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Electrophysiological Correlates of Visual Object Category Formation in a Prototype-Distortion Task

Stephanie Marie Long
University of Arkansas, Fayetteville

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Electrophysiological Correlates of Visual Object Category Formation
in a Prototype-Distortion Task

A thesis submitted in partial fulfillment
of the requirements for the degree of
Master of Arts in Psychology

by

Stephanie Long
University of Arkansas
Bachelor of Arts in Psychology, 2016
University of Arkansas
Bachelor of Arts in Biology, 2016

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University of Arkansas

This thesis is approved for recommendation to the Graduate Council.

Connie Lamm, Ph.D.
Thesis Director

Woodrow Shew, Ph.D.
Committee Member

William Levine, Ph.D.
Committee Member

Abstract

In perceptual learning studies, participants engage in extensive training in the discrimination of visual stimuli in order to modulate perceptual performance. Much of the literature in perceptual learning has looked at the induction of the reorganization of low-level representations in V1. However, much remains to be understood about the mechanisms behind how the adult brain (an expert in visual object categorization) extracts high-level visual objects from the environment and categorically represents them in the cortical visual hierarchy. Here, I used event-related potentials (ERPs) to investigate the neural mechanisms involved in object representation formation during a hybrid visual search and prototype distortion category learning task. EEG was continuously recorded while participants performed the hybrid task, in which a peripheral array of four dot patterns was briefly flashed on a computer screen. In half of the trials, one of the four dot patterns of the array contained the target, a distorted prototype pattern. The remaining trials contained only randomly generated patterns. After hundreds of trials, participants learned to discriminate the target pattern through corrective feedback. A multilevel modeling approach was used to examine the predictive relationship between behavioral performance over time and two ERP components, the N1 and the N250. The N1 is an early sensory component related to changes in visual attention and discrimination (Hopf et al., 2002; Vogel & Luck, 2000). The N250 is a component related to category learning and expertise (Krigolson et al., 2009; Scott et al., 2008; Tanaka et al., 2006). Results indicated that while N1 amplitudes did not change with improved performance, increasingly negative N250 amplitudes did develop over time and were predictive of improvements in pattern detection accuracy.

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Introduction

Background Literature

The human brain learns to process varying objects in the environment using the visual system, something that computer science is still attempting to accomplish computationally (Nguyen, Yosinski, & Clune, 2015). Yet by full maturation, the human visual system is highly efficient at pattern detection in a world cluttered by visual objects (Logothetis & Sheinberg, 1996). As humans, we have the extraordinary ability to interpret varying forms of an object and recognize them as the same thing, such as a horse being shown in two or three dimensions, in sketches or pictures, occluded by other elements, in detail or as a silhouette, or even shown overhead as opposed to the side. Though this seems trivial, there are patients with impairments in visual cortex that develop what is known as visual object agnosia who cannot perform these simple tasks. Although this impairment ranges in effects, it can prevent patients from correctly identifying a visual object even though they have the ability to see and draw the object (Zihl, 2003). Visual agnosia cases call into question how the brain is perceptually organized. In *The Mind's Eye*, Oliver Sacks (2010) describes a case where one woman was able to identify solid objects but not drawings of the same object. He wrote, '[Lillian] made me wonder whether she had a specific agnosia for representations. The recognition of representations may require a sort of learning, the grasping of a code or convention, beyond that needed for the recognition of objects' (p. 12). Dr. Sacks' insight highlights the complexity of the brain's ability to learn to represent objects in many forms. These cases reveal that damage to the visual cortex can cause disruption in the brain's ability to flexibly represent objects; however, the neural mechanism underlying this process is still largely unknown.

How object representations are encoded in the visual system and what the mechanism is which allows for the incredible flexibility in object identification are questions that are still being asked in vision science. Hubel and Wiesel (1962) famously began investigations in cats to study how the visual system learns to process its environment. In these studies they discovered that single cells in early visual areas such as V1 and V2 represent low-level features of the environment such as the orientation of edges. These early visual areas then feed into areas later in the visual hierarchy such as V3 and V4, where more complex visual representations are formed (Felleman & Van Essen, 1991; Martin, 2007). In humans, studies have shown impairments in both early and late areas in the visual system are involved in deficits related to visual agnosia (Behrmann & Kimchi, 2003). Neuroimaging has led to a greater understanding of the brain areas in the visual system involved in object processing (Ishai, Ungerleider, Martin, Schouten, & Haxby, 1999; Martin, 2007) and object category representations in high-level brain regions (Seeger & Miller, 2010). However, in cognitive neuroscience there is still a gap in understanding the development of these representations from start to finish. The brain is not preprogrammed with innate representations of objects but instead uses experience to become an expert object processor (Hirsch & Spinelli, 1970).

