a balanced chunk strength design. *Journal of Cognitive Neuroscience*, *16*(3), 427–438. http://doi.org/10.1162/089892904322926764

Loftus, G. R., & Masson, M. E. J. (1994). Using confidence intervals in within-subject designs. *Psychonomic Bulletin & Review*, *1*(4), 476–490.

Oostenveld, R., Fries, P., Maris, E., & Schoffelen, J.-M. (2011). FieldTrip: Open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. *Computational Intelligence and Neuroscience*, *2011*(156869), 1–9. http://doi.org/10.1155/2011/156869

Oostenveld, R., & Praamstra, P. (2001). The five percent electrode system for high-resolution EEG and ERP measurements. *Clinical Neurophysiology : Official Journal of the International Federation of Clinical Neurophysiology*, *112*(4), 713–719.

Pflieger, M. (2001). Theory of a spatial filter for removing ocular artifacts with preservation of EEG. *EMSE Workshop*, 7–8.

Powers, A. R., Hevey, M. A., & Wallace, M. T. (2012). Neural Correlates of Multisensory Perceptual Learning. *Journal of Neuroscience*, *32*(18), 6263–6274. http://doi.org/10.1523/JNEUROSCI.6138-11.2012

Raposo, D., Sheppard, J. P., Schrater, P. R., & Churchland, A. K. (2012). Multisensory decision-making in rats and humans. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *32*(11), 3726–35. http://doi.org/10.1523/JNEUROSCI.4998-11.2012

Reber, A. S. (1967). Implicit learning of artificial grammars. *Journal of Verbal Learning and Verbal Behavior*, *6*(6), 855–863. http://doi.org/10.1016/S0022-5371(67)80149-X

Romei, V., Gross, J., & Thut, G. (2012). Sounds reset rhythms of visual cortex and corresponding human visual perception. *Current Biology*, *22*(9), 807–813. http://doi.org/10.1016/j.cub.2012.03.025

Saffran, J. R., Aslin, R. N., & Newport, E. L. (1996). Statistical learning by 8-month-old infants. *Science*, *274*(5294), 1926–1928.

Sagi, D. (2011). Perceptual learning in Vision Research. *Vision Research*, *51*(13), 1552–1566. http://doi.org/10.1016/j.visres.2010.10.019

Sasaki, Y., Náñez, J., & Watanabe, T. (2012). Recent progress in perceptual learning research. *Wiley Interdisciplinary Reviews: Cognitive Science*, *3*(3), 293–299. http://doi.org/10.1002/wcs.1175.Recent

Schoups, A., Vogels, R., Qian, N., & Orban, G. (2001). Practising orientation identification improves orientation coding in V1 neurons. *Nature*, *412*(August), 549–553.

Seger, C., Prabhakaran, V., Poldrack, R. A., & Gabrieli, J. (2000). Neural activity differs between explicit and implicit learning of artificial grammar strings: An fMRI study. *Psychobiology*, *28*(3), 283–292.

Seitz, A. R., & Dinse, H. R. (2007). A common framework for perceptual learning. *Current Opinion in Neurobiology*, *17*, 148–153.

Seitz, A. R., Kim, R., & Shams, L. (2006). Sound facilitates visual learning. *Current Biology*, *16*, 1422–1427.

Seitz, A. R., Kim, R., van Wassenhove, V., & Shams, L. (2007). Simultaneous and independent acquisition of multisensory and unisensory associations. *Perception*, *36*(10), 1445–1453.

Shams, L., Kamitani, Y., & Shimojo, S. (2000). What you see is what you hear. *Nature*, *408*(December), 2000. http://doi.org/10.1038/35048669

Shams, L., & Seitz, A. R. (2008). Benefits of Multisensory Learning. *Trends in Cognitive Sciences*, *12*(11), 411–417.

Sheppard, J., Raposo, D., & Churchland, A. (2013). Dynamic weighting of multisensory stimuli shapes decision-making in rats and humans. *Journal of Vision*, *13(6)*(4), 1–19. http://doi.org/10.1167/13.6.4.doi

Shimojo, S., & Shams, L. (2001). Sensory modalities are not seperate modalities: plasticity and interactions. *Current Opinion in Neurobiology*, *11*, 505–509.

Sigala, R., Haufe, S., Roy, D., Dinse, H. R., & Ritter, P. (2014). The role of alpha-rhythm states in perceptual learning: insights from experiments and computational models. *Frontiers in Computational Neuroscience*, *8*(36), 1–19. http://doi.org/10.3389/fncom.2014.00036

Snyder, A. C., & Foxe, J. J. (2010). Anticipatory attentional suppression of visual features indexed by oscillatory alpha-band power increases: a high-density electrical mapping study. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *30*(11), 4024–4032. http://doi.org/10.1523/JNEUROSCI.5684-09.2010

Stein, B. E., & Stanford, T. R. (2008). Multisensory integration: current issues from the perspective of the single neuron. *Nature Reviews. Neuroscience*, *9*(4), 255–266. http://doi.org/10.1038/nrn2377

Turk-Browne, N. B. (2012). Statistical learning and its consequences. In M. D. Dodd & J. H. Flowers (Eds.), *The Influence of Attention, Learning, and Motivation on Visual Search* (pp. 117–146). New York, NY: Springer New York. http://doi.org/10.1007/978-1-4614-4794-8

Turk-Browne, N. B., Isola, P. J., Scholl, B., & Treat, T. A. (2008). Multidimensional visual statistical learning. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *34*(2), 399–407.

Turk-Browne, N. B., Jungé, J. A., & Scholl, B. J. (2005). The automaticity of visual statistical learning. *Journal of Experimental Psychology: General*, *134*(4), 552–564.

von Kriegstein, K., & Giraud, A. L. (2006). Implicit multisensory associations influence voice recognition. *PLoS Biology*, *4*(10), 1809–1820. http://doi.org/10.1371/journal.pbio.0040326

Watanabe, T., & Sasaki, Y. (2015). Perceptual learning: Toward a comprehensive theory. *Annual Review of Psychology*, *66*, 197–221. http://doi.org/10.1146/annurev-psych-010814-015214

Watson, A. B., & Pelli, D. G. (1983). QUEST: A Bayesian adaptive psychometric method. *Perception and Psychophysics*, *33*(2), 113–120.

Woodman, G. F. (2010). A brief introduction to the use of event-related potentials in studies of perception and attention. *Attention, Perception, & Psychophysics*, *72*(8), 2031–2046. http://doi.org/10.3758/APP

Xiao, L.-Q., Zhang, J.-Y., Wang, R., Klein, S. a, Levi, D. M., & Yu, C. (2008). Complete transfer of perceptual learning across retinal locations enabled by double training. *Current Biology : CB*, *18*(24), 1922–1926. http://doi.org/10.1016/j.cub.2008.10.030

Yang, T., & Maunsell, J. H. R. (2004). The effect of perceptual learning on neuronal responses in monkey visual area V4. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *24*(7), 1617–1626. http://doi.org/10.1523/JNEUROSCI.4442-03.2004

Yu, C., Klein, S. A., & Levi, D. M. (2004). Perceptual learning in contrast discrimination and the (minimal) role of context. *Journal of Vision*, *4*, 169–182. http://doi.org/10.1167/4.3.4

Zhang, J.-Y., Zhang, G.-L., Xiao, L.-Q., Klein, S. a, Levi, D. M., & Yu, C. (2010). Rule-based learning explains visual perceptual learning and its specificity and transfer. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *30*(37), 12323–12328. http://doi.org/10.1523/JNEUROSCI.0704-10.2010

Zhao, J., Al-Aidroos, N., & Turk-Browne, N. B. (2013). Attention is spontaneously biased toward regularities. *Psychological Science*, *24*(5), 667–677. http://doi.org/10.1177/0956797612460407

Figures

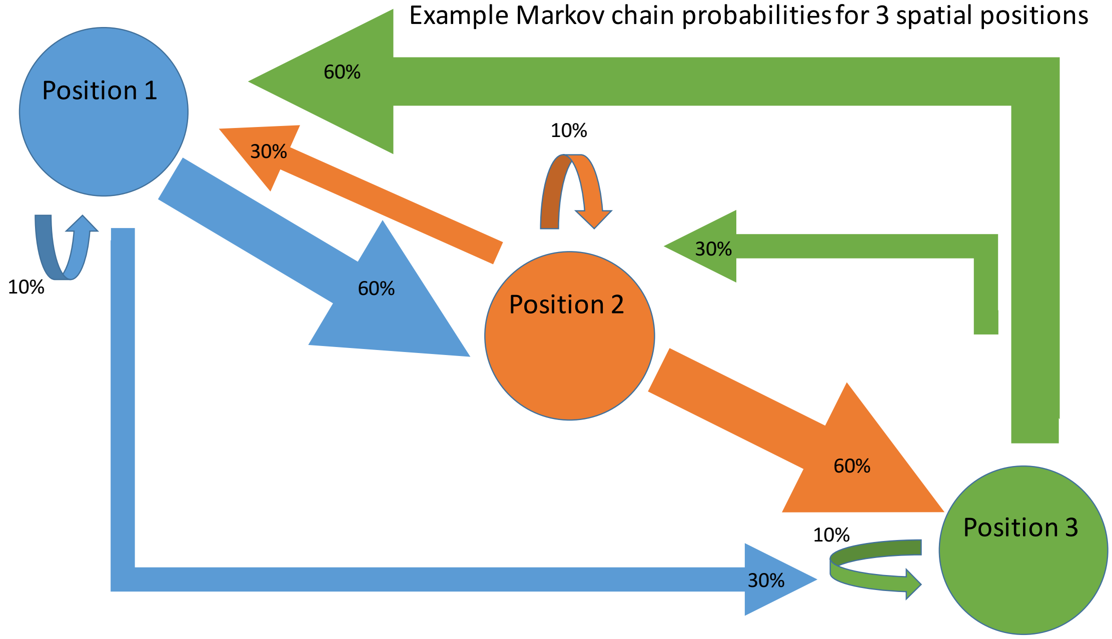

Figure 18 – Example of a modified Markov chain controlling the spatial transition probabilities for one participant. After a stimulus presentation at a location, there were a set of probabilities dictating where the next stimulus presentation would occur. See text for further details.

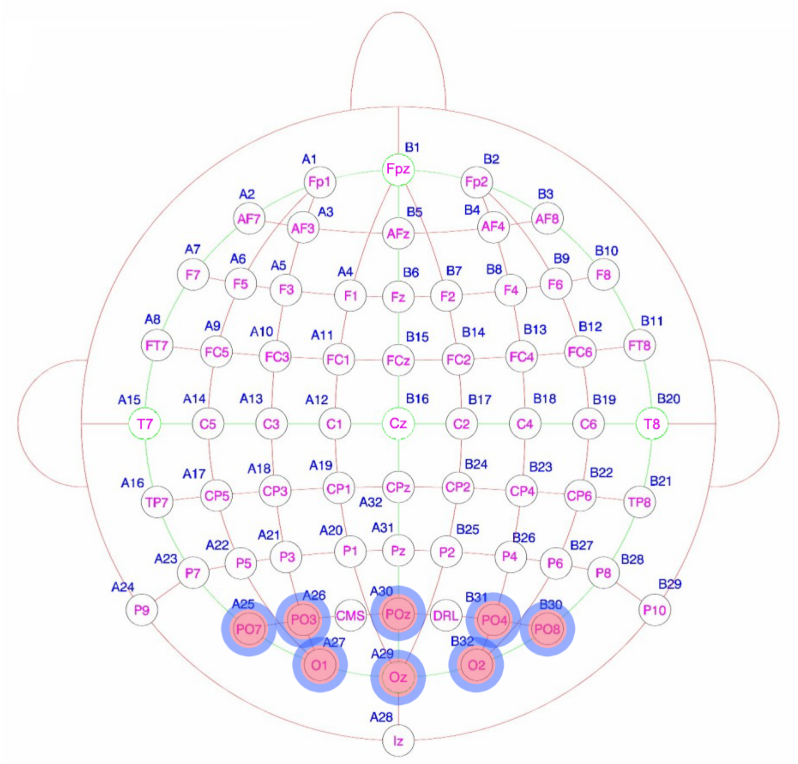

Figure 19 – Overhead view of the 64 electrode placement using the BioSemi ActiveTwo system. Red highlighted regions denote electrodes used in the alpha power analyses, corresponding approximately to sites Oz, O1, O2, POz, PO3, PO4, PO7, and PO8.

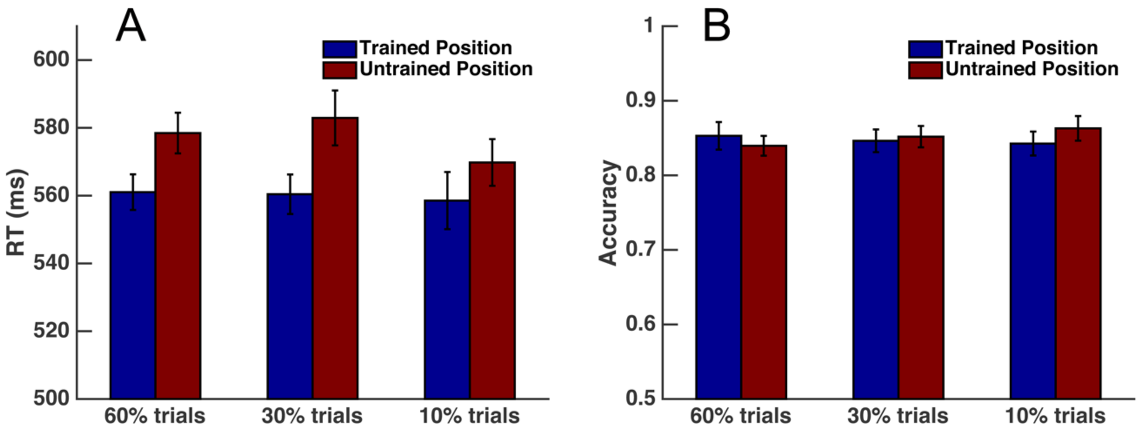

Figure 20 – (A) RT for trained and untrained positions in the second session of Experiment 1, split by transition probability. (B) Accuracy for trained and untrained positions in the second session of Experiment 1, split by transition probability. Blue bars denote trained positions; red bars denote untrained positions. Error bars denote +/- 1 within-subject SEM (Loftus & Masson, 1994). N = 15.

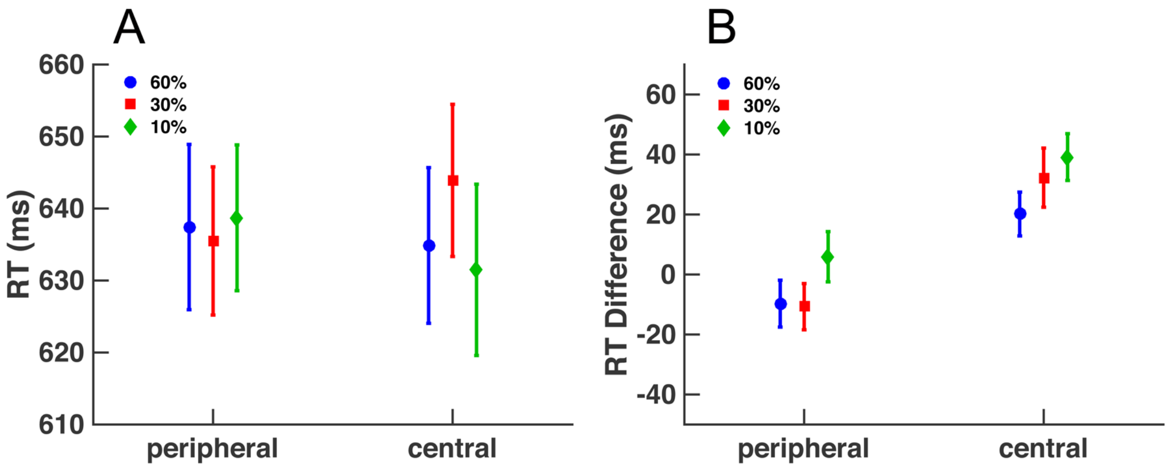

Figure 21 – Experiment 1 SL during training session. (A) RT in second half of the session split by transition probability and presentation location. (B) RT from the second half of the session minus the RT from the first half of the session, split by transition probability and presentation location. Blue circles denote 60% trials, red squares denote 30% trials, and green diamonds denote 10% trials. Error bars denote +/- 1 within-subject SEM. N = 15.

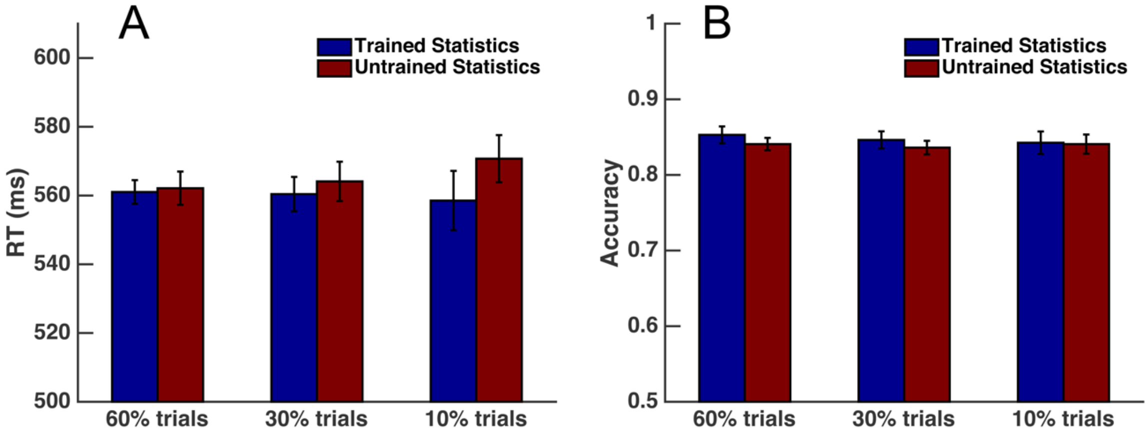

Figure 22 – (A) RT for trained and untrained statistics in the second session of Experiment 1, split by transition probability. (B) Accuracy for trained and untrained statistics in the second session of Experiment 1, split by transition probability. Blue bars denote trained statistics; red bars denote untrained statistics. Error bars denote +/- 1 within-subject SEM. N = 15.