Research into what is known as perceptual learning focuses on how early primary sensory areas (V1) functionally reorganize (the process known as neuroplasticity) due to extensive training and practice (Bao, Yang, Rios, He, & Engel, 2010). Perceptual learning is the term used to refer to adaptations to (and generally improved) perceptual performance following training and/or feedback (for review, see Fahle, 2005). Although perceptual learning provides insight into how areas early in the visual hierarchy flexibly adapt to visual experiences, generally

these effects are specific to V1 (Ramachandran & Braddick, 1973) and are not able to extend our understanding of the adaptability of later areas in the visual hierarchy.

Outside studies of V1 and its low-level feature discrimination of edges and Gabor tilt angles, studies of categorical learning are used to examine changes in higher-order visual areas. Category learning and research of visual object expertise both allow for the investigation of how the visual system forms representations for high-level visual objects. Object stimuli used in these studies range widely from artificial objects such as dot patterns (Posner & Keele, 1968) or morph blobs (Krigolson, Pierce, Holroyd, & Tanaka, 2009) to real-world objects such as birds (Scott, Tanaka, Sheinberg, & Curran, 2006) or cars (Gauthier, Skudlarski, Gore, & Anderson, 2000). There are several categorization paradigms according to Seger and Miller (2010). In particular, prototype distortion tasks allow for the study of the development of novel object representations. During these tasks, participants learn to discriminate between a distorted prototype pattern and randomly distorted patterns (Homa, Sterling, & Trepel, 1981), and this can be learned through feedback alone, eliminating the need to show the prototype (Ashby & Alfonso-Reese, 1998). Neuroimaging research (functional magnetic resonance imaging) of categorical learning using dot patterns has shown neuronal activation changes in the visual cortex during learning, such that as participants improve in performance their activations decrease (Little, Klein, Shobat, McClure, & Thulborn, 2004). This provides evidence that as the visual system gains experience categorizing objects, the brain is undergoing high-level neuroplasticity, where processing becomes more efficient and adapts to this experience.

To further understand how representations for prototype distortion categories change in the brain it is essential to investigate the gradual changes in category learning with temporal precision using event-related potentials (ERPs). Using EEG, researchers can examine

millisecond changes in electrical potential in the cortex related to changes in visual field. These specific potentials are referred to as visual evoked potentials (VEPs). Further, components of these VEPs can be decomposed and potentially reveal the underlying neural dynamics involved in a visual task. In this study, VEPs were used to examine the neural object representation being formed and refined over the course of a category learning task. Two components in particular were expected to play a role in these changes in the visual system, the N1 and the N250.

The N1, or N100, is an early sensory component that is a negative deflection which onsets around 100 to 200 milliseconds post-stimulus onset at the posterior midline (Luck, 2013). When investigating perceptual changes early in visual processing, this is a common component analyzed for changes due to its role in attentional processes. It has been theorized to be reflective of changes in visual attention (Hillyard & Anllo-Vento, 1998; Luck, 2013) as well as perceptual discrimination (Hopf, Bogel, Woodman, Heinze & Luck, 2002; Vogel & Luck, 2000). In categorical learning specifically, N1 has been shown to increase in negativity for category stimuli after learning compared to non-category stimuli (Curran, Tanaka, & Weiskopf, 2002). The N250, an inferior temporal component associated with object category learning, is a negative deflection that follows stimulus onset by 200-300 milliseconds (Schweinberger, Huddy, & Burton, 2004). Several studies have shown that changes in the amplitude of this component are associated with the acquisition of perceptual expertise in object recognition (Scott et al., 2006; Scott, Tanaka, Sheinberg, & Curran, 2008; Tanaka, Curran, Porterfield, & Collins, 2006). Both components are integral to understanding the temporal changes in object representations during learning within the visual system.

The Current Investigation

As part of an undergraduate honors thesis, I collected data and preliminarily analyzed the data to investigate the short-term plasticity mechanisms in the brain, while participants learned to represent a novel prototype pattern through category learning (Long, 2016). In that investigation, we crudely developed a timeline of category learning and found changes in the N250 component similar to previous studies (Scott et al., 2006; Tanaka et al., 2006). As predicted, the N250 amplitude increased (became more negative) as participants improved in object recognition across learning. All methods, procedures, and data described in this thesis were used previously for my undergraduate thesis (Long, 2016). However, the current investigation describes an improved analysis procedure to capture a more refined time course of learning to compare changes in N1 and N250 in conjunction with changes in behavioral performance.

Here, I describe the results of my investigation into the underlying perceptual mechanisms that develop in the visual hierarchy as the brain gains experience in recognizing a prototype pattern, using a multilevel model (MLM) of behavioral outcomes. In the preliminary analysis of the data we used signal-averaging and repeated measures ANOVAs to test component changes over several blocks of time. This is a very common technique used across EEG research (Luck, 2014; Picton et al., 2000). However, MLM is becoming increasingly popular in psychophysical studies as well as in ERP research because it is a more flexible technique that allows for the incorporation of subjects as a source of variability (Volpert-Esmond, Merkle, Levsen, Ito, & Bartholow, 2018) and this potentially allows for more power to detect fixed effects (Vossen, Van Breukelen, Hermens, Van Os, & Lousberg, 2011). Critical to this study, however, is that MLM allows for the inclusion of time as a continuous variable, while testing other effects at the subject level. This enables the modeling of learning over time, while

also accounting for differences in subjects' learning rates. Using MLM to model data that is time-series in nature, such as ERPs and learning, allowed for a much more precise and detailed analyses in this study.

In this study, I used MLM with predictor variables including *time*, to model changes in perceptual learning over the course of the experiment, *N1*, to model early visual discrimination processing, and *N250*, to model object category formation. The relationships between these predictors and the outcome variable, behavioral performance (as measured by d'), were analyzed to evaluate changes in object representation formation over time. I hypothesized that all three predictors would have significant main effects such that perceptual learning, N1, and N250 would all significantly increase with behavioral performance. I also hypothesized two significant interactions between both ERP component amplitudes and time. If these ERP components reflect the development of visual object processing, then the amplitude changes in these components should vary in conjunction with performance across time (both ERP components should increase in amplitude as performance increases over time).

Methods

Participants

Forty-four participants with normal or corrected-to-normal vision were recruited from the University of Arkansas undergraduate population (age $M = 20.8$, $SD = 2.52$, range = 18-29 years, 23 females). Each participant completed one session lasting three hours and was compensated with psychology course credit. Additionally to incentivize accuracy, participants received monetary reward (one cent for each correct response trial and one cent subtracted for each incorrect response trial) with a total average bonus of \$5.48. Two participants were excluded

from all analyses due to technical failures preventing physiological recordings. Twenty-three participants were excluded from analysis for one of three reasons, (1) data containing artifacts ($N = 3$), (2) large amounts of missing data ($N = 3$), or (3) non-learners/outliers ($N = 17$). The details of the exclusion criteria can be found in the “Statistical Analyses” section below. A final total of 19 participants were used in the analyses (age $M = 20$, $SD = 1.8$, range = 18-26, 11 females). The University of Arkansas International Review Board approved all procedures described in this thesis.

Stimuli

All experimental sessions were conducted in a laboratory under low levels of ambient light. All stimuli were presented on a 21-inch CRT monitor (85 Hz vertical refresh, 1024 x 768 resolution), electrically shielded in a grounded aluminum Faraday cage. A chinrest was used for all participants to maintain a viewing distance from the monitor at 57 cm.

The stimuli presented during the experiment were designed for participants to perform a hybrid category learning (an “A, not A” version of prototype distortion category learning reviewed in Ashby & Maddox, 2005) and visual search task (Neisser, 1967; Wolfe, 1994) that I developed and detail in the next section. While participants fixated on a central yellow dot (0.2° diameter), four sets of white square stimuli (each at an eccentricity of 6.4° from fixation) flashed briefly in the four quadrants of peripheral vision: upper left, lower left, upper right, and lower right. Each set of stimuli was contained within a $2.3^\circ \times 2.3^\circ$ area and included 48 white squares ($0.12^\circ \times 0.12^\circ$ each), for a total of 192 white squares displayed on each trial. Participants viewed stimuli from two conditions: Target Absent and Target Present. In the Target Absent condition, participants viewed small white squares positioned as random noise in all four peripheral quadrants (see examples in Figure 1C). The positions of the small white squares in each $2.3^\circ \times$

2.3° quadrant were formed by first randomly extracting the x- and y- coordinates of each square from a uniform distribution and then each x- and y- coordinate was shifted by a pseudo randomly-generated number extracted from a normal distribution ($M = 0^\circ$, $SD = 0.25^\circ$). In the Target Present condition, participants viewed the same four peripheral quadrants, three of which contained random noise (generated as previously described in the Absent condition), while one (which varied randomly from trial to trial) contained the target stimulus. The target stimulus was a statistically distorted version of a prototype object pattern roughly resembling an “X” (Figure 1A). Critically, the target stimulus that participants viewed was *never* the prototype pattern itself. Participants solely viewed the target stimulus as distortions of the prototype (see examples in Figure 1B). The target stimulus was created for each Target Present trial by taking the x- and y- coordinates of each white square from the original coordinates of the prototype pattern and shifting each square’s coordinates via the same normally distributed distortion used in the Absent condition.