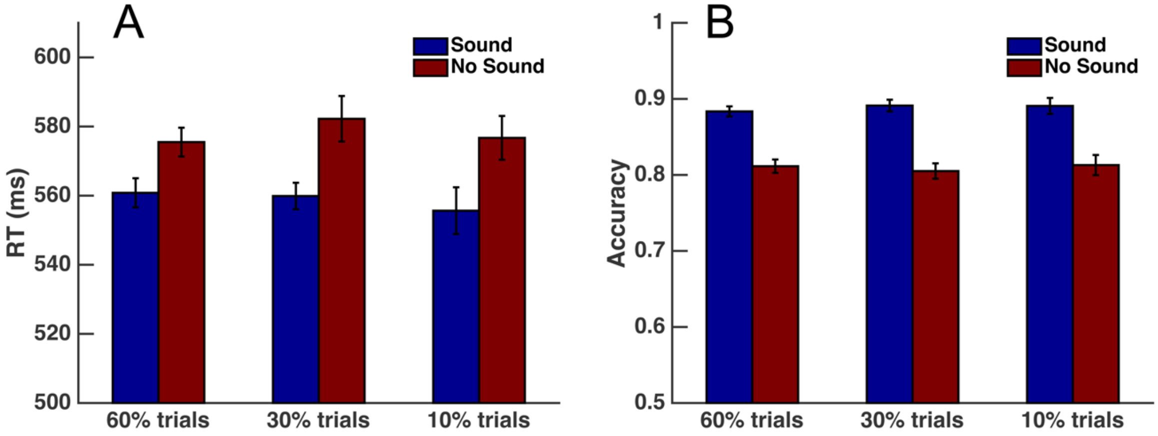

Figure 23 – (A) RT for trials with and without sound in the second session of Experiment 1, split by transition probability. (B) Accuracy for trials with and without sound in the second session of Experiment 1, split by transition probability. Blue bars denote trials with sound; red bars denote trials without sound. Error bars denote +/- 1 within-subject SEM. N = 15.

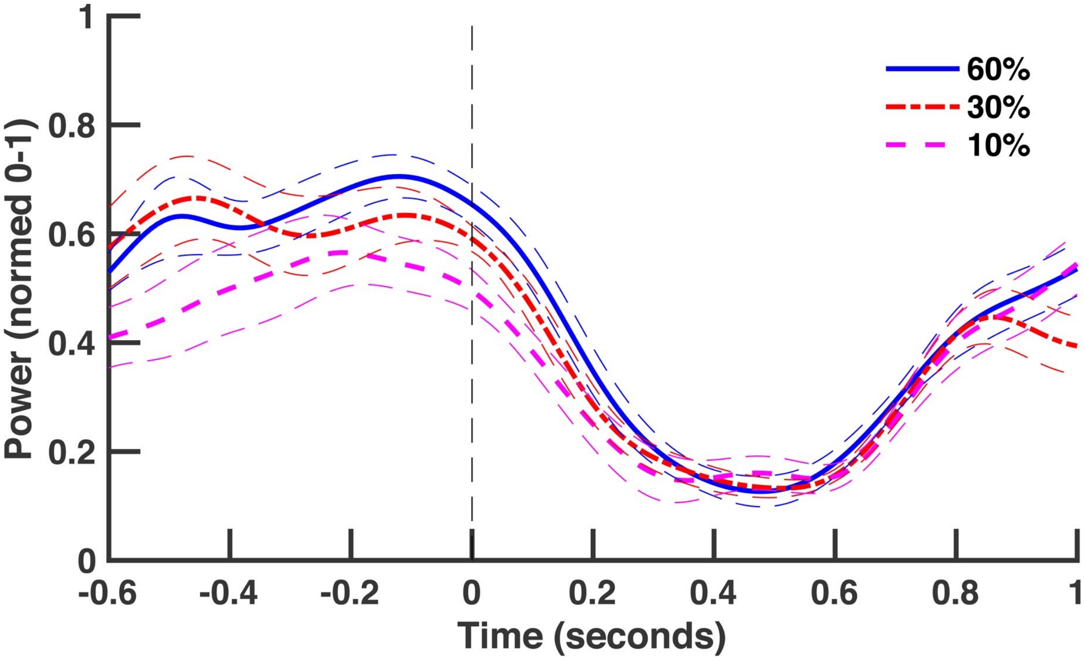

Figure 24 – Alpha power for 60% trials (thick blue solid line), 30% trials (thick red dotted line), and 10% trials (thick pink dashed line) in the second session of Experiment 1. Thinner dashed lines denote +/- 1 within-subject SEM for the respective color. N = 15.

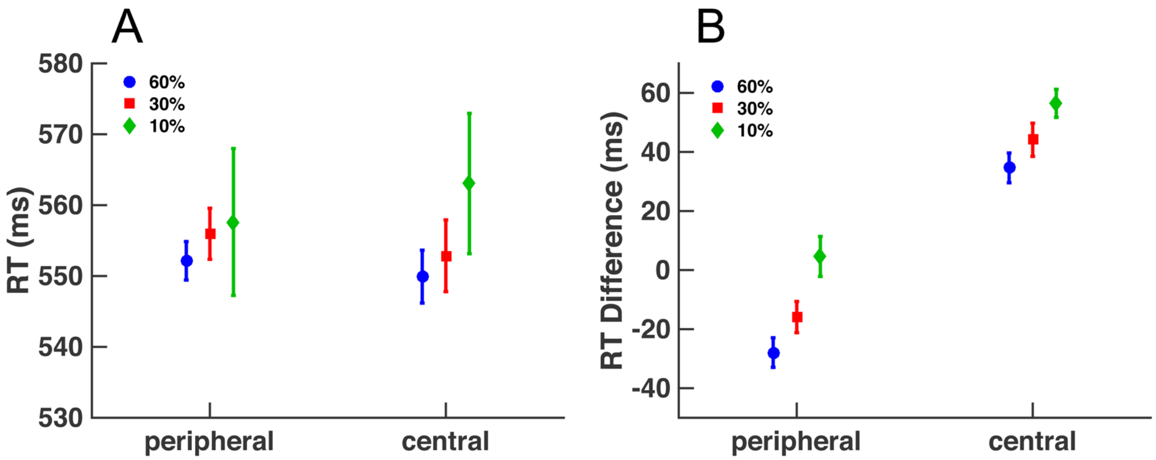

Figure 25 – Experiment 1 control study (non-adaptive contrast) SL during training session. (A) RT in second half of the session split by transition probability and presentation location. (B) RT from the second half of the session minus the RT from the first half of the session, split by transition probability and presentation location. Blue circles denote 60% trials, red squares denote 30% trials, and green diamonds denote 10% trials. Error bars denote +/- 1 within-subject SEM. N = 15.

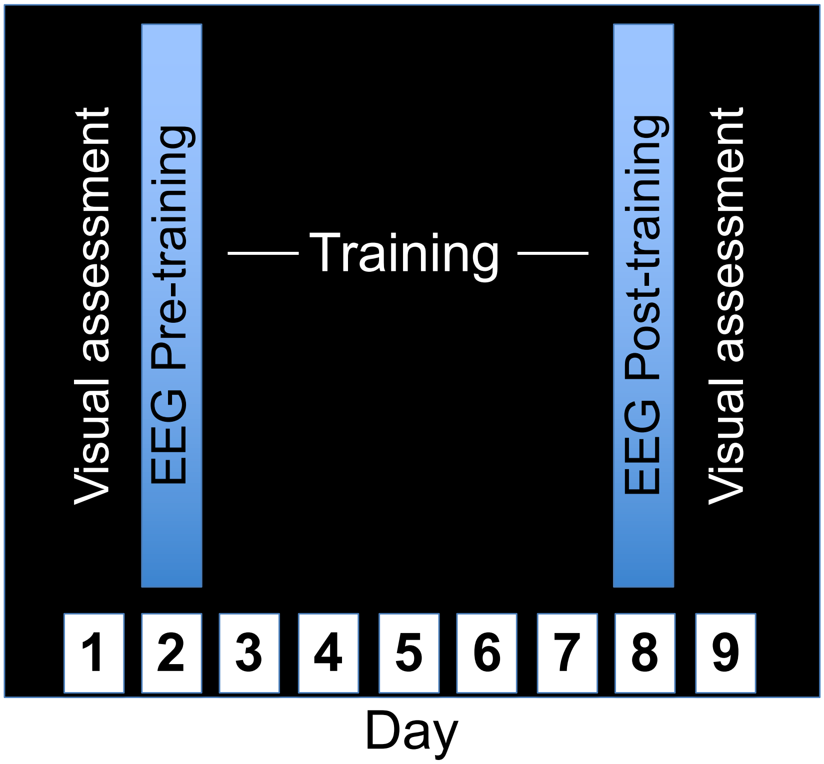

Figure 26 – Schedule of the experimental sessions for Experiment 2. Days 1 and 9 consisted of visual assessments before and after training, Days 2 and 8 consisted of EEG recordings before and after training, and Days 3-7 consisted of the training sessions. See text for descriptions of each session type.

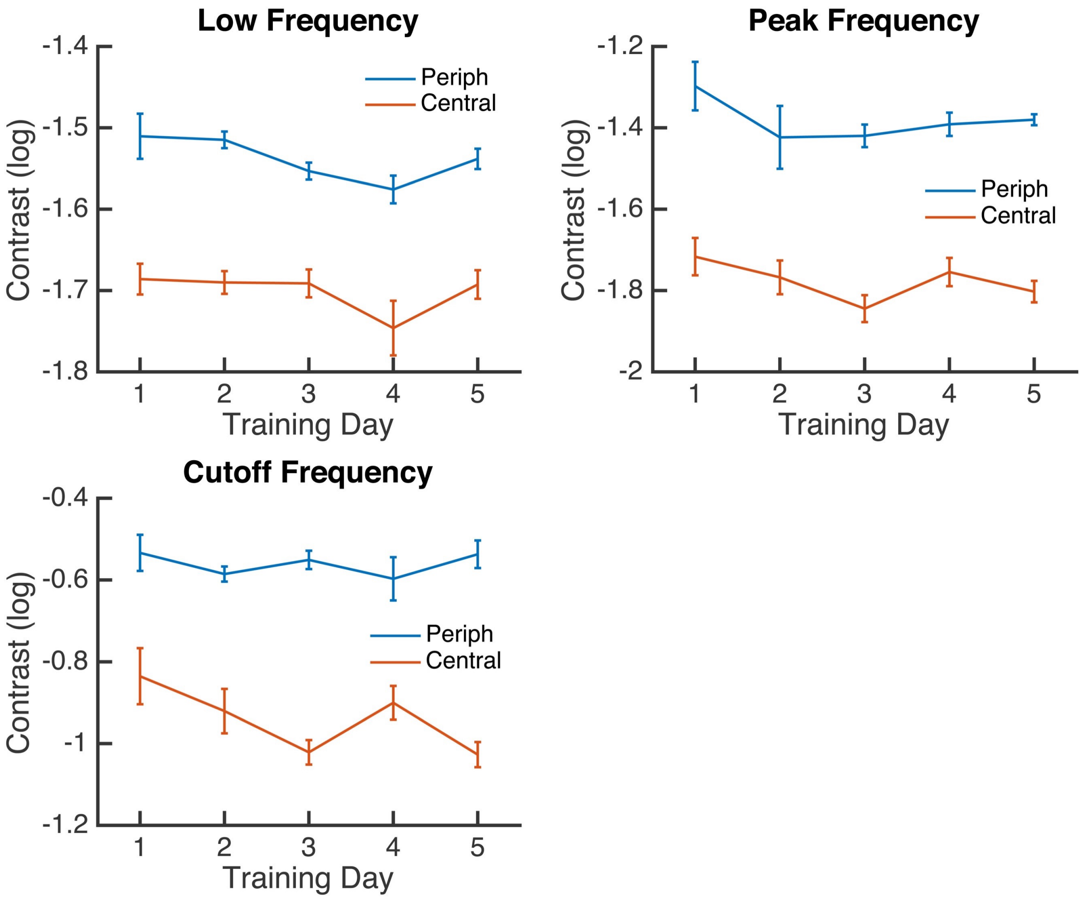

Figure 27 – Contrast threshold in logarithmic units as a function of training day, spatial frequency, and position. (A) Low spatial frequency, (B) peak spatial frequency, (C) cutoff spatial frequency. Blue curves denote peripheral trials; red curves denote central trials. Error bars denote +/- 1 within-subject SEM. N = 6.

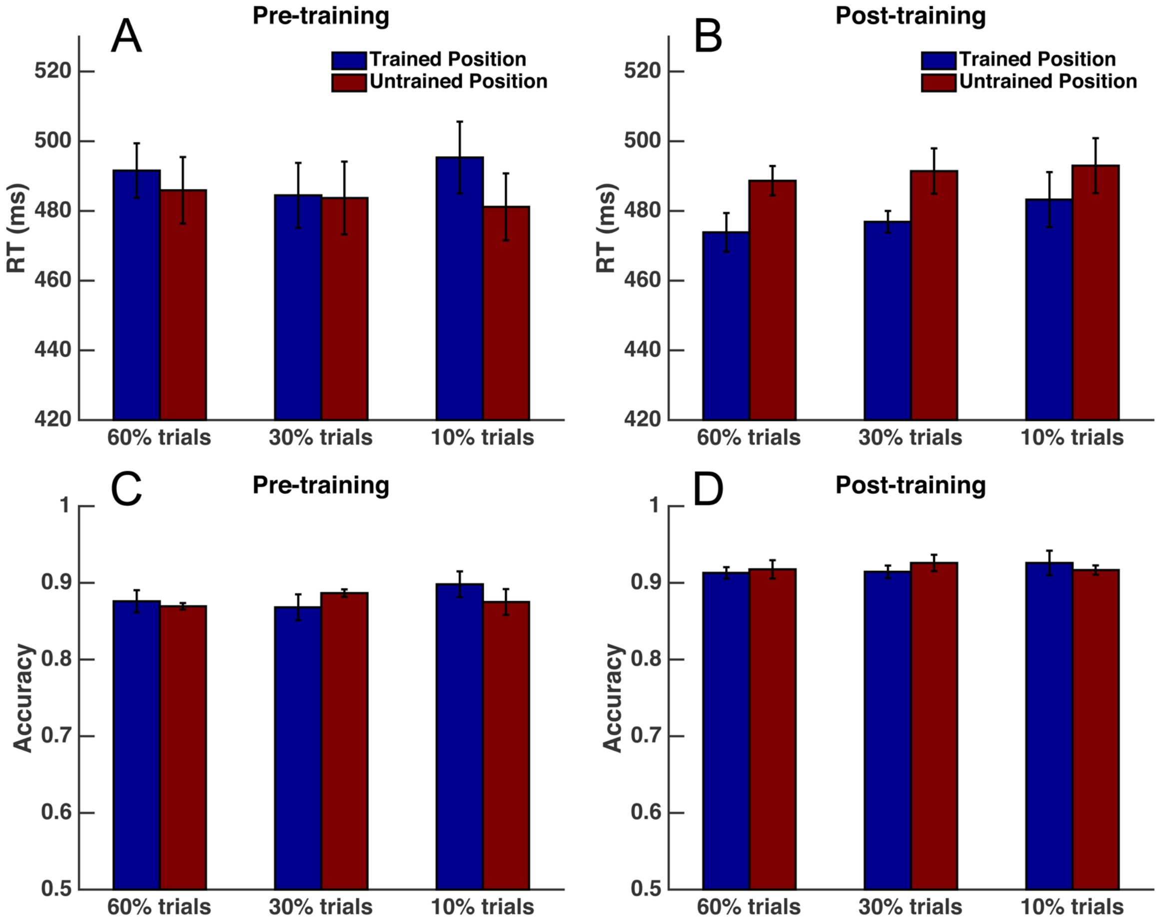

Figure 28 – Trained vs. untrained positions, split by session and transition probability. (A) Mean RT in pre-training session; (B) Mean RT in post-training session; (C) Mean accuracy in pre-training session; (D) Mean accuracy in post-training session. Blue bars denote trials using trained positions, red bars denote trials using untrained positions. Error bars denote +/- 1 within-subject SEM. N = 6.

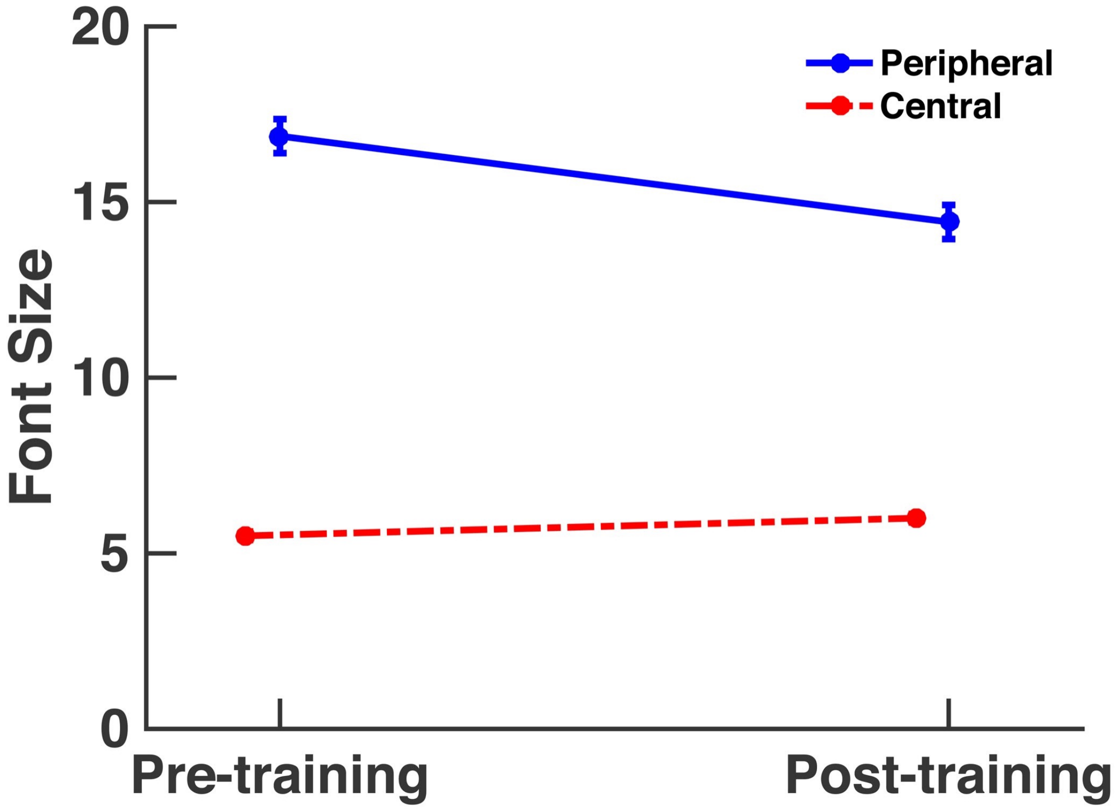

Figure 29 – Landolt C results, split by session and presentation location. Blue solid curves denote peripheral trials; red dashed curves denote central trials. Error bars (which may be obscured by the data markers) denote +/- 1 within-subject SEM. N = 6.

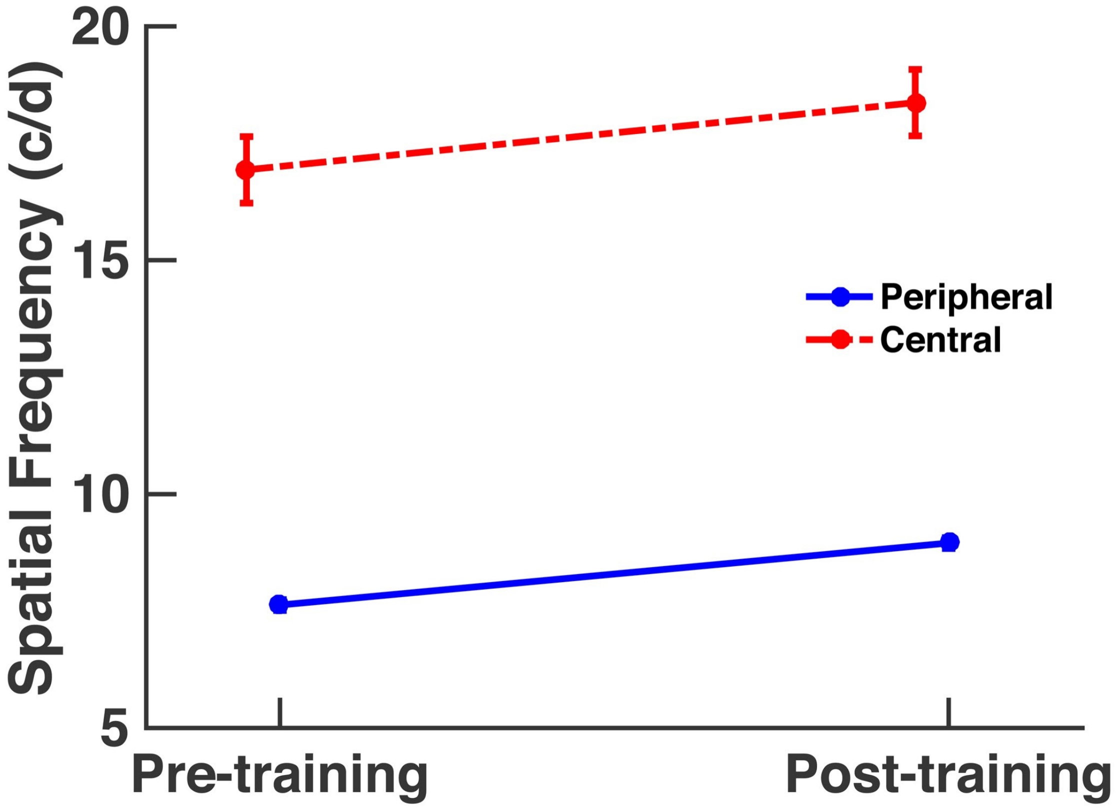

Figure 30 – Cutoff spatial frequency results, split by session and presentation location. Blue solid curves denote peripheral trials; red dashed curves denote central trials. Error bars (which may be obscured by the data markers) denote +/- 1 within-subject SEM. N = 6.

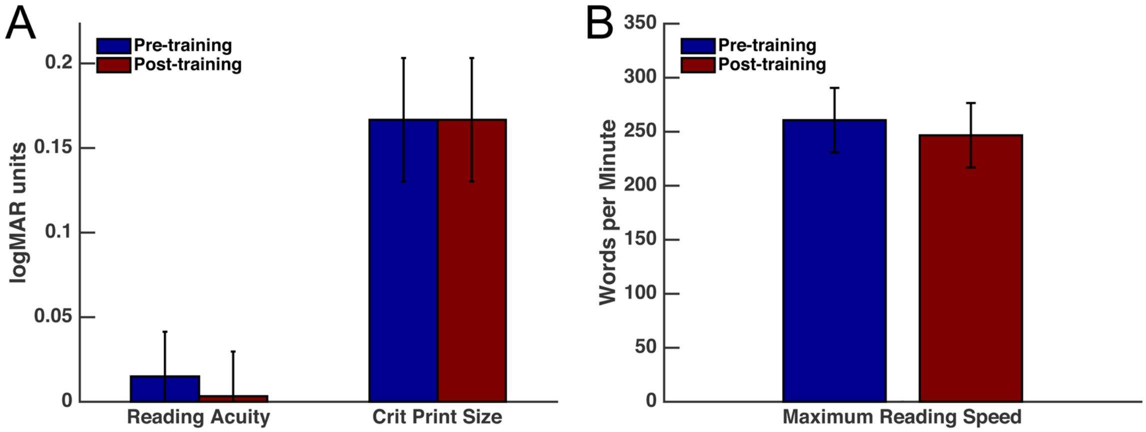

Figure 31 – MN Read results for each of the three administered tests. (A) Reading acuity (left) and critical print size (right), split by session. logMAR units measure print size, where smaller values indicate smaller print. (B) Maximum reading speed, measured in words per minute and split by session. In all plots blue bars denote pre-training sessions and red bars denote post-training sessions. Error bars denote +/- 1 within-subject SEM. N = 6.

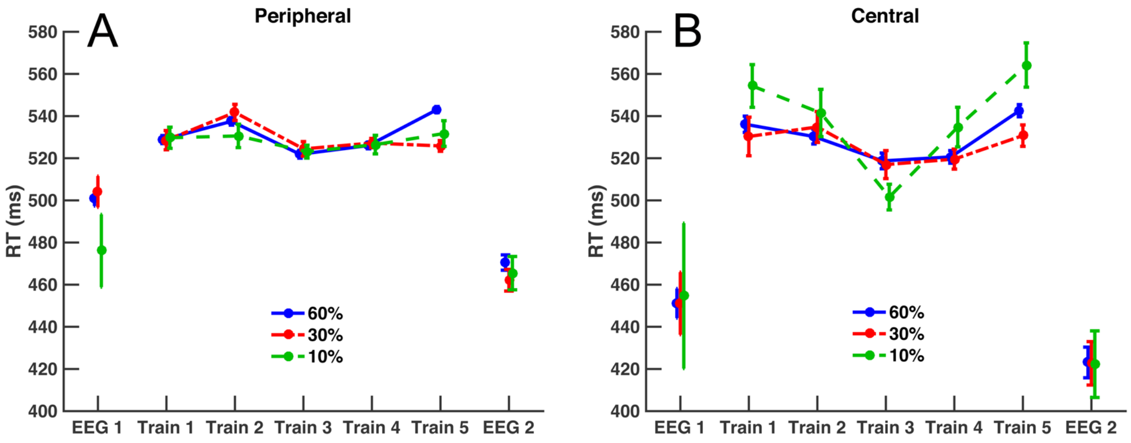

Figure 32 – SL effects across session days in (A) peripheral trials and (B) central trials. The abscissa denotes session days, beginning with the pre-training session (EEG 1), continuing through the five training sessions, and ending with the post-training session (EEG 2). The pre- and post-training data come from the first block of the session which used trained statistics. The training session data come from the second half of each session. Solid blue curves denote 60% trials, red dotted curves denote 30% trials, and green dashed curves denote 10% trials. Error bars denote +/- 1 within-subject SEM. N = 6.

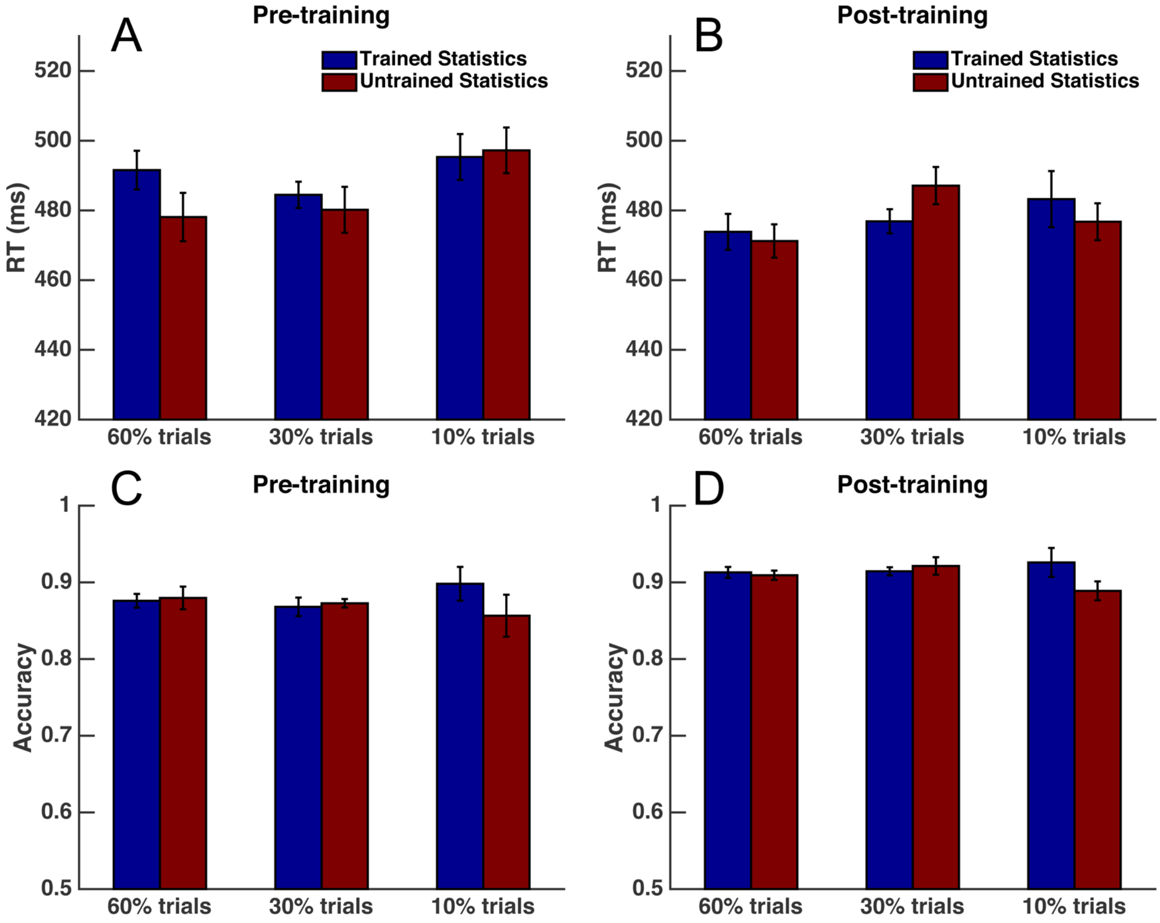

Figure 33 - Trained vs. untrained statistics, split by session and transition probability. (A) Mean RT in pre-training session; (B) Mean RT in post-training session; (C) Mean accuracy in pre-training session; (D) Mean accuracy in post-training session. Blue bars denote trials using trained statistics, red bars denote trials using untrained statistics. Error bars denote +/- 1 within-subject SEM. N = 6.

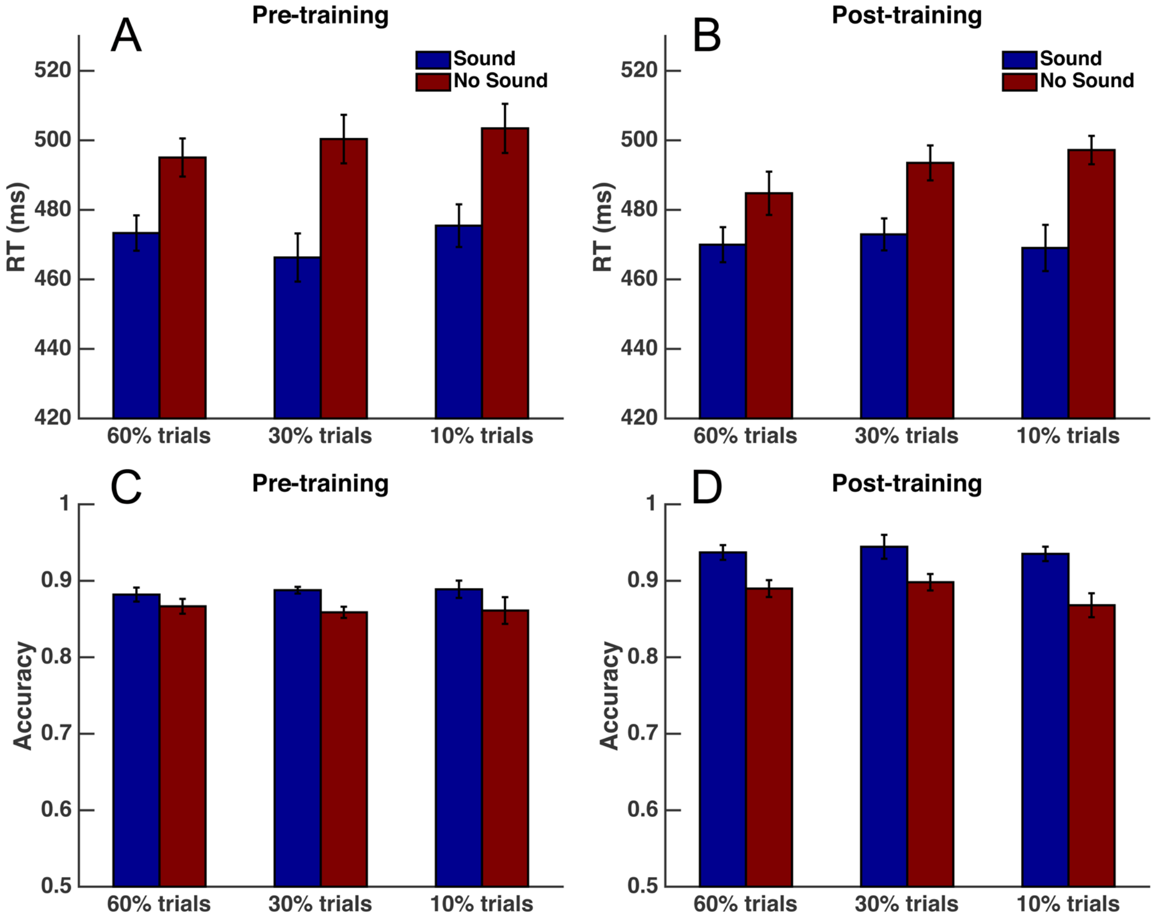

Figure 34 – Trials with sound vs. trials without sound, split by session and transition probability. (A) Mean RT in pre-training session; (B) Mean RT in post-training session; (C) Mean accuracy in pre-training session; (D) Mean accuracy in post-training session. Blue bars denote trials with sound, red bars denote trials without sound. Error bars denote +/- 1 within-subject SEM. N = 6.