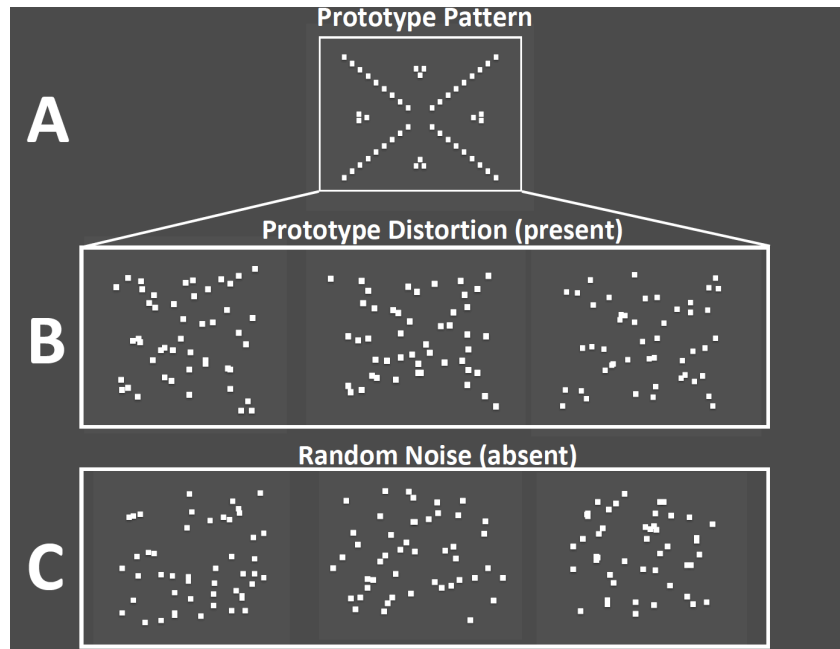


Figure 1. The target stimulus was a prototype pattern that was displayed distorted in one of the four peripheral locations, while the rest contained random noise during the Target Present trials. In the Target Absent trials, all four locations contained random noise.

Procedure

Ashby et al. (1998) reviewed four main tasks used to study human perceptual category learning including prototype distortion. The type of category learning used in this experiment was similar to a prototype distortion task, specifically the “A, not A” type. Like other prototype distortion tasks this experiment used distortions of prototype dot patterns as visual targets for categorization (Little, Shin, Sisco, & Thulborn, 2006; Posner & Keele, 1968). Participants either responded with a ‘1’ on the keyboard number pad if the target was present, indicating that the target they saw was part of category “A,” or responded with ‘2’ if the target was absent, indicating that all the stimuli presented were random and thus not category “A.”

However, the task used in my study was not designed solely as a category learning task. It was important to closely mimic how the visual system extracts object categories from a cluttered visual environment. Other vision scientists have used visual search tasks to study the visual system in this environment (Wolfe, Oliva, Horowitz, Butcher & Bompas, 2002; Yang &

Zelinsky, 2009). Similarly, my laboratory task also included elements of visual search and perceptual learning. At the beginning of each experiment, participants were instructed to look for a “pattern” that would appear on half of the trials. The prototype pattern was not described or shown to participants in any way. Instead, participants learned categorization through corrective feedback. Through the process of perceptual learning, over time most participants learned to correctly detect the target pattern (subjects had an average accuracy of 71% over the course of the experiment). Unlike other category learning tasks, participants were not asked to categorize a single object. Instead they had to perform a task with visual search, where they were presented with four peripheral objects and asked to categorize the environment as one that included a version of the target category or not. This provided a more ecologically valid experience to study the visual system learning to extract objects from the environment and categorize them.