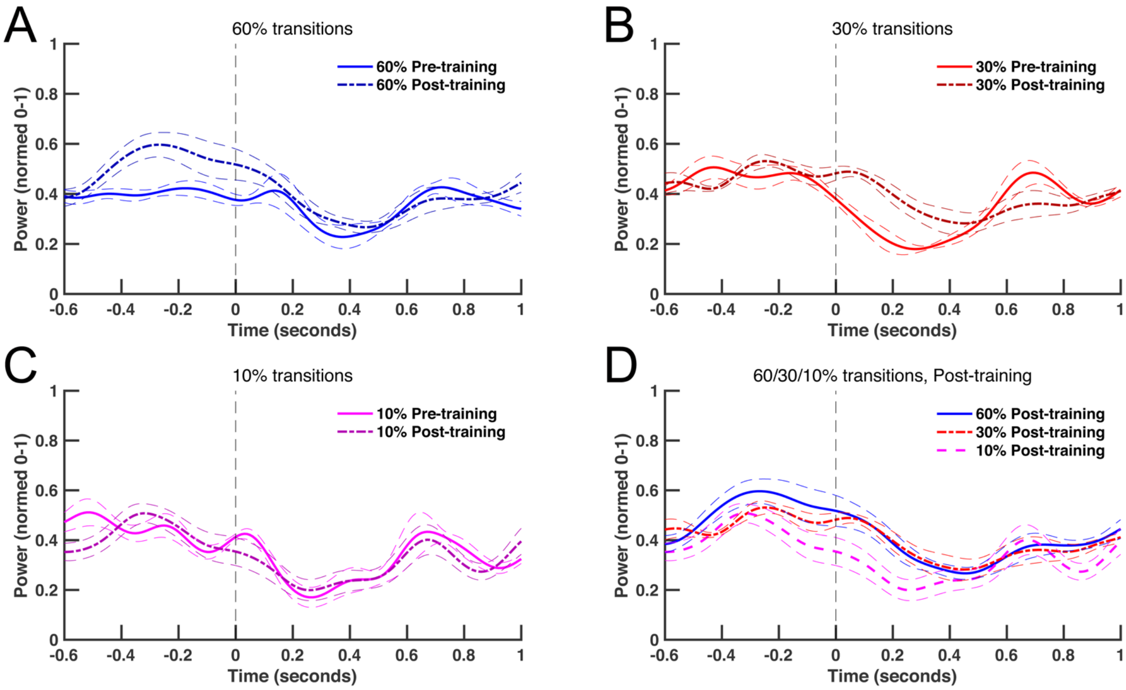

Figure 35 – Alpha power split by transition probability and session. (A) 60% trials pre-training (thick solid light blue curve) and post-training (thick dashed dark blue curve); (B) 30% trials pre-training (thick solid light red curve) and post-training (thick dashed dark red curve); (C) 10% trials pre-training (thick solid light purple curve) and post-training (thick dashed dark purple curve); (D) All three trial probabilities post-training – 60% in thick solid blue, 30% in thick dashed red, 10% in thick dotted purple. These are the thick dashed lines from A-C on the same axes. Thin dashed lines around all curves denote +/- 1 within-subject SEM in the respective color. N = 6.

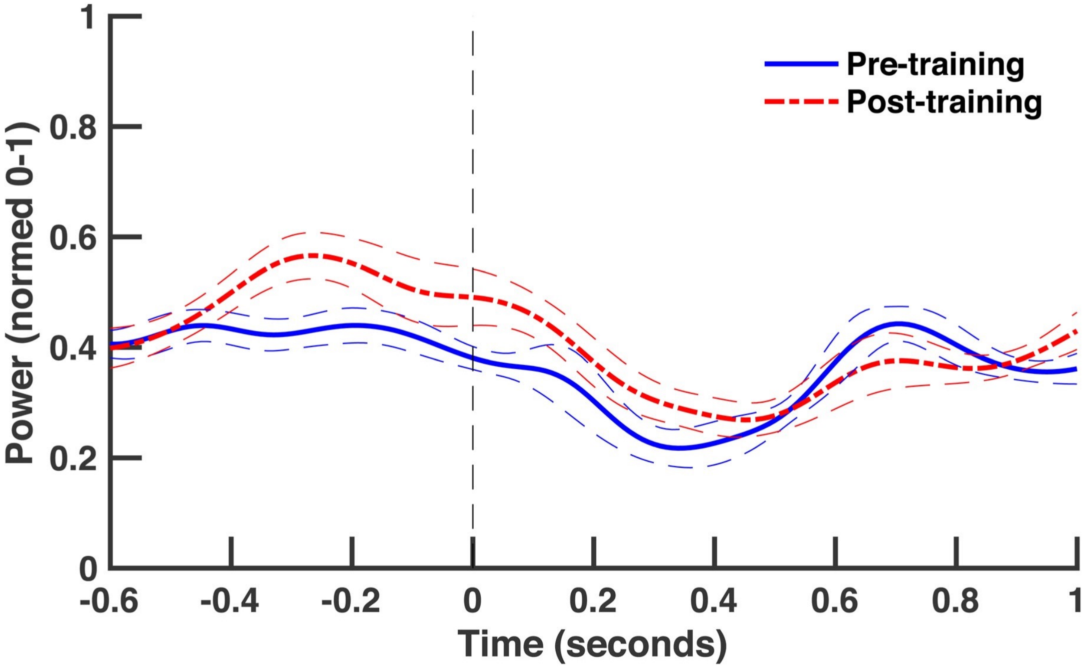

Figure 36 – Alpha power for all visible trials before training (thick blue solid line) and all visible trials after training (thick red dotted line). Thinner dashed lines denote +/- 1 within-subject SEM for the respective color. N = 6.

Tables of Means

Chapter 3 - Experiment 1 & Control Study

Variable	*M*	*SD*
2nd Session Trained Pos. RT (ms)		
60% Trials	561.0308	13.3617
30% Trials	560.4227	19.3603
10% Trials	558.5340	33.4332
2nd Session Trained Pos. Acc. (%)		
60% Trials	85.2963	7.1598
30% Trials	84.6296	5.8981
10% Trials	84.2592	6.2138
2nd Session Untrained Pos. RT (ms)		
60% Trials	578.4644	18.7343
30% Trials	582.9292	22.1594
10% Trials	569.7809	26.5703
2nd Session Untrained Pos. Acc. (%)		
60% Trials	83.9630	5.1462
30% Trials	85.1852	5.5432
10% Trials	86.2963	6.4151
1st Session SL RT (ms)		
Peripheral		
60%	637.4259	88.9406
30%	635.4876	79.7204
10%	638.7044	78.4459
Central		
60%	634.8689	83.7482
30%	643.8998	81.8824
10%	631.4805	92.1412
1st Session SL RT Difference (ms)		
Peripheral		
60%	-9.7113	60.3980
30%	-10.7342	59.6054
10%	5.9244	64.9090
Central		
60%	20.1598	56.6486
30%	32.2834	76.2953
10%	39.1377	60.3983
2nd Session Trained Stat. RT (ms)		
60% Trials	561.0308	13.3617

30% Trials	560.4227	19.3604
10% Trials	558.5340	33.4332
2nd Session Trained Stat. Acc. (%)		
60% Trials	85.2963	4.3128
30% Trials	84.6296	4.3887
10% Trials	84.2592	5.7683
2nd Session Untrained Stat. RT (ms)		
60% Trials	562.1341	18.7343
30% Trials	564.1185	22.1594
10% Trials	570.7241	26.5703
2nd Session Untrained Stat. Acc. (%)		
60% Trials	84.0741	3.1796
30% Trials	83.6111	3.4774
10% Trials	84.0741	4.9183
2nd Session Sound RT (ms)		
60% Trials	560.8261	16.3374
30% Trials	559.8963	14.8213
10% Trials	555.6536	26.2104
2nd Session Sound Acc. (%)		
60% Trials	88.3518	2.5605
30% Trials	89.1204	2.9942
10% Trials	89.0741	4.0732
2nd Session No Sound RT (ms)		
60% Trials	575.4968	16.1138
30% Trials	582.2467	25.5017
10% Trials	576.7221	24.5597
2nd Session No Sound Acc. (%)		
60% Trials	81.1481	33.9186
30% Trials	80.5092	39.1359
10% Trials	81.2963	51.2675
Alpha Power Post-stim. (Normalized)		
60%	0.1682	0.2060
30%	0.1641	0.1694
10%	0.1592	0.1324
Control Study		
1st Session SL RT (ms)		
Peripheral		
60%	552.1453	8.0863
30%	555.9562	10.7386
10%	557.6162	30.8726
Central		

60%	549.9104	11.1086
30%	552.8503	15.0847
10%	563.0437	29.4956
1st Session SL RT Difference (ms)		
Peripheral		
60%	-27.9366	58.2737
30%	-15.9276	61.3863
10%	4.6146	78.8075
Central		
60%	34.6112	58.5193
30%	44.1153	65.3156
10%	56.4636	55.2169

Table 6 – Means and within-subject standard deviations for analyses in Experiment 1 and the Control Study of Chapter 3, listed in order of discussion. SD is within-subjects SD, calculated according to Loftus and Masson (1994).

Chapter 3 - Experiment 2

Variable	*M*	*SD*
Contrast Threshold (Log Units)		
Low Frequency		
Peripheral		
Day 1	-1.5104	0.0679
Day 2	-1.5148	0.0250
Day 3	-1.5533	0.0255
Day 4	-1.5758	0.0416
Day 5	-1.5382	0.0306
Central		
Day 1	-1.6859	0.0464
Day 2	-1.6901	0.0343
Day 3	-1.6912	0.0420
Day 4	-1.7462	0.0823
Day 5	-1.6926	0.0431
Peak Frequency		
Peripheral		
Day 1	-1.2975	0.1462
Day 2	-1.4236	0.1892
Day 3	-1.4199	0.0680
Day 4	-1.3915	0.0701
Day 5	-1.3803	0.0329
Central		
Day 1	-1.7167	0.1123
Day 2	-1.7676	0.1017
Day 3	-1.8445	0.0810
Day 4	-1.7545	0.0851
Day 5	-1.8027	0.0648
Cutoff Frequency		
Peripheral		
Day 1	-0.5337	0.1083
Day 2	-0.5856	0.0452
Day 3	-0.5509	0.0549
Day 4	-0.5972	0.1295
Day 5	-0.5371	0.0827
Central		
Day 1	-0.8354	0.1679
Day 2	-0.9206	0.1331
Day 3	-1.0214	0.0736
Day 4	-0.9003	0.1010
Day 5	-1.0270	0.0755

Pre-Training Trained Pos. RT (ms)		
60% Trials	491.5716	19.1737
30% Trials	484.4715	22.8189
10% Trials	495.3326	25.2292
Pre-Training Trained Pos. Acc. (%)		
60% Trials	87.5926	3.5489
30% Trials	86.8056	4.1408
10% Trials	89.8148	4.1154
Pre-Training Untrained Pos. RT (ms)		
60% Trials	485.9121	23.3753
30% Trials	483.7037	25.6062
10% Trials	481.1662	23.5253
Pre-Training Untrained Pos. Acc. (%)		
60% Trials	86.9444	1.0338
30% Trials	88.6574	1.1928
10% Trials	87.5000	4.1112
Post-Training Trained Pos. RT (ms)		
60% Trials	473.8574	13.5918
30% Trials	476.8781	7.6089
10% Trials	483.2454	19.3412
Post-Training Trained Pos. Acc. (%)		
60% Trials	91.2963	1.8171
30% Trials	91.4352	2.0004
10% Trials	92.5926	3.9226
Post-Training Untrained Pos. RT (ms)		
60% Trials	488.6619	10.3457
30% Trials	491.4284	15.9645
10% Trials	492.9812	19.3367
Post-Training Untrained Pos. Acc. (%)		
60% Trials	91.7592	2.9223
30% Trials	92.5926	2.6168
10% Trials	91.6667	1.4778
Landolt C (Font Size)		
Pre-training		
Peripheral	16.8750	1.1884
Central	5.5000	0.2934
Post-training		
Peripheral	14.4306	1.1884
Central	6.0000	0.2934
Cutoff Spatial Frequency (c/deg.)		
Pre-training		
Peripheral	7.6300	0.2852

Central	16.9307	1.7399
Post-training		
Peripheral	8.9553	0.2852
Central	18.3676	1.7399
MN Read - Reading Acuity (logMAR)		
Pre-test	0.0150	0.0646
Post-test	0.0033	0.0646
MN Read - Crit. Print Size (logMAR)		
Pre-test	0.1667	0.0894
Post-test	0.1667	0.0894
MN Read – Max.Read. Speed (wpm)		
Pre-test	260.6667	73.1683
Post-test	246.6667	73.1683
SL Across Sessions (ms)		
Peripheral Location		
60%		
EEG 1	500.8094	21.0341
Train 1	528.8578	11.5306
Train 2	537.4980	10.8018
Train 3	521.8908	11.1664
Train 4	526.0350	9.3522
Train 5	543.0616	8.7993
EEG 2	470.5026	21.8080
30%		
EEG 1	504.1224	44.5307
Train 1	528.5713	27.4825
Train 2	541.7506	22.8946
Train 3	524.4243	20.9159
Train 4	527.1979	13.2016
Train 5	525.8402	15.2987
EEG 2	462.1108	30.9111
10%		
EEG 1	476.0950	103.5331
Train 1	529.7175	30.1054
Train 2	530.5827	33.2044
Train 3	523.1236	18.3298
Train 4	526.4572	26.4755
Train 5	531.7190	36.5006
EEG 2	465.4590	47.4203
Central Location		
60%		
EEG 1	451.1456	42.0682

Train 1	536.1100	23.1739
Train 2	530.2895	21.1807
Train 3	518.7308	22.4374
Train 4	520.6253	17.9318
Train 5	542.5494	17.3578
EEG 2	423.0942	43.6161
30%		
EEG 1	451.1164	89.0614
Train 1	530.3278	55.0211
Train 2	534.8408	44.0443
Train 3	516.9853	39.7894
Train 4	519.5781	28.4159
Train 5	530.7419	30.5178
EEG 2	422.6878	61.8222
10%		
EEG 1	454.6990	207.0661
Train 1	554.3023	60.8597
Train 2	541.4753	67.3538
Train 3	501.5683	36.4990
Train 4	534.8003	56.4267
Train 5	564.2380	63.0380
EEG 2	422.2607	94.8406
Pre-Training Trained Stats RT (ms)		
60% Trials	491.5716	13.5861
30% Trials	484.4715	9.2721
10% Trials	495.3326	16.1311
Pre-Training Trained Stats Acc. (%)		
60% Trials	87.5926	2.1971
30% Trials	86.8056	2.9609
10% Trials	89.8148	5.3856
Pre-Training Untrained Stats RT (ms)		
60% Trials	478.1040	16.9731
30% Trials	480.1784	16.1533
10% Trials	497.2400	16.0532
Pre-Training Untrained Stats Acc. (%)		
60% Trials	87.9630	3.6226
30% Trials	87.2685	1.3563
10% Trials	85.6481	6.6969
Post-Training Trained Stats RT (ms)		
60% Trials	473.8574	12.6344
30% Trials	476.8781	8.5073
10% Trials	483.2454	19.6807

Post-Training Trained Stats Acc. (%)		
60% Trials	91.2963	1.7402
30% Trials	91.4352	1.3004
10% Trials	92.5926	4.6234
Post-Training Untrained Stats RT (ms)		
60% Trials	471.2204	11.7358
30% Trials	487.1167	13.0912
10% Trials	476.7637	12.9488
Post-Training Untrain. Stats Acc. (%)		
60% Trials	90.9259	1.4862
30% Trials	92.1296	2.8088
10% Trials	88.8889	3.0192
Pre-Training Sound RT (ms)		
60% Trials	473.3302	12.4479
30% Trials	466.2922	16.9704
10% Trials	475.4521	15.0144
Pre-Training Sound Acc. (%)		
60% Trials	88.1944	2.2396
30% Trials	88.7731	1.0754
10% Trials	88.8889	2.7753
Pre-Training No Sound RT (ms)		
60% Trials	495.0648	13.4253
30% Trials	500.3668	17.0885
10% Trials	503.4415	17.3123
Pre-Training No Sound Acc. (%)		
60% Trials	86.6667	2.3769
30% Trials	85.8796	1.8000
10% Trials	86.1111	4.2912
Post-Training Sound RT (ms)		
60% Trials	469.9902	12.3600
30% Trials	472.9499	11.2806
10% Trials	469.0502	16.3169
Post-Training Sound Acc. (%)		
60% Trials	93.7037	2.3667
30% Trials	94.4444	3.8199
10% Trials	93.5185	2.2998
Post-Training No Sound RT (ms)		
60% Trials	484.7758	15.2574
30% Trials	493.5110	12.3413
10% Trials	497.2062	10.0210
Post-Training No Sound Acc. (%)		
60% Trials	88.9815	2.7007

30% Trials	89.8148	2.6376
10% Trials	86.8056	3.8350
Alpha Power Post-stim. (Normalized)		
Pre-Training		
60%	0.2486	0.1243
30%	0.2125	0.0970
10%	0.2151	0.1768
Post-Training		
60%	0.2900	0.2324
30%	0.3043	0.2650
10%	0.2263	0.2789
Overall Alpha Power (Normalized)		
Pre-stimulus Interval		
Pre-Training	0.4230	0.2449
Post-Training	0.5294	0.2249
Post-stimulus Interval		
Pre-Training	0.2345	0.1012
Post-Training	0.2879	0.2372

Table 7 – Means and within-subject standard deviations for analyses in Experiment 2 of Chapter 3, listed in order of discussion. SD is within-subjects SD, calculated according to Loftus and Masson (1994).

GENERAL DISCUSSION

The goal of this dissertation was to examine the mechanisms underlying sensory learning and perceptual processes, namely perceptual learning (PL), statistical learning (SL), and multisensory integration (MI), in order to address outstanding questions in the literature about whether the underlying mechanisms are unitary or multifaceted, and whether the mechanisms might intersect. In the first chapter we used a series of experiments to show that SL, often treated as a unitary process, may in fact comprise multiple processes and further, that those processes may act in competition with each other. In the second chapter we used a combination of PL training and EEG recordings to show that multiple attentional factors affect PL and that it is most likely not a unitary, low level process as some have hypothesized. In the third chapter, we designed a novel training paradigm that combined PL, SL, and MI and although we found that the data were able to confirm some of the results from the previous two chapters, a number of limitations prevented us from making strong conclusions.

The common thread among all three chapters is that the processes studied here are neither simple nor unitary but are instead complex and multifaceted. The double dissociation seen in behavior across the different SL tasks used in Chapter 1 is classical evidence for multiple underlying processes (Chun, 1997; Gabrieli, Fleischman, Keane, Reminger, & Morrell, 1995). The behavioral patterns demonstrate that different tasks can reveal different information about SL and not only are these sources of information not redundant but the suppression of each behavioral pattern by the other suggests that these processes may be in competition with one another. While we do not know of any model of

SL that accounts for this, the results are highly consistent with neurological evidence that relates to SL, such as the striatum and medial temporal lobe displaying competing activation during learning (Packard, 1999; Poldrack et al., 2001) and the frontal cortex and striatum displaying different time courses of learning (Pasupathy & Miller, 2005). Neuroimaging studies of SL have shown that the striatum, the medial temporal lobe, and the left inferior frontal cortex support SL (Durrant, Cairney, & Lewis, 2013; Karuza et al., 2013; Schapiro, Gregory, Landau, McCloskey, & Turk-Browne, 2014; Schapiro, Kustner, & Turk-Browne, 2012; Turk-Browne, Scholl, Chun, & Johnson, 2009; Turk-Browne, Scholl, Johnson, & Chun, 2010), suggesting that the mechanisms underlying SL may express different patterns of learning. Others have also proposed that SL should be examined in terms of different time courses of learning instead of a single outcome measure (Karuza, Emberson, & Aslin, 2014) and have shown that SL can affect other perceptual and attentional processes (Barakat, Seitz, & Shams, 2013; Zhao, Al-Aidroos, & Turk-Browne, 2013). Our behavioral results, together with previous behavioral and neurological results, suggest that SL is indeed a multifaceted learning process and thus treating SL as a unitary process disregards valuable information about it. The results further suggest that future research would benefit from using multiple behavioral measures of learning instead of a single outcome measure, as multiple measures can help to capture typically disregarded variance.

Similarly, the increase in alpha power after PL training in Chapter 2 indicates that not all aspects of PL can be accounted for by low level learning processes. Instead, at least some aspects of PL appear to stem from higher level reallocation of attentional resources.

This is consistent with some models of PL that specifically incorporate attentional resources (Ahissar & Hochstein, 2004; Byers & Serences, 2012). The results also help to answer the open question of where activation and plasticity in response to PL occur. There is extensive neurological evidence for low level plasticity (Bao, Yang, Rios, He, & Engel, 2010; Gilbert, Li, & Piech, 2009; Gilbert, Sigman, & Crist, 2001; Hua et al., 2010) but also behavioral evidence for higher areas of plasticity (Hung & Seitz, 2014; Jeter, Dosher, Liu, & Lu, 2010; Xiao et al., 2008; Zhang et al., 2010) and models which can account for the data without low level plasticity (Dosher, Jeter, Liu, & Lu, 2013; Petrov, Dosher, & Lu, 2005). An elegant, data-driven explanation for these conflicting results is that PL is composed of multiple processes which occur at different stages of processing. The neurological results of our study, demonstrating overall increased alpha power, provide further evidence for this explanation. Our behavioral data clearly indicated greater learning for trained stimuli compared to untrained stimuli, yet the electrophysiological data indicated that attentional resources were used more efficiently across all trials after training, not solely trials with trained stimuli, suggesting that multiple learning processes were at work. It should also be noted that although trained stimuli demonstrated the largest behavioral improvements, untrained stimuli also showed improvement after training, once again suggesting that multiple processes may have been at work. Future PL research would benefit by considering these results and investigating which mechanisms of PL might be affecting the data, as this may help answer currently debated issues like location and stimulus specificity.

The combined PL/SL/MI paradigm used in Chapter 3 did not provide us with results that were as clear as we predicted, yet some aspects of the two studies provide us with evidence of the multifaceted nature of the perceptual processes. In Experiment 1 of Chapter 3, different RTs to trained and untrained positions begin to appear after a single day of training even though PL studies typically require multiple days of training, which has been shown to be particularly true when training contrast perception (Furmanski, Schluppeck, & Engel, 2004; Li, Polat, Makous, & Bavelier, 2009; Yu, Klein, & Levi, 2004). As with models of SL, these different time courses of learning within PL could signify the presence of multiple regions of plasticity and multiple underlying processes. In Experiment 2 of Chapter 3, partial transfer of learning to the untrained cutoff spatial frequency task and Landolt C task suggests that all plasticity did not take place in low level areas, providing further evidence for multiple brain regions and processes supporting PL. Further, some explanations for our scarcity of significant results would imply that multiple processes were at work during PL. For example, the small effect sizes seen throughout both experiments could be a direct result of interference between SL, PL, and MI. If that were the case then it would imply that they share common or competitive mechanisms and are not isolated, unitary processes. This would, however, be contradictory to previous research which has shown the ability to combine PL and MI (Seitz, Kim, & Shams, 2006; Shams & Seitz, 2008) and SL and MI (Seitz, Kim, van Wassenhove, & Shams, 2007). Another explanation for the small effects seen in Chapter 3 is that the combination of so many parameters into a single paradigm created divided attentional effects. As discussed above in relation to Chapter 2, if attentional effects were at play in PL then it would imply that it is not a unitary low level process and similarly if divided attention affected SL and MI then it might imply that there are different mechanisms within them that work with and without attentional resources. Providing some supporting evidence for this is the alpha power pattern seen in Experiment 2 of Chapter 3 which is similar to that seen in Chapter 2, where alpha power increased overall after training as compared to before training, although the effect in Chapter 3 was not as strong as in Chapter 2. As with many of the results of Chapter 3, further experimentation is required to determine if any of these postulates are correct.

The need for replication, further experimentation, and further analyses exist for all three sets of studies. Chapter 1 failed to sufficiently answer the question of whether SL is a result of associative processes, representational processes, or both. Prior evidence exists for both explanations of SL (Barakat et al., 2013; Turk-Browne et al., 2010) and our results seem to suggest that both may be at work but further research is required to clarify our results. Chapter 2 failed to answer the question of why alpha power would increase for the task in general but not correlate with trained stimuli specifically. Although there are possible explanations for this, such as the possibility that alpha power increases in a nonlinear fashion or that participants are able to regulate alpha in some way, our experimental design was not able to address the question and again, only further research would be able to add to the discussion.

The need for further research and analyses is particularly strong for Chapter 3. There are numerous reasons why the results may not have been as informative as predicted, including the size of the cohorts, the parameters used for QUEST, the very use of QUEST instead of other methods to estimate contrast threshold, and the highly complex design and combination of stimuli. The complex experimental design also means that there are numerous other analyses that could be informative. For example, if we were to determine a feature that we could use to classify the stimuli into "learned" and "non-learned" stimuli, as was done in Chapter 1, then we might also discover dissociable effects of learning within PL and/or SL, or interactions with MI. There are other analyses of interactions between PL, SL, and MI that could also reveal more about the three processes, for instance by looking at how SL is expressed at different stages of PL or vice versa. Additionally, the EEG data is a rich source of unrealized analyses. Previous unpublished data from our research has suggested that machine learning algorithms – computer-controlled mathematical algorithms designed to find patterns in highly complex datasets – may reveal learning patterns in EEG data that is not readily apparent in behavioral results (Bays & Seitz, unpublished). Applying algorithms such as those to the EEG data in Chapter 3 may reveal underlying processes that behavioral and alpha power analyses failed to show. Finally, the results of the control study of Experiment 1 of Chapter 3 suggest that future studies may benefit from simpler designs at first, e.g., combining PL and MI before adding a third process to the paradigm. Ultimately, only further research can inform us as to how these various parameters affected the results reported here.

Altogether, we have provided evidence that sensory learning processes and other perceptual processes should not be treated as simple, unitary mechanisms but instead should be investigated in terms of their manifold natures. Discussing the processes in terms of a single outcome measure obfuscates underlying multiple mechanisms and hinders attempts to create models and test theories. In addition, understanding that the processes are complex and multifaceted paves the way to understanding how they might overlap with other learning processes in the brain. In this instance, embracing complexity does not create problems but instead helps to provide sought-after solutions.

References

Ahissar, M., & Hochstein, S. (2004). The reverse hierarchy theory of visual perceptual learning. *Trends in Cognitive Sciences*, *8*(10), 457–64. http://doi.org/10.1016/j.tics.2004.08.011

Bao, M., Yang, L., Rios, C., He, B., & Engel, S. A. (2010). Perceptual learning increases the strength of the earliest signals in visual cortex. *Journal of Neuroscience*, *30*(45), 15080–15084.

Barakat, B. K., Seitz, A. R., & Shams, L. (2013). The effect of statistical learning on internal stimulus representations: Predictable items are enhanced even when not predicted. *Cognition*, *129*(2), 205–211. http://doi.org/10.1016/j.cognition.2013.07.003

Byers, A., & Serences, J. T. (2012). Exploring the relationship between perceptual learning and top-down attentional control. *Vision Research*, *74*, 30–39. http://doi.org/10.1016/j.visres.2012.07.008

Chun, M. M. (1997). Types and tokens in visual processing: A double dissociation between the attentional blink and repetition blindness. *Journal of Experimental Psychology: Human Perception and Performance*, *23*(3), 738–755. http://doi.org/10.1037/0096-1523.23.3.738

Dosher, B. A., Jeter, P., Liu, J., & Lu, Z.-L. (2013). An integrated reweighting theory of perceptual learning. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(33), 13678–13683. http://doi.org/10.1073/pnas.1312552110

Durrant, S. J., Cairney, S. A., & Lewis, P. A. (2013). Overnight consolidation aids the transfer of statistical knowledge from the medial temporal lobe to the striatum. *Cerebral Cortex*, *23*(10), 2467–2478. http://doi.org/10.1093/cercor/bhs244

Furmanski, C. S., Schluppeck, D., & Engel, S. A. (2004). Learning strengthens the response of primary visual cortex to simple patterns. *Current Biology*, *14*, 573–578. http://doi.org/10.1016/j

Gabrieli, J. D. E., Fleischman, D. A., Keane, M. M., Reminger, S. L., & Morrell, F. (1995). Double dissociation between memory systems underlying explicit and implicit memory in the human brain. *Psychological Science*, *6*(2), 76–82.

Gilbert, C. D., Li, W., & Piech, V. (2009). Perceptual learning and adult cortical plasticity. *Journal of Physiology*, *587*(12), 2743–2751.

Gilbert, C. D., Sigman, M., & Crist, R. E. (2001). The Neural Basis of Perceptual Learning. *Neuron*, *31*, 681–697.

Hua, T., Bao, P., Huang, C.-B., Wang, Z., Xu, J., Zhou, Y., & Lu, Z.-L. (2010). Perceptual Learning Improves Contrast Sensitivity of V1 Neurons in Cats. *Current Biology*, *20*, 887–894.

Hung, S.-C., & Seitz, A. R. (2014). Prolonged training at threshold promotes robust retinotopic specificity in perceptual learning. *The Journal of Neuroscience*, *34*(25), 8423–8431. http://doi.org/10.1523/JNEUROSCI.0745-14.2014

Jeter, P. E., Dosher, B. A., Liu, S.-H., & Lu, Z.-L. (2010). Specificity of perceptual learning increases with increased training. *Vision Research*, *50*(19), 1928–1940. http://doi.org/10.1016/j.visres.2010.06.016

Karuza, E. A., Emberson, L. L., & Aslin, R. N. (2014). Combining fMRI and behavioral measures to examine the process of human learning. *Neurobiology of Learning and Memory*, *109*, 193–206. http://doi.org/10.1016/j.nlm.2013.09.012

Karuza, E. A., Newport, E. L., Aslin, R. N., Starling, S. J., Tivarus, M. E., & Bavelier, D. (2013). The neural correlates of statistical learning in a word segmentation task: An fMRI study. *Brain and Language*, *127*(1), 46–54. http://doi.org/10.1016/j.bandl.2012.11.007

Li, R., Polat, U., Makous, W., & Bavelier, D. (2009). Enhancing the contrast sensitivity function through action video game training. *Nat Neurosci*, *12*(5), 549–551. http://doi.org/10.1038/nn.2296

Packard, M. G. (1999). Glutamate infused posttraining into the hippocampus or caudate-putamen differentially strengthens place and response learning. *Proceedings of the National Academy of Sciences*, *96*(22), 12881–12886.

Pasupathy, A., & Miller, E. K. (2005). Different time courses of learning-related activity in the prefrontal cortex and striatum. *Nature*, *433*(7028), 873–876. http://doi.org/10.1038/nature03287

Petrov, A. A., Dosher, B. A., & Lu, Z.-L. (2005). The dynamics of perceptual learning: an incremental reweighting model. *Psychological Review*, *112*(4), 715–743. http://doi.org/10.1037/0033-295X.112.4.715

Poldrack, R. A., Clark, J., Paré-Blagoev, E. J., Shohamy, D., Creso Moyano, J., Myers, C., & Gluck, M. A. (2001). Interactive memory systems in the human brain. *Nature*, *414*(6863), 546–550. http://doi.org/10.1038/35107080

Schapiro, A. C., Gregory, E., Landau, B., McCloskey, M., & Turk-Browne, N. B. (2014). The necessity of the medial temporal lobe for statistical learning. *Journal of Cognitive Neuroscience*, *26*(8), 1736–1747. http://doi.org/doi:10.1162/jocn_a_00578

Schapiro, A. C., Kustner, L. V, & Turk-Browne, N. B. (2012). Shaping of object representations in the human medial temporal lobe based on temporal regularities. *Current Biology*, *22*(17), 1622–1627. http://doi.org/10.1016/j.cub.2012.06.056

Seitz, A. R., Kim, R., & Shams, L. (2006). Sound facilitates visual learning. *Current Biology*, *16*, 1422–1427.

Seitz, A. R., Kim, R., van Wassenhove, V., & Shams, L. (2007). Simultaneous and independent acquisition of multisensory and unisensory associations. *Perception*, *36*(10), 1445–1453.

Shams, L., & Seitz, A. R. (2008). Benefits of Multisensory Learning. *Trends in Cognitive Sciences*, *12*(11), 411–417.

Turk-Browne, N. B., Scholl, B. J., Chun, M. M., & Johnson, M. K. (2009). Neural evidence of statistical learning: Efficient detection of visual regularities without awareness. *Journal of Cognitive Neuroscience*, *21*(10), 1934–1945.

Turk-Browne, N. B., Scholl, B., Johnson, M. K., & Chun, M. M. (2010). Implicit perceptual anticipation triggered by statistical learning. *Journal of Neuroscience*, *30*(33), 11177–11187.

Xiao, L.-Q., Zhang, J.-Y., Wang, R., Klein, S. a, Levi, D. M., & Yu, C. (2008). Complete transfer of perceptual learning across retinal locations enabled by double training. *Current Biology : CB*, *18*(24), 1922–1926. http://doi.org/10.1016/j.cub.2008.10.030

Yu, C., Klein, S. A., & Levi, D. M. (2004). Perceptual learning in contrast discrimination and the (minimal) role of context. *Journal of Vision*, *4*, 169–182. http://doi.org/10.1167/4.3.4

Zhang, J.-Y., Zhang, G.-L., Xiao, L.-Q., Klein, S. a, Levi, D. M., & Yu, C. (2010). Rule-based learning explains visual perceptual learning and its specificity and transfer. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *30*(37), 12323–12328. http://doi.org/10.1523/JNEUROSCI.0704-10.2010

Zhao, J., Al-Aidroos, N., & Turk-Browne, N. B. (2013). Attention is spontaneously biased toward regularities. *Psychological Science*, *24*(5), 667–677. http://doi.org/10.1177/0956797612460407

Complete References

Abla, D., Katahira, K., & Okanoya, K. (2008). On-line assessment of statistical learning by event-related potentials. *Journal of Cognitive Neuroscience*, *20*(6), 952–64. http://doi.org/10.1162/jocn.2008.20058

Abla, D., & Okanoya, K. (2009). Visual statistical learning of shape sequences: An ERP study. *Neuroscience Research*, *64*(2), 185–90. http://doi.org/10.1016/j.neures.2009.02.013

Adini, Y., Sagi, D., & Tsodyks, M. (2002). Context-enabled learning in the human visual system. *Nature*, *415*(6873), 790–793. http://doi.org/10.1038/415790a

Ahissar, M., & Hochstein, S. (2004). The reverse hierarchy theory of visual perceptual learning. *Trends in Cognitive Sciences*, *8*(10), 457–64. http://doi.org/10.1016/j.tics.2004.08.011

Aslin, R. N., Saffran, J. R., & Newport, E. L. (1998). Computation of conditional probability statistics by 8-month-old infants. *Psychological Science*, *9*(4), 321–324.

Baker, C. I., Olson, C. R., & Behrmann, M. (2004). Role of Attention and Perceptual Grouping in Visual Statistical Learning. *Psychological Science*, *15*(7), 460–466.

Bao, M., Yang, L., Rios, C., He, B., & Engel, S. A. (2010). Perceptual learning increases the strength of the earliest signals in visual cortex. *Journal of Neuroscience*, *30*(45), 15080–15084.

Barakat, B. K., Seitz, A. R., & Shams, L. (2013). The effect of statistical learning on internal stimulus representations: Predictable items are enhanced even when not predicted. *Cognition*, *129*(2), 205–211. http://doi.org/10.1016/j.cognition.2013.07.003

Bays, B. C., Turk-Browne, N. B., & Seitz, A. R. (2016). Dissociable behavioural outcomes of visual statistical learning. *Visual Cognition*, *6285*(February), 1–26. http://doi.org/10.1080/13506285.2016.1139647

Bays, B. C., Visscher, K. M., Le Dantec, C. C., & Seitz, A. R. (2015). Alpha-band EEG activity in perceptual learning. *Journal of Vision*, *15*(10), 1–12. http://doi.org/10.1167/15.10.7.doi

Berger, H. (1929). Über das elektrenkephalogramm des menschen. *Archiv Für Psychiatrie*, *87*(1), 527–570.