To familiarize participants with the timing and response procedures, they first completed six practice trials. No instructions or explanations were given on what was being displayed, they were only told when to respond. Participants then viewed a total of 1792 trials in the hybrid category learning and visual search task, half of which were either Target Present trials (896) or Target Absent trials (896). Within each trial, participants began by fixating on the yellow fixation for a random interval between 1500 and 2500 milliseconds (ms). Then the four peripheral quadrants, each containing 48 white square stimuli, were flashed on the screen for 200 ms. Following the stimulus presentation, participants responded with a button press to indicate if the target was present or absent. Then after a random interval between 300 and 500 ms, a feedback stimulus (a green square for correct responses or a red square for incorrect responses) was displayed at fixation for 2000 ms. The experiment was composed of 16 blocks and following each was a display of the participant’s accuracy and total bonus money. Following the

experiment, participants were asked to fill out a survey to draw and describe the target pattern if they saw one.

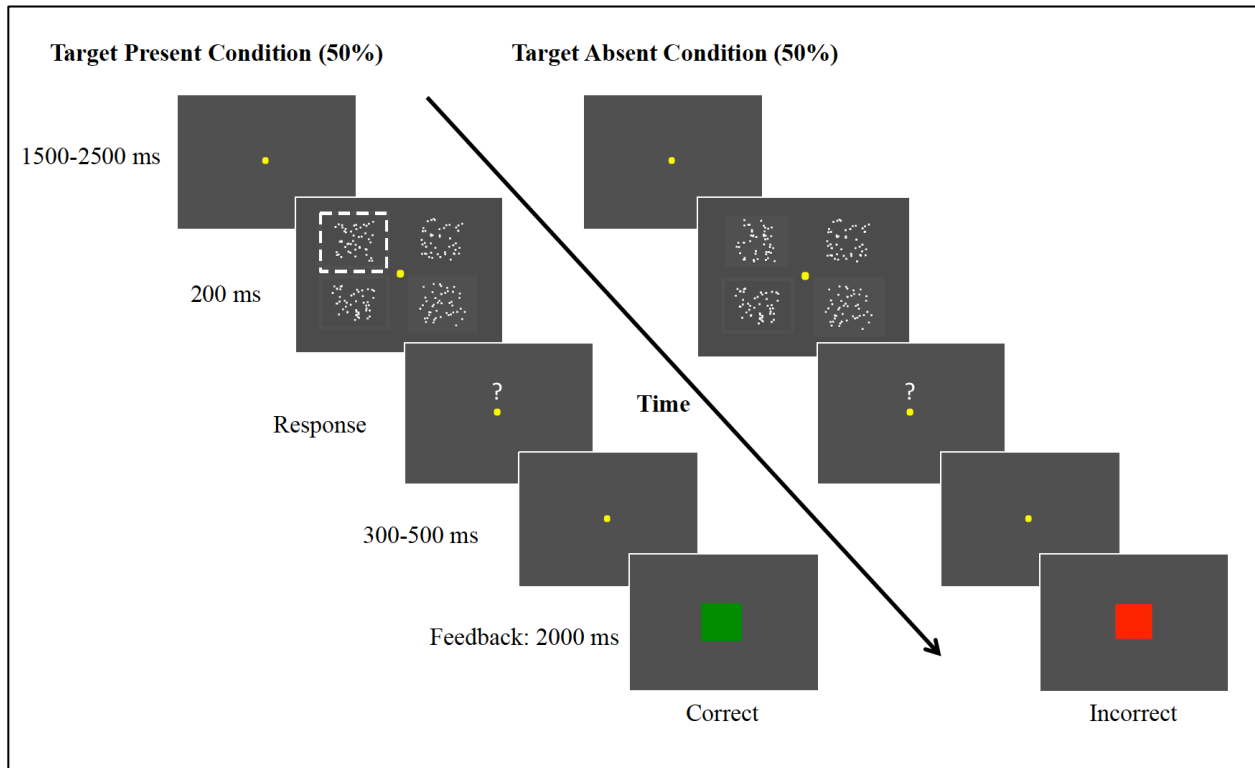


Figure 2. All trials began with a fixation screen and then were either Target Present trials or Target Absent trials. Participants responded on a keyboard after each stimulus presentation to indicate whether the target was present or absent. Corrective feedback was then displayed to complete the trial. *Note that the dashed white square in the Present condition is merely a demonstration of the target; participants were never shown the target during the task.

EEG recording. A 64-channel BrainAmp DC ActiCap active EEG system was used while each participant completed the experiment. Scalp-recorded Ag/AgCl electrodes were placed according to the standard 10-10 system. The electrodes were recorded from positions: AF3/4, AF7/8, Fz, F1/2, F3/4, F5/6, F7/8, FCz, FC1/2, FC3/4, FC5/6, FT7/8, Cz, C1/2, C3/4, C5/6, T7/8, CPz, CP1/2, CP3/4, CP5/6, TP7/8, Pz, P1/2, P3/4, P5/6, P7/8, POz, PO3/4, PO7/8, PO9/10, Oz, O1/2, and M1/2. Four bipolar electrode pairs were placed on the face of each participant to record electrooculogram (EOG) at the following locations: left and right canthi and above and below the left eye. Before EEG recording began, all electrode channels were verified

to have impedance levels at or below 5 k Ω . During continuous EEG recording, all electrodes were referenced to a common reference electrode (FCz), digitally sampled at 1000 Hz, and low-pass filtered at 250 Hz.