Bertels, J., Franco, A., & Destrebecqz, A. (2012). How implicit is visual statistical learning? *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *38*(5), 1425–1431. http://doi.org/10.1037/a0027210

Bollimunta, A., Chen, Y., Schroeder, C. E., & Ding, M. (2008). Neuronal mechanisms of cortical alpha oscillations in awake-behaving macaques. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *28*(40), 9976–9988. http://doi.org/10.1523/JNEUROSCI.2699-08.2008

Bonnefond, M., & Jensen, O. (2012). Alpha oscillations serve to protect working memory maintenance against anticipated distracters. *Current Biology*, *22*(20), 1969–1974. http://doi.org/10.1016/j.cub.2012.08.029

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*, 433–436.

Byers, A., & Serences, J. T. (2012). Exploring the relationship between perceptual learning and top-down attentional control. *Vision Research*, *74*, 30–39. http://doi.org/10.1016/j.visres.2012.07.008

Campbell, K. L., Healey, M. K., Lee, M. M. S., Zimerman, S., & Hasher, L. (2012). Age Differences in Visual Statistical Learning. *Psychology and Aging*, *27*(3), 650–656. http://doi.org/10.1037/a0026780.Age

Chalk, M., Seitz, A. R., & Seriès, P. (2010). Rapidly learned stimulus expectations alter perception of motion. *Journal of Vision*, *10*(8), 1–18. http://doi.org/10.1167/10.8.2

Chaumon, M., & Busch, N. (2014). Prestimulus Neural Oscillations Inhibit Visual Perception via Modulation of Response Gain. *Journal of Cognitive Neuroscience*, *26*(11), 2514–2529. http://doi.org/10.1162/jocn_a_00653

Chun, M. M. (1997). Types and tokens in visual processing: A double dissociation between the attentional blink and repetition blindness. *Journal of Experimental Psychology: Human Perception and Performance*, *23*(3), 738–755. http://doi.org/10.1037/0096-1523.23.3.738

Cleeremans, A., & McClelland, J. L. (1991). Learning the structure of event sequences. *Journal of Experimental Psychology. General*, *120*(3), 235–253. http://doi.org/10.1037/0096-3445.120.3.235

Conway, C. M., & Christiansen, M. H. (2005). Modality-constrained statistical learning of tactile, visual, and auditory sequences. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *31*(1), 24–39.

Conway, C. M., & Christiansen, M. H. (2006). Statistical learning within and between modalities. *Psychological Science*, *17*(10), 905–912.

Das, K., Giesbrecht, B., & Eckstein, M. P. (2010). Predicting variations of perceptual performance across individuals from neural activity using pattern classifiers. *NeuroImage*, *51*(4), 1425–1437. http://doi.org/10.1016/j.neuroimage.2010.03.030

De Valois, K. (1977). Spatial frequency adaptation can enhance contrast sensitivity. *Vision Research*, *17*(9), 1057–1065.

Deveau, J., Lovcik, G., & Seitz, A. R. (2014). Broad-based visual benefits from training with an integrated perceptual-learning video game. *Vision Research*, *99*, 134–140. http://doi.org/10.1016/j.visres.2013.12.015

Deveau, J., Ozer, D. J., & Seitz, A. R. (2014). Improved vision and on-field performance in baseball through perceptual learning. *Current Biology*, *24*(4), R146–R147. http://doi.org/10.1016/j.cub.2014.01.004

Dobres, J., & Seitz, A. R. (2010). Perceptual learning of oriented gratings as revealed by classification images. *Journal of Vision*, *10*(13), 8–11. http://doi.org/10.1167/10.13.8.Introduction

Dosher, B. A., Jeter, P., Liu, J., & Lu, Z.-L. (2013). An integrated reweighting theory of perceptual learning. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(33), 13678–13683. http://doi.org/10.1073/pnas.1312552110

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 of the United States of America*, *95*(23), 13988–13993.

Durrant, S. J., Cairney, S. A., & Lewis, P. A. (2013). Overnight consolidation aids the transfer of statistical knowledge from the medial temporal lobe to the striatum. *Cerebral Cortex*, *23*(10), 2467–2478. http://doi.org/10.1093/cercor/bhs244

Durrant, S. J., Taylor, C., Cairney, S. A., & Lewis, P. A. (2011). Sleep-dependent consolidation of statistical learning. *Neuropsychologia*, *49*(5), 1322–1331. http://doi.org/10.1016/j.neuropsychologia.2011.02.015

Elman, J. L. (1990). Finding structure in time. *Cognitive Science*, *14*(2), 179–211. http://doi.org/10.1207/s15516709cog1402_1

Ergenoglu, T., Demiralp, T., Bayraktaroglu, Z., Ergen, M., Beydagi, H., & Uresin, Y. (2004). Alpha rhythm of the EEG modulates visual detection performance in humans. *Cognitive Brain Research*, *20*(3), 376–383. http://doi.org/10.1016/j.cogbrainres.2004.03.009

Fahle, M. (2004). Perceptual learning: a case for early selection. *Journal of Vision*, *4*(10), 879–890. http://doi.org/10.1167/4.10.4

Fahle, M. (2005). Perceptual learning: specificity versus generalization. *Current Opinion in Neurobiology*, *15*(2), 154–160. http://doi.org/10.1016/j.conb.2005.03.010

Fahle, M., Edelman, S., & Poggio, T. (1995). Fast perceptual learning in hyperacuity. *Vision Research*, *35*(21), 3003–3013.

Fiorentini, A., & Berardi, N. (1980). Perceptual learning specific for orientation and spatial frequency. *Nature*, *287*(5777), 43–44.

Fiser, J., & Aslin, R. N. (2001). Unsupervised statistical learning of higher-order spatial structures from visual scenes. *Psychological Science*, *12*(6), 499–504.

Fiser, J., & Aslin, R. N. (2002). Statistical learning of higher-order temporal structure from visual shape sequences. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *28*(3), 458–467.

Fiser, J., & Aslin, R. N. (2005). Encoding multielement scenes: Statistical learning of visual feature hierarchies. *Journal of Experimental Psychology: General*, *134*(4), 521–537.

Fletcher, P., Büchel, C., Josephs, O., Friston, K., & Dolan, R. (1999). Learning-related neuronal responses in prefrontal cortex studied with functional neuroimaging. *Cerebral Cortex*, *9*(2), 168–178.

Foxe, J. J., & Snyder, A. C. (2011). The role of alpha-band brain oscillations as a sensory suppression mechanism during selective attention. *Frontiers in Psychology*, *2*(154), 1–13. http://doi.org/10.3389/fpsyg.2011.00154

French, R. M., Addyman, C., & Mareschal, D. (2011). TRACX: A recognition-based connectionist framework for sequence segmentation and chunk extraction. *Psychological Review*, *118*(4), 614–636. http://doi.org/10.1037/a0025255

Freyer, F., Becker, R., Dinse, H. R., & Ritter, P. (2013). State-dependent perceptual learning. *The Journal of Neuroscience*, *33*(7), 2900–2907. http://doi.org/10.1523/JNEUROSCI.4039-12.2013

Frost, R., Siegelman, N., Narkiss, A., & Afek, L. (2013). What predicts successful literacy acquisition in a second language? *Psychological Science*, *24*(7), 1243–1252. http://doi.org/10.1177/0956797612472207

Gabrieli, J. D. E., Fleischman, D. A., Keane, M. M., Reminger, S. L., & Morrell, F. (1995). Double dissociation between memory systems underlying explicit and implicit memory in the human brain. *Psychological Science*, *6*(2), 76–82.

Ghose, G. M. (2004). Learning in mammalian sensory cortex. *Current Opinion in Neurobiology*, *14*(4), 513–8. http://doi.org/10.1016/j.conb.2004.07.003

Gilbert, C. D., Li, W., & Piech, V. (2009). Perceptual learning and adult cortical plasticity. *Journal of Physiology*, *587*(12), 2743–2751.

Gilbert, C. D., Sigman, M., & Crist, R. E. (2001). The Neural Basis of Perceptual Learning. *Neuron*, *31*, 681–697.

Hanslmayr, S., Aslan, A., Staudigl, T., Klimesch, W., Herrmann, C. S., & Bäuml, K.-H. (2007). Prestimulus oscillations predict visual perception performance between and within subjects. *NeuroImage*, *37*(4), 1465–1473. http://doi.org/10.1016/j.neuroimage.2007.07.011

Hanslmayr, S., Gross, J., Klimesch, W., & Shapiro, K. L. (2011). The role of alpha oscillations in temporal attention. *Brain Research Reviews*, *67*(1-2), 331–343. http://doi.org/10.1016/j.brainresrev.2011.04.002

Hauser, M. D., Newport, E. L., & Aslin, R. N. (2001). Segmentation of the speech stream in a non-human primate: Statistical learning in cotton-top tamarins. *Cognition*, *78*(3), B53–B64.

Hua, T., Bao, P., Huang, C.-B., Wang, Z., Xu, J., Zhou, Y., & Lu, Z.-L. (2010). Perceptual Learning Improves Contrast Sensitivity of V1 Neurons in Cats. *Current Biology*, *20*, 887–894.

Hughes, S. W., & Crunelli, V. (2005). Thalamic mechanisms of EEG alpha rhythms and their pathological implications. *The Neuroscientist*, *11*(4), 357–372. http://doi.org/10.1177/1073858405277450

Hung, S.-C., & Seitz, A. R. (2014). Prolonged training at threshold promotes robust retinotopic specificity in perceptual learning. *The Journal of Neuroscience*, *34*(25), 8423–8431. http://doi.org/10.1523/JNEUROSCI.0745-14.2014

Hunt, R., & Aslin, R. (2001). Statistical learning in a serial reaction time task: Access to separable statistical cues by individual learners. *Journal of Experimental Psychology: General*, *130*(4), 658–680.

Hussain, Z., Sekuler, A. B., & Bennett, P. J. (2011). Superior identification of familiar visual patterns a year after learning. *Psychological Science*, *22*(6), 724–730. http://doi.org/10.1177/0956797611409591

Ingram, K. M., Mickes, L., & Wixted, J. T. (2012). Recollection can be weak and familiarity can be strong. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *38*(2), 325–339.

Jacoby, L. L. (1991). A process dissociation framework: Separating automatic from intentional uses of memory. *Journal of Memory and Language*, *30*, 513–541.

Jensen, O., Gelfand, J., Kounios, J., & Lisman, J. E. (2002). Oscillations in the alpha band (9-12 Hz) increase with memory load during retention in a short-term memory task. *Cerebral Cortex*, *12*(8), 877–882. http://doi.org/10.1093/cercor/12.8.877

Jensen, O., & Mazaheri, A. (2010). Shaping functional architecture by oscillatory alpha activity: gating by inhibition. *Frontiers in Human Neuroscience*, *4*(186), 1–8. http://doi.org/10.3389/fnhum.2010.00186

Jensen, O., Spaak, E., & Zumer, J. M. (2014). Human brain oscillations : from physiological mechanisms to analysis and cognition. In S. Supek & C. J. Aine (Eds.), *Magnetoencephalography. From Signals to Dynamic Cortical Networks* (pp. 359–404). Springer Berlin.

Jeter, P. E., Dosher, B. A., Liu, S.-H., & Lu, Z.-L. (2010). Specificity of perceptual learning increases with increased training. *Vision Research*, *50*(19), 1928–1940. http://doi.org/10.1016/j.visres.2010.06.016

Jones, S. R., Pritchett, D. L., Stufflebeam, S. M., Hämäläinen, M., & Moore, C. I. (2007). Neural correlates of tactile detection: a combined magnetoencephalography and biophysically based computational modeling study. *The Journal of Neuroscience*, *27*(40), 10751–10764. http://doi.org/10.1523/JNEUROSCI.0482-07.2007

Karuza, E. A., Newport, E. L., Aslin, R. N., Starling, S. J., Tivarus, M. E., & Bavelier, D. (2013). The neural correlates of statistical learning in a word segmentation task: An fMRI study. *Brain and Language*, *127*(1), 46–54. http://doi.org/10.1016/j.bandl.2012.11.007

Keil, A., Debener, S., Gratton, G., Junghöfer, M., Kappenman, E. S., Luck, S. J., … Yee, C. M. (2014). Committee report: publication guidelines and recommendations for studies using electroencephalography and magnetoencephalography. *Psychophysiology*, *51*(1), 1–21. http://doi.org/10.1111/psyp.12147

Kelly, S. P., Lalor, E. C., Reilly, R. B., & Foxe, J. J. (2006). Increases in alpha oscillatory power reflect an active retinotopic mechanism for distracter suppression during sustained visuospatial attention. *Journal of Neurophysiology*, *95*(6), 3844–3851. http://doi.org/10.1152/jn.01234.2005

Kim, R., Seitz, A., Feenstra, H., & Shams, L. (2009). Testing assumptions of statistical learning: Is it long-term and implicit? *Neuroscience Letters*, *461*(2), 145–149. http://doi.org/10.1016/j.neulet.2009.06.030

Kim, R., Seitz, A., & Shams, L. (2008). Benefits of Stimulus Congruency for Multisensory Facilitation of Visual Learning. *PloS One*, *3*(1), e1532.

Kirkham, N. Z., Slemmer, J. A., & Johnson, S. P. (2002). Visual statistical learning in infancy: Evidence for a domain general learning mechanism. *Cognition*, *83*(2), B35–B42.

Kleiner, M., Brainard, D. H., & Pelli, D. G. (2007). What's new in Psychtoolbox-3? *Perception*, *36*(ECVP Abstract Supplement).

Klimesch, W. (1999). EEG alpha and theta oscillations reflect cognitive and memory performance: a review and analysis. *Brain Research. Brain Research Reviews*, *29*(2-3), 169–195.

Klimesch, W. (2012). Alpha-band oscillations, attention, and controlled access to stored information. *Trends in Cognitive Sciences*, *16*(12), 606–617. http://doi.org/10.1016/j.tics.2012.10.007

Klimesch, W., Sauseng, P., & Hanslmayr, S. (2007). EEG alpha oscillations: the inhibition-timing hypothesis. *Brain Research Reviews*, *53*(1), 63–88. http://doi.org/10.1016/j.brainresrev.2006.06.003

Koelewijn, T., Bronkhorst, A., & Theeuwes, J. (2010). Attention and the multiple stages of multisensory integration: A review of audiovisual studies. *Acta Psychologica*, *134*(3), 372–384. http://doi.org/10.1016/j.actpsy.2010.03.010

Lange, J., Keil, J., Schnitzler, A., van Dijk, H., & Weisz, N. (2014). The role of alpha oscillations for illusory perception. *Behavioural Brain Research*, *271*, 294–301. http://doi.org/10.1016/j.bbr.2014.06.015

Law, C.-T., & Gold, J. I. (2008). Neural correlates of perceptual learning in a sensory-motor, but not a sensory, cortical area. *Nature Neuroscience*, *11*(4), 505–13. http://doi.org/10.1038/nn2070

Le Dantec, C. C., Melton, E. E., & Seitz, A. R. (2012). A triple dissociation between learning of target , distractors , and spatial contexts. *Journal of Vision*, *12*(2), 1–12. http://doi.org/10.1167/12.2.5.Introduction

Le Dantec, C. C., & Seitz, A. R. (2012). High resolution, high capacity, spatial specificity in perceptual learning. *Frontiers in Psychology*, *3*(222), 1–7. http://doi.org/10.3389/fpsyg.2012.00222

Lieberman, M. D., Chang, G. Y., Chiao, J., Bookheimer, S. Y., & Knowlton, B. J. (2004). An event-related fMRI study of artificial grammar learning in a balanced chunk strength design. *Journal of Cognitive Neuroscience*, *16*(3), 427–438. http://doi.org/10.1162/089892904322926764

Loftus, G. R., & Masson, M. E. J. (1994). Using confidence intervals in within-subject designs. *Psychonomic Bulletin & Review*, *1*(4), 476–490.

Logan, G. D. (1992). Attention and preattention in theories of automaticity. *American Journal of Psychology*, *105*(2), 317–339.

Lopes da Silva, F. H., van Lierop, T. H. M. T., Schrijer, C. F., & Storm van Leeuwen, W. (1973). Organization of thalamic and cortical alpha rhythms: spectra and coherences. *Electroencephalography and Clinical Neurophysiology*, *35*, 627–639.

Nenert, R., Viswanathan, S., Dubuc, D. M., & Visscher, K. M. (2012). Modulations of ongoing alpha oscillations predict successful short-term visual memory encoding. *Frontiers in Human Neuroscience*, *6*(May), 1–11. http://doi.org/10.3389/fnhum.2012.00127

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.

Oostenveld, R., Fries, P., Maris, E., & Schoffelen, J.-M. (2011). FieldTrip: Open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. *Computational Intelligence and Neuroscience*, *2011*(156869), 1–9. http://doi.org/10.1155/2011/156869

Oostenveld, R., & Praamstra, P. (2001). The five percent electrode system for high-resolution EEG and ERP measurements. *Clinical Neurophysiology : Official Journal of the International Federation of Clinical Neurophysiology*, *112*(4), 713–719.

Packard, M. G. (1999). Glutamate infused posttraining into the hippocampus or caudate-putamen differentially strengthens place and response learning. *Proceedings of the National Academy of Sciences*, *96*(22), 12881–12886.

Palva, S., & Palva, J. M. (2011). Functional roles of alpha-band phase synchronization in local and large-scale cortical networks. *Frontiers in Psychology*, *2*(204), 1–15. http://doi.org/10.3389/fpsyg.2011.00204

Pasupathy, A., & Miller, E. K. (2005). Different time courses of learning-related activity in the prefrontal cortex and striatum. *Nature*, *433*(7028), 873–876. http://doi.org/10.1038/nature03287

Payne, L., & Sekuler, R. (2014). The Importance of Ignoring: Alpha Oscillations Protect Selectivity. *Current Directions in Psychological Science*, *23*(3), 171–177. http://doi.org/10.1177/0963721414529145

Perruchet, P., & Pacton, S. (2006). Implicit learning and statistical learning: One phenomenon, two approaches. *Trends in Cognitive Sciences*, *10*(5), 233–8. http://doi.org/10.1016/j.tics.2006.03.006

Perruchet, P., & Vinter, A. (1998). PARSER: A model for word segmentation. *Journal of Memory and Language*, *39*(2), 246–263. http://doi.org/10.1006/jmla.1998.2576

Petrov, A. A., Dosher, B. A., & Lu, Z.-L. (2005). The dynamics of perceptual learning: an incremental reweighting model. *Psychological Review*, *112*(4), 715–743. http://doi.org/10.1037/0033-295X.112.4.715

Pflieger, M. (2001). Theory of a spatial filter for removing ocular artifacts with preservation of EEG. *EMSE Workshop*, 7–8.

Pilly, P. K., Grossberg, S., & Seitz, A. R. (2010). Low-level sonsory plasticity during task-irrelevant perceptual learning: Evidence from conventional and double training procedures. *Vision Research*, *50*, 424–432.

Poldrack, R. A., Clark, J., Paré-Blagoev, E. J., Shohamy, D., Creso Moyano, J., Myers, C., & Gluck, M. A. (2001). Interactive memory systems in the human brain. *Nature*, *414*(6863), 546–550. http://doi.org/10.1038/35107080

Posner, M. I., & Petersen, S. E. (1990). The attention system of the human brain. *Annual Review of Neuroscience*, *13*, 25–42. http://doi.org/10.1146/annurev.ne.13.030190.000325

Posner, M. I., & Snyder, C. R. R. (1975). Attention and cognitive control. In R. L. Solso (Ed.), *Information processing and cognition: The Loyola symposium* (pp. 55–85). Hillsdale, NJ: Erlbaum.

Powers, A. R., Hevey, M. A., & Wallace, M. T. (2012). Neural Correlates of Multisensory Perceptual Learning. *Journal of Neuroscience*, *32*(18), 6263–6274. http://doi.org/10.1523/JNEUROSCI.6138-11.2012

process. (2015). Retrieved August 09, 2015, from http://www.merriam-webster.com/dictionary/process.

Ramachandran, V. S., & Braddick, O. (1973). Orientation-specific learning in stereopsis. *Perception*, *2*(3), 371–376.

Raposo, D., Sheppard, J. P., Schrater, P. R., & Churchland, A. K. (2012). Multisensory decision-making in rats and humans. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *32*(11), 3726–35. http://doi.org/10.1523/JNEUROSCI.4998-11.2012

Reber, A. S. (1967). Implicit learning of artificial grammars. *Journal of Verbal Learning and Verbal Behavior*, *6*(6), 855–863. http://doi.org/10.1016/S0022-5371(67)80149-X

Romei, V., Gross, J., & Thut, G. (2010). On the role of prestimulus alpha rhythms over occipito-parietal areas in visual input regulation: correlation or causation? *The Journal of Neuroscience*, *30*(25), 8692–8697. http://doi.org/10.1523/JNEUROSCI.0160-10.2010

Romei, V., Gross, J., & Thut, G. (2012). Sounds reset rhythms of visual cortex and corresponding human visual perception. *Current Biology*, *22*(9), 807–813. http://doi.org/10.1016/j.cub.2012.03.025

Ronnqvist, K. C., McAllister, C. J., Woodhall, G. L., Stanford, I. M., & Hall, S. D. (2013). A multimodal perspective on the composition of cortical oscillations. *Frontiers in Human Neuroscience*, *7*(April), 132. http://doi.org/10.3389/fnhum.2013.00132

Sadeh, T., Shohamy, D., Levy, D. R., Reggev, N., & Maril, A. (2011). Cooperation between the hippocampus and the striatum during episodic encoding. *Journal of Cognitive Neuroscience*, *23*(7), 1597–1608.

Saffran, J. R., Aslin, R. N., & Newport, E. L. (1996). Statistical learning by 8-month-old infants. *Science*, *274*(5294), 1926–1928.

Saffran, J. R., Johnson, E., Aslin, R. N., & Newport, E. L. (1999). Statistical learning of tone sequences by human infants and adults. *Cognition*, *70*(1), 27–52.

Saffran, J. R., Newport, E. L., Aslin, R. N., Tunick, R. A., & Barrueco, S. (1997). Incidental language learning: Listening (and learning) out of the corner of your ear. *Psychological Science*, *8*(2), 101–105.

Saffran, J. R., & Thiessen, E. (2003). Pattern induction by infant language learners. *Developmental Psychology*, *39*(3), 484–494.

Sagi, D. (2011). Perceptual learning in Vision Research. *Vision Research*, *51*(13), 1552–1566. http://doi.org/10.1016/j.visres.2010.10.019

Sasaki, Y., Náñez, J., & Watanabe, T. (2012). Recent progress in perceptual learning research. *Wiley Interdisciplinary Reviews: Cognitive Science*, *3*(3), 293–299. http://doi.org/10.1002/wcs.1175.Recent

Schapiro, A. C., Gregory, E., Landau, B., McCloskey, M., & Turk-Browne, N. B. (2014). The necessity of the medial temporal lobe for statistical learning. *Journal of Cognitive Neuroscience*, *26*(8), 1736–1747. http://doi.org/doi:10.1162/jocn_a_00578

Schapiro, A. C., Kustner, L. V, & Turk-Browne, N. B. (2012). Shaping of object representations in the human medial temporal lobe based on temporal regularities. *Current Biology*, *22*(17), 1622–1627. http://doi.org/10.1016/j.cub.2012.06.056

Schapiro, A. C., & Turk-Browne, N. B. (2015). Statistical learning. In A. W. Toga & R. A. Poldrack (Eds.), *Brain Mapping: An Encyclopedic Reference* (pp. 501–506). Academic Press.

Schoups, A., Vogels, R., Qian, N., & Orban, G. (2001). Practising orientation identification improves orientation coding in V1 neurons. *Nature*, *412*(August), 549–553.

Seger, C., Prabhakaran, V., Poldrack, R. A., & Gabrieli, J. (2000). Neural activity differs between explicit and implicit learning of artificial grammar strings: An fMRI study. *Psychobiology*, *28*(3), 283–292.

Seitz, A. R., & Dinse, H. R. (2007). A common framework for perceptual learning. *Current Opinion in Neurobiology*, *17*, 148–153.

Seitz, A. R., Kim, R., & Shams, L. (2006). Sound facilitates visual learning. *Current Biology*, *16*, 1422–1427.

Seitz, A. R., Kim, R., van Wassenhove, V., & Shams, L. (2007). Simultaneous and independent acquisition of multisensory and unisensory associations. *Perception*, *36*(10), 1445–1453.

Seitz, A. R., & Watanabe, T. (2005). A unified model for perceptual learning. *Trends in Cognitive Sciences*, *9*(7), 329–334.

Shams, L., Kamitani, Y., & Shimojo, S. (2000). What you see is what you hear. *Nature*, *408*(December), 2000. http://doi.org/10.1038/35048669

Shams, L., & Seitz, A. R. (2008). Benefits of Multisensory Learning. *Trends in Cognitive Sciences*, *12*(11), 411–417.

Sheppard, J., Raposo, D., & Churchland, A. (2013). Dynamic weighting of multisensory stimuli shapes decision-making in rats and humans. *Journal of Vision*, *13(6)*(4), 1–19. http://doi.org/10.1167/13.6.4.doi

Shimojo, S., & Shams, L. (2001). Sensory modalities are not seperate modalities: plasticity and interactions. *Current Opinion in Neurobiology*, *11*, 505–509.

Sigala, R., Haufe, S., Roy, D., Dinse, H. R., & Ritter, P. (2014). The role of alpha-rhythm states in perceptual learning: insights from experiments and computational models. *Frontiers in Computational Neuroscience*, *8*(36), 1–19. http://doi.org/10.3389/fncom.2014.00036

Silva, L., Amitai, Y., & Connors, B. (1991). Intrinsic oscillations of neocortex generated by layer 5 pyramidal neurons. *Science*, *251*(4992), 432–435.

Snyder, A. C., & Foxe, J. J. (2010). Anticipatory attentional suppression of visual features indexed by oscillatory alpha-band power increases: a high-density electrical mapping study. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *30*(11), 4024–4032. http://doi.org/10.1523/JNEUROSCI.5684-09.2010

Stein, B. E., & Stanford, T. R. (2008). Multisensory integration: current issues from the perspective of the single neuron. *Nature Reviews. Neuroscience*, *9*(4), 255–266. http://doi.org/10.1038/nrn2377

Thut, G., Nietzel, A., Brandt, S. a, & Pascual-Leone, A. (2006). Alpha-band electroencephalographic activity over occipital cortex indexes visuospatial attention bias and predicts visual target detection. *The Journal of Neuroscience*, *26*(37), 9494–9502. http://doi.org/10.1523/JNEUROSCI.0875-06.2006

Toro, J. M., Sinnett, S., & Soto-Faraco, S. (2005). Speech segmentation by statistical learning depends on attention. *Cognition*, *97*(2), B25–B34.

Turk-Browne, N. B. (2012). Statistical learning and its consequences. In M. D. Dodd & J. H. Flowers (Eds.), *The Influence of Attention, Learning, and Motivation on Visual Search* (pp. 117–146). New York, NY: Springer New York. http://doi.org/10.1007/978-1-4614-4794-8

Turk-Browne, N. B., Isola, P. J., Scholl, B., & Treat, T. A. (2008). Multidimensional visual statistical learning. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *34*(2), 399–407.

Turk-Browne, N. B., Jungé, J. A., & Scholl, B. J. (2005). The automaticity of visual statistical learning. *Journal of Experimental Psychology: General*, *134*(4), 552–564.

Turk-Browne, N. B., & Scholl, B. (2009). Flexible visual statistical learning: transfer across space and time. *Journal of Experimental Psychology: Human Perception and Performance*, *35*(1), 195–202.

Turk-Browne, N. B., Scholl, B. J., Chun, M. M., & Johnson, M. K. (2009). Neural evidence of statistical learning: Efficient detection of visual regularities without awareness. *Journal of Cognitive Neuroscience*, *21*(10), 1934–1945.

Turk-Browne, N. B., Scholl, B., Johnson, M. K., & Chun, M. M. (2010). Implicit perceptual anticipation triggered by statistical learning. *Journal of Neuroscience*, *30*(33), 11177–11187.

Vaden, R. J., Hutcheson, N. L., McCollum, L. a, Kentros, J., & Visscher, K. M. (2012). Older adults, unlike younger adults, do not modulate alpha power to suppress irrelevant information. *NeuroImage*, *63*(3), 1127–1133. http://doi.org/10.1016/j.neuroimage.2012.07.050

Van Winsum, W., Sergeant, J., & Geuze, R. (1984). The functional significance of event-related desynchronization of alpha rhythm in attentional and activating tasks. *Electroencephalography and Clinical Neurophysiology*, *58*(6), 519–524. http://doi.org/10.1016/0013-4694(84)90042-7

von Kriegstein, K., & Giraud, A. L. (2006). Implicit multisensory associations influence voice recognition. *PLoS Biology*, *4*(10), 1809–1820. http://doi.org/10.1371/journal.pbio.0040326

Watanabe, T., & Sasaki, Y. (2015). Perceptual learning: Toward a comprehensive theory. *Annual Review of Psychology*, *66*, 197–221. http://doi.org/10.1146/annurev-psych-010814-015214

Watson, A. B., & Pelli, D. G. (1983). QUEST: A Bayesian adaptive psychometric method. *Perception and Psychophysics*, *33*(2), 113–120.

Wixted, J. T. (2007). Dual-process theory and signal-detection theory of recognition memory. *Psychological Review*, *114*(1), 152–176.

Woodman, G. F. (2010). A brief introduction to the use of event-related potentials in studies of perception and attention. *Attention, Perception, & Psychophysics*, *72*(8), 2031–2046. http://doi.org/10.3758/APP

Xiao, L.-Q., Zhang, J.-Y., Wang, R., Klein, S. a, Levi, D. M., & Yu, C. (2008). Complete transfer of perceptual learning across retinal locations enabled by double training. *Current Biology : CB*, *18*(24), 1922–1926. http://doi.org/10.1016/j.cub.2008.10.030

Yang, C. D. (2004). Universal Grammar, statistics or both? *Trends in Cognitive Sciences*, *8*(10), 451–456.

Yang, J., & Li, P. (2012). Brain networks of explicit and implicit learning. *PloS One*, *7*(8), e42993. http://doi.org/10.1371/journal.pone.0042993

Yang, T., & Maunsell, J. H. R. (2004). The effect of perceptual learning on neuronal responses in monkey visual area V4. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *24*(7), 1617–1626. http://doi.org/10.1523/JNEUROSCI.4442-03.2004

Yonelinas, A. P. (1994). Receiver-operating characteristics in recognition memory: evidence for a dual-process model. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *20*(6), 1341–1354.

Yu, C., Klein, S. A., & Levi, D. M. (2004). Perceptual learning in contrast discrimination and the (minimal) role of context. *Journal of Vision*, *4*, 169–182. http://doi.org/10.1167/4.3.4

Zhang, J.-Y., Zhang, G.-L., Xiao, L.-Q., Klein, S. a, Levi, D. M., & Yu, C. (2010). Rule-based learning explains visual perceptual learning and its specificity and transfer. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *30*(37), 12323–12328. http://doi.org/10.1523/JNEUROSCI.0704-10.2010

Zhao, J., Al-Aidroos, N., & Turk-Browne, N. B. (2013). Attention is spontaneously biased toward regularities. *Psychological Science*, *24*(5), 667–677. http://doi.org/10.1177/0956797612460407

Zhao, J., Ngo, N., McKendrick, R., & Turk-Browne, N. B. (2011). Mutual interference between statistical summary perception and statistical learning. *Psychological Science*, *22*(9), 1212–1219. http://doi.org/10.1177/0956797611419304

Zohary, E., Celebrini, S., Britten, K. H., & Newsome, W. T. (1994). Neuronal plasticity that underlies improvement in perceptual performance. *Science (New York, N.Y.)*, *263*(5151), 1289–1292.

Complete Tables of Means

Chapter 1 - Experiment 1	Shape 1	Shape 2	
Variable	*M*	*M*	*SD*
Search Task RT (ms)	535.0016	519.9835	27.0906
Search Learned RT (ms)	677.8779	684.3018	41.9448
Search Learned Accuracy (%)	84.2453	83.9623	6.5993
Search Non-learned RT (ms)	670.7070	645.7044	45.8544
Search Non-learned Accuracy (%)	85.5696	87.7215	6.5374

Table 1 – Means and within-subject standard deviations for the search task and the detection task as split by the search task in Experiment 1. Note that within-subject SD is calculated according to Loftus and Masson (1994) and involves subtracting a participant's overall mean RT from each condition's mean RT, thus resulting in the same within-subjects SD for each condition.

Chapter 1 - Experiment 2	Shape 1	Shape 2	
Variable	*M*	*M*	*SD*
Recog. Learned RT (ms)	601.0396	603.3661	33.4764
Recog. Learned Acc. (%)	90.5755	87.1942	6.3290
Recog. Non-learned RT (ms)	608.3596	579.8756	34.8195
Recog. Non-learned Acc. (%)	91.0606	90.7576	6.1998
Recog. Learned (Fam.) RT (ms)	616.7955	615.7430	36.8466
Recog. Learned (Fam.) Acc. (%)	89.3590	84.7436	7.0569
Recog. Learned (Rem.) RT (ms)	580.8928	587.5400	28.7532
Recog. Learned (Rem.) Acc. (%)	92.1311	90.3279	5.2048

Table 2 – Means and within-subject standard deviations for the detection task as split by the recognition task (Recog.) in Experiment 2 and as further split by Familiar (Fam.)/Remember (Rem.) ratings in the recognition task. Note that within-subjects SD is calculated according to Loftus and Masson (1994) and involves subtracting a participant's overall mean RT from each condition's mean RT, thus resulting in the same within-subjects SD for each condition.

Chapter 1 - Experiment 3	Shape 1	Shape 2	
Variable	*M*	*M*	*SD*
Search Task (Intact) RT (ms)	441.8604	424.6667	15.1232
Search Task (Foil) RT (ms)	434.9080	422.0179	16.8743
Search Task (Mismatched) RT (ms)	-	429.8590	13.6318
Detect. Learned (Intact) RT (ms)	561.0158	556.5837	44.9820
Detect. Learned (Intact) Acc. (%)	88.7151	88.9944	10.4170
Detect. Learned (Foil) RT (ms)	-	571.1587	43.5238
Detect. Learned (Foil) Acc. (%)	-	90.0000	9.0451
Detect. Learned (Mis.) RT (ms)	-	564.1364	46.8164
Detect. Learned (Mis.) Acc. (%)	-	89.3855	9.4754
Detect. Non-learn. (Intact) RT (ms)	553.5948	542.5806	46.4856
Detect. Non-learn. (Intact) Acc. (%)	87.8981	88.2802	10.4046
Detect. Non-learn. (Foil) RT (ms)	-	549.0857	37.0857
Detect. Non-learn. (Foil) Acc. (%)	-	88.7898	8.9181
Detect. Non-learn. (Mis.) RT (ms)	-	553.7758	37.7127
Detect. Non-learn. (Mis.) Acc. (%)	-	90.5096	8.7767

Table 3 – Means and within-subject standard deviations for the search task and the detection task as split by the search task in Experiment 3. The detection task split by the search task only included the second shapes of the intact and mismatched pairs. Note that within-subjects SD is calculated according to Loftus and Masson (1994) and involves subtracting a participant's overall mean RT from each condition's mean RT, thus resulting in the same within-subjects SD for each condition.