Statistical Analyses

Psychophysical data. To assess each participant's progress of perceptual learning, his or her behavioral responses were averaged over time using a moving average. The moving average encompassed a 20 trial window with 10 trials of overlap between each window (88 windows total). This windowing was used in the electrophysiological data as well to match the brain activity in time with the behavioral responses. This windowing sought to both optimize the signal-to-noise ratio of the ERPs as well as capture varying learning rates in the behavioral data. There was a wide range of learning rates across participants, with some taking as few as 10 trials to detect the target pattern with high accuracy, while others took many more trials. To capture participants' change in perceptual sensitivity over time, d' was calculated for each window (Wickens, 2002). This procedure allowed for the measurement of each participant's ability to discriminate between Target Present and Target Absent trials, while remaining uninfluenced by individual bias towards either condition.

ERP data. Offline, all data processing was performed with custom scripts in MATLAB. Using the EEGLAB toolbox (Delorme & Makeig, 2004; <http://www.sccn.ucsd.edu/eeglab>), all EEG channels were re-referenced to the average of the left and right mastoid channels (M1/2) and low-pass filtered at 50 Hz. Horizontal EOG (HEOG) was calculated by averaging the left and right canthi channels and vertical EOG (VEOG) was calculated by averaging EOG channels above and below the left eye.

Separate processing was performed on the scalp channels to clean the data for identification of ocular artifacts with extended Infomax ICA (Lee, Girolami, & Sejnowski, 1999) using *runica* (Makeig, Jung, Bell, Ghahremani, & Sejnowski, 1997) from the EEGLAB toolbox. First, all channel data were resampled at 250 Hz, then high pass filtered at 1 Hz, and segmented into non-overlapping segments from 200 ms before stimulus onset until 2000 ms after stimulus. On the segmented data, DC-offset was removed and epochs containing peak amplitudes of ± 250 mV were removed to minimize contamination of ICs by bad channels and muscle artifacts. The *runica* function was then applied to this cleaned data and 55 ICs were calculated from the scalp channels. The weights of this ICA were then applied to the continuous data and ICs containing ocular artifacts (eye blinks and eye movements) were identified through visual inspection and removed. The continuous data, free of ocular artifacts, was then processed outside of EEGLAB with custom scripting in MATLAB.

To extract visual evoked potentials (VEPs), the continuous EEG data was time-locked to the presentation of the white square stimuli and segmented from 200 ms before the onset of the stimuli until 400 ms after this onset (-200 – 400 ms). All segments were then baseline corrected 200 ms prior to stimulus onset (-200 – 0 ms). In the target present trials, the target locations were collapsed across the left and right visual fields. Artifact rejection was performed to reject segments with an absolute difference greater than 200 microvolts (μV). If any participant had greater than 20% of segments rejected then electrodes were evaluated across segments for noisiness by calculating root-mean-square (RMS). Only three subjects fit these criteria. Any electrode with greater than two SDs from the mean RMS was considered an outlier and removed from analysis, which resulted in up to two electrodes being removed from analysis (none were electrodes of interest).

Similar to the psychophysical data, the ERP data was averaged using a moving average with the same window of 20 trials with 10 overlapping trials. From these moving averages, components N250 and N1 were quantified as the average voltage within a specific time window, visually identified from grand averaged ERP waveforms collapsed across experimental manipulations. The components were also evaluated by pooling electrodes that were crosschecked within the literature (N250: Scott et al., 2006; Tanaka et al., 2006; N1: Hopf et al., 2002; Luck, 2013) as well as visual inspection of scalp distributions to identify electrodes with maximum amplitude (Figure 3C and 3F). Each participants' mean N250 component amplitude (μV) over time was calculated by a peak difference of Target Absent trials subtracted from Target Present trials at 225 – 335 ms following stimulus onset (Figure 3D and 3E), from pooled electrodes (collapsed contralateral to the visual field) PO7/8 and P7/8 (Figure 3F). This difference was calculated to measure the N250 activity that was related to target presence instead of calculating and comparing the two conditions separately, consistent with the procedure used by Scott et al. (2008) and Tanaka et al. (2006). The N1 component was identified at 150 – 180 ms post-stimulus (Figure 3A and 3B), from pooled electrodes (collapsed contralateral to the visual field) P5/6, P7/8, PO3/4, PO7/8, and O1/2 (Figure 3C). A mean N1 peak difference amplitude (μV) was calculated over time by subtracting Target Absent from Target Present to look at N1 change over time that was unique to target presence by removing baseline N1 activity occurring in the absent condition.