Chapter 1 - Supplemental Data

Variable	*M*	*SD*
Position 2 < 1 Learned RT	3.8019	1.0458
Position 2 < 1 Non-learned RT	2.1772	1.0593
Exp. 1 Detect. Task RT (ms)		
Shape 1	674.5226	22.0731
Shape 2	666.7086	22.0731
Exp. 1 Detect. Task Acc. (%)		
Shape 1	84.8108	3.3529
Shape 2	85.5676	3.3529
Exp. 2 Detect. Task RT (ms)		
Shape 1	603.6415	13.7694
Shape 2	596.3334	13.7694
Exp. 2 Detect. Task Acc. (%)		
Shape 1	90.7317	2.8215
Shape 2	88.3415	2.8215
Exp. 3 Detect. Task RT (ms)		
Shape 1 (Intact)	557.2170	19.6873
Shape 2 (Intact)	550.0484	19.6873
Shape 1 (Foil)	560.7402	18.1728
Shape 2 (Foil)	561.0014	18.1728
Shape 2 (Mismatched)	559.0566	18.7134
Exp. 3 Detect. Task Acc. (%)		
Shape 1 (Intact)	88.3333	3.6446
Shape 2 (Intact)	88.6607	3.6446
Shape 1 (Foil)	89.6726	3.7797
Shape 2 (Foil)	89.4345	2.6689
Shape 2 (Mismatched)	89.9107	3.2004
Exp. 1 Search Task Triplet RT (ms)		
Shape 1	535.0016	33.7906
Shape 2	519.9835	23.4039
Shape 3	502.0861	21.0593
Exp. 1 Detect. Task Triplet RT (ms)		
Shape 1 (Learned)	668.9590	44.6678
Shape 2 (Learned)	672.9014	49.9690
Shape 3 (Learned)	682.8752	39.5317
Exp. 1 Detect. Task Triplet Acc. (%)		
Shape 1 (Learned)	86.2651	6.9939
Shape 2 (Learned)	85.6626	7.3337
Shape 3 (Learned)	86.9880	7.7871
Exp. 1 Detect. Task Triplet RT (ms)		
Shape 1 (Non-learned)	679.5779	50.6901

Shape 2 (Non-learned)	663.6845	49.4496
Shape 3 (Non-learned)	666.2951	44.4885
Exp. 1 Detect. Task Triplet Acc. (%)		
Shape 1 (Non-learned)	83.6274	8.0554
Shape 2 (Non-learned)	85.4902	8.1072
Shape 3 (Non-learned)	85.4902	8.1072
Exp. 2 Detect. Task Triplet RT (ms)		
Shape 1 (Learned Familiar)	616.7955	39.8886
Shape 2 (Learned Familiar)	615.7430	44.4447
Shape 3 (Learned Familiar)	621.9238	41.2576
Exp. 2 Detect. Task Triplet Acc. (%)		
Shape 1 (Learned Familiar)	89.3590	8.7093
Shape 2 (Learned Familiar)	84.7436	7.9623
Shape 3 (Learned Familiar)	87.4359	8.9050
Exp. 2 Detect. Task Triplet RT (ms)		
Shape 1 (Learned Remember)	580.8928	37.6057
Shape 2 (Learned Remember)	587.5400	30.8788
Shape 3 (Learned Remember)	584.2880	37.7941
Exp. 2 Detect. Task Triplet Acc. (%)		
Shape 1 (Learned Remember)	92.1311	6.3053
Shape 2 (Learned Remember)	90.3279	6.3728
Shape 3 (Learned Remember)	90.9836	7.2374
Exp. 2 Detect. Task Triplet RT (ms)		
Shape 1 (Non-learned)	608.3596	39.9798
Shape 2 (Non-learned)	579.8756	42.1087
Shape 3 (Non-learned)	596.9038	43.5140
Exp. 2 Detect. Task Triplet Acc. (%)		
Shape 1 (Non-learned)	91.0606	6.5666
Shape 2 (Non-learned)	90.7576	7.1425
Shape 3 (Non-learned)	92.4242	5.8753

Table 4 – Means and within-subject standard deviations for the Supplemental data of Chapter 1, listed in order of discussion within the Supplemental data section. Note that with the exception of the first two variables, all SD is within-subjects SD, which is calculated according to Loftus and Masson (1994) and involves subtracting a participant's overall mean RT from each condition's mean RT. For situations in which there are only two conditions this results in the same within-subjects SD for each condition.

Chapter 2 - All

Variable	*M*	*SD*
Orientation Offset Threshold (deg.)		
Day 1	28.4414	7.8831
Day 2	24.5411	6.3218
Day 3	25.1930	9.0739
Day 4	22.9928	5.4176
Day 5	20.9841	4.7902
Day 6	20.9403	5.5054
Day 7	15.3559	8.8280
Day 8	11.9638	4.4865
Pre-test RT (ms)		
Trained	906.1055	41.7535
Untrained	892.1720	37.6136
Pre-test Accuracy (%)		
Trained	61.6267	1.4175
Untrained	64.3044	2.8019
Post-test RT (ms)		
Trained	695.3097	41.7535
Untrained	808.5520	37.6136
Post-test Accuracy (%)		
Trained	72.2555	1.4175
Untrained	64.3967	2.8019
Pre-test Alpha Power (Normalized)		
Pre-stimulus Period (Overall)	0.3864	0.1860
Stim. Processing Period (Overall)	0.0662	0.0752
Post-test Alpha Power (Normalized)		
Pre-stimulus Period (Overall)	0.6748	0.1126
Pre-stimulus Period (Trained)	0.6253	0.0910
Pre-stimulus Period (Untrained)	0.6342	0.1355
Stim. Processing Period (Overall)	0.1315	0.1030
Stim. Processing Period (Trained)	0.1107	0.1054
Stim. Processing Period (Untrained)	0.0854	0.0955

Table 5 – Means and within-subject standard deviations for analyses in Chapter 2, listed in order of discussion. SD is within-subjects SD, calculated according to Loftus and Masson (1994).

Chapter 3 - Experiment 1 & Control Study

Variable	*M*	*SD*
2nd Session Trained Pos. RT (ms)		
60% Trials	561.0308	13.3617
30% Trials	560.4227	19.3603
10% Trials	558.5340	33.4332
2nd Session Trained Pos. Acc. (%)		
60% Trials	85.2963	7.1598
30% Trials	84.6296	5.8981
10% Trials	84.2592	6.2138
2nd Session Untrained Pos. RT (ms)		
60% Trials	578.4644	18.7343
30% Trials	582.9292	22.1594
10% Trials	569.7809	26.5703
2nd Session Untrained Pos. Acc. (%)		
60% Trials	83.9630	5.1462
30% Trials	85.1852	5.5432
10% Trials	86.2963	6.4151
1st Session SL RT (ms)		
Peripheral		
60%	637.4259	88.9406
30%	635.4876	79.7204
10%	638.7044	78.4459
Central		
60%	634.8689	83.7482
30%	643.8998	81.8824
10%	631.4805	92.1412
1st Session SL RT Difference (ms)		
Peripheral		
60%	-9.7113	60.3980
30%	-10.7342	59.6054
10%	5.9244	64.9090
Central		
60%	20.1598	56.6486
30%	32.2834	76.2953
10%	39.1377	60.3983
2nd Session Trained Stat. RT (ms)		
60% Trials	561.0308	13.3617
30% Trials	560.4227	19.3604
10% Trials	558.5340	33.4332
2nd Session Trained Stat. Acc. (%)		
60% Trials	85.2963	4.3128

30% Trials	84.6296	4.3887
10% Trials	84.2592	5.7683
2nd Session Untrained Stat. RT (ms)		
60% Trials	562.1341	18.7343
30% Trials	564.1185	22.1594
10% Trials	570.7241	26.5703
2nd Session Untrained Stat. Acc. (%)		
60% Trials	84.0741	3.1796
30% Trials	83.6111	3.4774
10% Trials	84.0741	4.9183
2nd Session Sound RT (ms)		
60% Trials	560.8261	16.3374
30% Trials	559.8963	14.8213
10% Trials	555.6536	26.2104
2nd Session Sound Acc. (%)		
60% Trials	88.3518	2.5605
30% Trials	89.1204	2.9942
10% Trials	89.0741	4.0732
2nd Session No Sound RT (ms)		
60% Trials	575.4968	16.1138
30% Trials	582.2467	25.5017
10% Trials	576.7221	24.5597
2nd Session No Sound Acc. (%)		
60% Trials	81.1481	33.9186
30% Trials	80.5092	39.1359
10% Trials	81.2963	51.2675
Alpha Power Post-stim. (Normalized)		
60%	0.1682	0.2060
30%	0.1641	0.1694
10%	0.1592	0.1324
Control Study		
1st Session SL RT (ms)		
Peripheral		
60%	552.1453	8.0863
30%	555.9562	10.7386
10%	557.6162	30.8726
Central		
60%	549.9104	11.1086
30%	552.8503	15.0847
10%	563.0437	29.4956
1st Session SL RT Difference (ms)		

Peripheral		
60%	-27.9366	58.2737
30%	-15.9276	61.3863
10%	4.6146	78.8075
Central		
60%	34.6112	58.5193
30%	44.1153	65.3156
10%	56.4636	55.2169

Table 6 – Means and within-subject standard deviations for analyses in Experiment 1 and the Control Study of Chapter 3, listed in order of discussion. SD is within-subjects SD, calculated according to Loftus and Masson (1994).

Chapter 3 - Experiment 2

Variable	*M*	*SD*
Contrast Threshold (Log Units)		
Low Frequency		
Peripheral		
Day 1	-1.5104	0.0679
Day 2	-1.5148	0.0250
Day 3	-1.5533	0.0255
Day 4	-1.5758	0.0416
Day 5	-1.5382	0.0306
Central		
Day 1	-1.6859	0.0464
Day 2	-1.6901	0.0343
Day 3	-1.6912	0.0420
Day 4	-1.7462	0.0823
Day 5	-1.6926	0.0431
Peak Frequency		
Peripheral		
Day 1	-1.2975	0.1462
Day 2	-1.4236	0.1892
Day 3	-1.4199	0.0680
Day 4	-1.3915	0.0701
Day 5	-1.3803	0.0329
Central		
Day 1	-1.7167	0.1123
Day 2	-1.7676	0.1017
Day 3	-1.8445	0.0810
Day 4	-1.7545	0.0851
Day 5	-1.8027	0.0648
Cutoff Frequency		
Peripheral		
Day 1	-0.5337	0.1083
Day 2	-0.5856	0.0452
Day 3	-0.5509	0.0549
Day 4	-0.5972	0.1295
Day 5	-0.5371	0.0827
Central		
Day 1	-0.8354	0.1679
Day 2	-0.9206	0.1331
Day 3	-1.0214	0.0736
Day 4	-0.9003	0.1010
Day 5	-1.0270	0.0755

Pre-Training Trained Pos. RT (ms)		
60% Trials	491.5716	19.1737
30% Trials	484.4715	22.8189
10% Trials	495.3326	25.2292
Pre-Training Trained Pos. Acc. (%)		
60% Trials	87.5926	3.5489
30% Trials	86.8056	4.1408
10% Trials	89.8148	4.1154
Pre-Training Untrained Pos. RT (ms)		
60% Trials	485.9121	23.3753
30% Trials	483.7037	25.6062
10% Trials	481.1662	23.5253
Pre-Training Untrained Pos. Acc. (%)		
60% Trials	86.9444	1.0338
30% Trials	88.6574	1.1928
10% Trials	87.5000	4.1112
Post-Training Trained Pos. RT (ms)		
60% Trials	473.8574	13.5918
30% Trials	476.8781	7.6089
10% Trials	483.2454	19.3412
Post-Training Trained Pos. Acc. (%)		
60% Trials	91.2963	1.8171
30% Trials	91.4352	2.0004
10% Trials	92.5926	3.9226
Post-Training Untrained Pos. RT (ms)		
60% Trials	488.6619	10.3457
30% Trials	491.4284	15.9645
10% Trials	492.9812	19.3367
Post-Training Untrained Pos. Acc. (%)		
60% Trials	91.7592	2.9223
30% Trials	92.5926	2.6168
10% Trials	91.6667	1.4778
Landolt C (Font Size)		
Pre-training		
Peripheral	16.8750	1.1884
Central	5.5000	0.2934
Post-training		
Peripheral	14.4306	1.1884
Central	6.0000	0.2934
Cutoff Spatial Frequency (c/deg.)		
Pre-training		
Peripheral	7.6300	0.2852

Central	16.9307	1.7399
Post-training		
Peripheral	8.9553	0.2852
Central	18.3676	1.7399
MN Read - Reading Acuity (logMAR)		
Pre-test	0.0150	0.0646
Post-test	0.0033	0.0646
MN Read - Crit. Print Size (logMAR)		
Pre-test	0.1667	0.0894
Post-test	0.1667	0.0894
MN Read – Max.Read. Speed (wpm)		
Pre-test	260.6667	73.1683
Post-test	246.6667	73.1683
SL Across Sessions (ms)		
Peripheral Location		
60%		
EEG 1	500.8094	21.0341
Train 1	528.8578	11.5306
Train 2	537.4980	10.8018
Train 3	521.8908	11.1664
Train 4	526.0350	9.3522
Train 5	543.0616	8.7993
EEG 2	470.5026	21.8080
30%		
EEG 1	504.1224	44.5307
Train 1	528.5713	27.4825
Train 2	541.7506	22.8946
Train 3	524.4243	20.9159
Train 4	527.1979	13.2016
Train 5	525.8402	15.2987
EEG 2	462.1108	30.9111
10%		
EEG 1	476.0950	103.5331
Train 1	529.7175	30.1054
Train 2	530.5827	33.2044
Train 3	523.1236	18.3298
Train 4	526.4572	26.4755
Train 5	531.7190	36.5006
EEG 2	465.4590	47.4203
Central Location		
60%		
EEG 1	451.1456	42.0682

Train 1	536.1100	23.1739
Train 2	530.2895	21.1807
Train 3	518.7308	22.4374
Train 4	520.6253	17.9318
Train 5	542.5494	17.3578
EEG 2	423.0942	43.6161
30%		
EEG 1	451.1164	89.0614
Train 1	530.3278	55.0211
Train 2	534.8408	44.0443
Train 3	516.9853	39.7894
Train 4	519.5781	28.4159
Train 5	530.7419	30.5178
EEG 2	422.6878	61.8222
10%		
EEG 1	454.6990	207.0661
Train 1	554.3023	60.8597
Train 2	541.4753	67.3538
Train 3	501.5683	36.4990
Train 4	534.8003	56.4267
Train 5	564.2380	63.0380
EEG 2	422.2607	94.8406
Pre-Training Trained Stats RT (ms)		
60% Trials	491.5716	13.5861
30% Trials	484.4715	9.2721
10% Trials	495.3326	16.1311
Pre-Training Trained Stats Acc. (%)		
60% Trials	87.5926	2.1971
30% Trials	86.8056	2.9609
10% Trials	89.8148	5.3856
Pre-Training Untrained Stats RT (ms)		
60% Trials	478.1040	16.9731
30% Trials	480.1784	16.1533
10% Trials	497.2400	16.0532
Pre-Training Untrained Stats Acc. (%)		
60% Trials	87.9630	3.6226
30% Trials	87.2685	1.3563
10% Trials	85.6481	6.6969
Post-Training Trained Stats RT (ms)		
60% Trials	473.8574	12.6344
30% Trials	476.8781	8.5073
10% Trials	483.2454	19.6807

Post-Training Trained Stats Acc. (%)		
60% Trials	91.2963	1.7402
30% Trials	91.4352	1.3004
10% Trials	92.5926	4.6234
Post-Training Untrained Stats RT (ms)		
60% Trials	471.2204	11.7358
30% Trials	487.1167	13.0912
10% Trials	476.7637	12.9488
Post-Training Untrain. Stats Acc. (%)		
60% Trials	90.9259	1.4862
30% Trials	92.1296	2.8088
10% Trials	88.8889	3.0192
Pre-Training Sound RT (ms)		
60% Trials	473.3302	12.4479
30% Trials	466.2922	16.9704
10% Trials	475.4521	15.0144
Pre-Training Sound Acc. (%)		
60% Trials	88.1944	2.2396
30% Trials	88.7731	1.0754
10% Trials	88.8889	2.7753
Pre-Training No Sound RT (ms)		
60% Trials	495.0648	13.4253
30% Trials	500.3668	17.0885
10% Trials	503.4415	17.3123
Pre-Training No Sound Acc. (%)		
60% Trials	86.6667	2.3769
30% Trials	85.8796	1.8000
10% Trials	86.1111	4.2912
Post-Training Sound RT (ms)		
60% Trials	469.9902	12.3600
30% Trials	472.9499	11.2806
10% Trials	469.0502	16.3169
Post-Training Sound Acc. (%)		
60% Trials	93.7037	2.3667
30% Trials	94.4444	3.8199
10% Trials	93.5185	2.2998
Post-Training No Sound RT (ms)		
60% Trials	484.7758	15.2574
30% Trials	493.5110	12.3413
10% Trials	497.2062	10.0210
Post-Training No Sound Acc. (%)		
60% Trials	88.9815	2.7007

30% Trials	89.8148	2.6376
10% Trials	86.8056	3.8350
Alpha Power Post-stim. (Normalized)		
Pre-Training		
60%	0.2486	0.1243
30%	0.2125	0.0970
10%	0.2151	0.1768
Post-Training		
60%	0.2900	0.2324
30%	0.3043	0.2650
10%	0.2263	0.2789
Overall Alpha Power (Normalized)		
Pre-stimulus Interval		
Pre-Training	0.4230	0.2449
Post-Training	0.5294	0.2249
Post-stimulus Interval		
Pre-Training	0.2345	0.1012
Post-Training	0.2879	0.2372

Table 7 – Means and within-subject standard deviations for analyses in Experiment 2 of Chapter 3, listed in order of discussion. SD is within-subjects SD, calculated according to Loftus and Masson (1994).