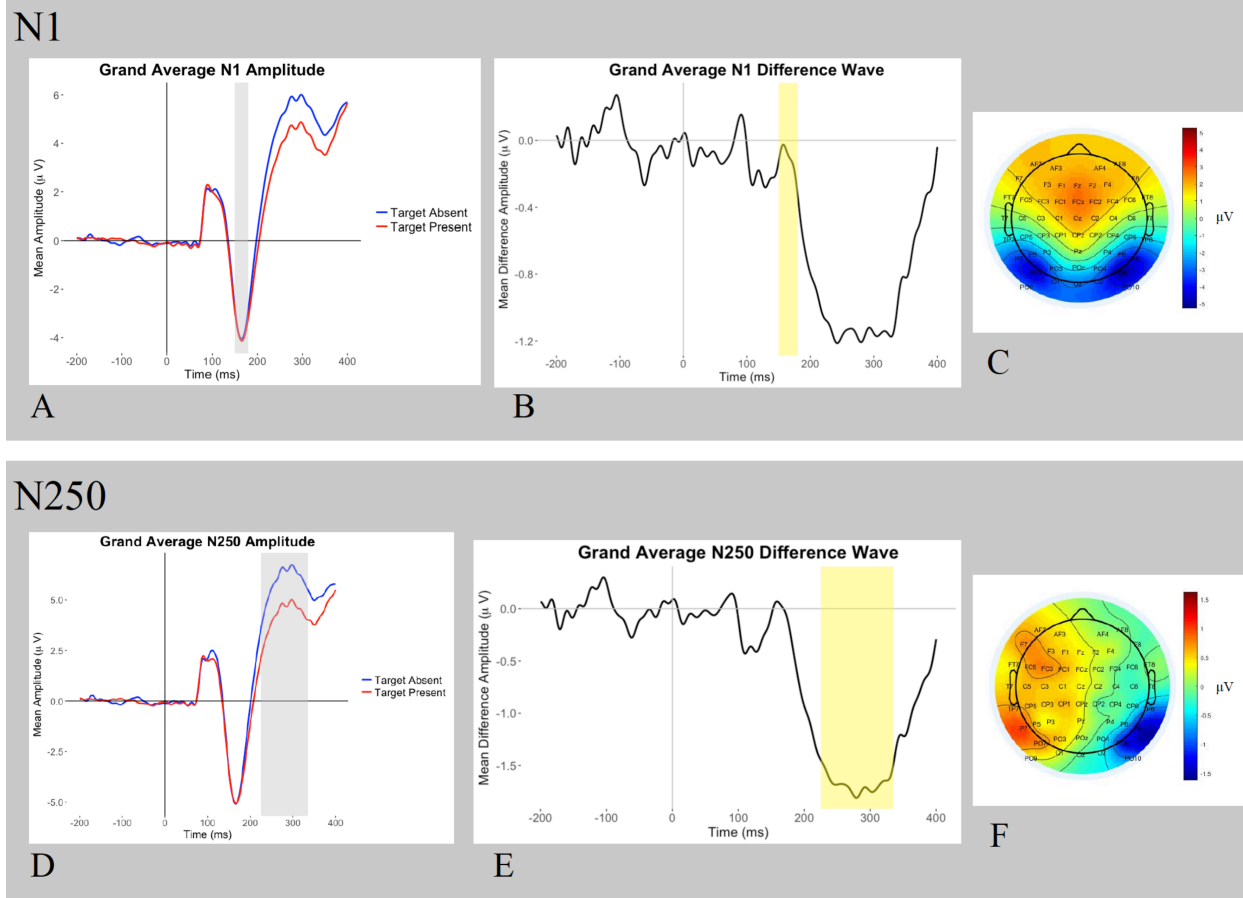


Figure 3. Grand averaged waveforms for the N1 and N250 components for both Target Present and Target Absent conditions (A and D) as well as the difference waveforms (Present – Absent) (B and E). These grand averages were used to identify the timeframe to analyze each component at. The N1 was pooled across electrodes showing maximum amplitude (C) and the N250 was pooled in the same way (F).

Participant exclusion. Artifactual data was classified as data that contained so much noise and/or sweat artifact that no eye-blink component could be visually identified from extracted ICA components. Missing data was defined as data containing more than 20 missing trials, as this could have impacted the interpretation of the time-series analysis. Non-learners were identified using two methods. First, a moving average of d' over 20 trials advancing one trial at a time was calculated to capture as much of the data as possible as well as capture the learning curve of those who learned the pattern within the first 20 trials. Then a pairwise one-tailed t-test was performed to compare the first 20 moving average windows to the last 20

windows. If there was no significant ($p < .05$) difference between the beginning and the end of participant's d' over time then that participant was categorized as a non-learner (this followed a similar procedure performed by Yamashita, Kawato, and Imamizu, 2015). Following the t-test, participants with a mean d' difference from beginning to end less than 0.5 were excluded as non-learners, since their d' value did not increase enough over time to indicate learning. Finally, the remaining participants were removed as outliers if their d' difference from beginning to end was found to be greater than two standard deviations from the mean d' difference of all remaining participants.

Multilevel modeling (MLM). The remaining participants that met the learning criterion ($N = 19$) were included in further analyses using MLM to examine if behavioral performance changes could be predicted by changes in N250 and N1 mean peak amplitude over time.

The *lme* function from the R package *nlme* (Pinheiro & Bates, 2002) was used to fit multilevel models via restricted maximum likelihood estimation for data analysis. Bagiella, Sloan, and Heitjan (2000) outlined the benefits to using MLM in psychophysiological studies. One critical benefit is the flexibility to set an appropriate variance-covariance matrix to model variance for time-series data such as EEG data. The matrix used in this model was the first-order autoregressive moving average, or ARMA(1,2) matrix, combining an AR1 covariance structure with a moving average covariance structure, which accounts for measures close in time being more highly correlated. The goodness-of-fit of the model containing this particular covariance structure was significantly better than models containing only an AR1 covariance structure or allowing unstructured covariance.

To predict the outcome variable of behavior (d'), three predictors were included in the model: time window (88 moving average windows), mean peak N1 difference amplitude

(present – absent; from now on will be referred to as “N1”), and mean peak N250 difference amplitude (present – absent; from now on will be referred to as “N250”). Additionally, interactions between time and each component were added for identification of the optimal model. The neural component predictors, N1 and N250, were each group mean-centered by subject, so that changes in either component were specific to differences within subjects. To find the optimal model, each predictor was added sequentially to compare progressively more complex models to simpler nested models using log-likelihood ratio testing. Since this was a within-subjects design, by-subject random adjustments were included for the intercept and for each predictor (i.e., random slopes) during model comparison to find the optimal model.

Model comparison began with a maximal model (one which included all possible random effects varying by subject), which failed to converge. Then random effects were removed sequentially to make the model simpler. If including a random effect only explained a small portion of variance then instead it was treated as a fixed effect to create a more parsimonious model. Each subsequently less complex model was compared to the previous model until the optimal model was identified. Model comparison was assessed using the chi-square likelihood ratio test.

The final optimal model contained fixed effect predictors of time window, both neural components (both mean-centered by subject), and two interactions between time and each component. The only random effect varying by subject included in the final model was for the by-subject intercept. The N1 and N250 predictors both provided significantly better model fit regardless of which order they were entered into the model. Residuals for the final model were tested for normality using the Shapiro-Wilk test for normality and found to not significantly deviate from normal, $W = 0.999$, $p = 0.401$. Finally, to investigate any interaction effects of time

window, two models were created to compare differences from the beginning to the end of learning. The models differed by centering the time window predictor in one model at the first time window (1) and in the other model at the last time window (88). Statistical significance was set at $p < .05$.

Results

The base model, in which the outcome variable of behavioral performance (d') had a single random intercept varying by subject, had an intraclass correlation coefficient (ICC) value of 0.34, indicating that MLM was an appropriate method of analysis because there is clustering in the data at the subject level. Therefore, modeling a random intercept for behavioral performance provided a better fitting model. The variability in behavioral performance intercepts is illustrated in Figure 4. Additionally, the final model provided a significantly better fit to the data than a linear regression model, $\chi^2(3) = 2162.65, p < .0001$. This indicated that allowing the intercept of behavioral performance to vary randomly at the subject level provided a significantly better fit than including all predictors at single level such as in a linear regression. Finally, pseudo- R^2 for the final model in comparison with the base model was 0.25. Although there is still unexplained variance left in the model, by adding the fixed effect-predictors a quarter of the variance was further explained.

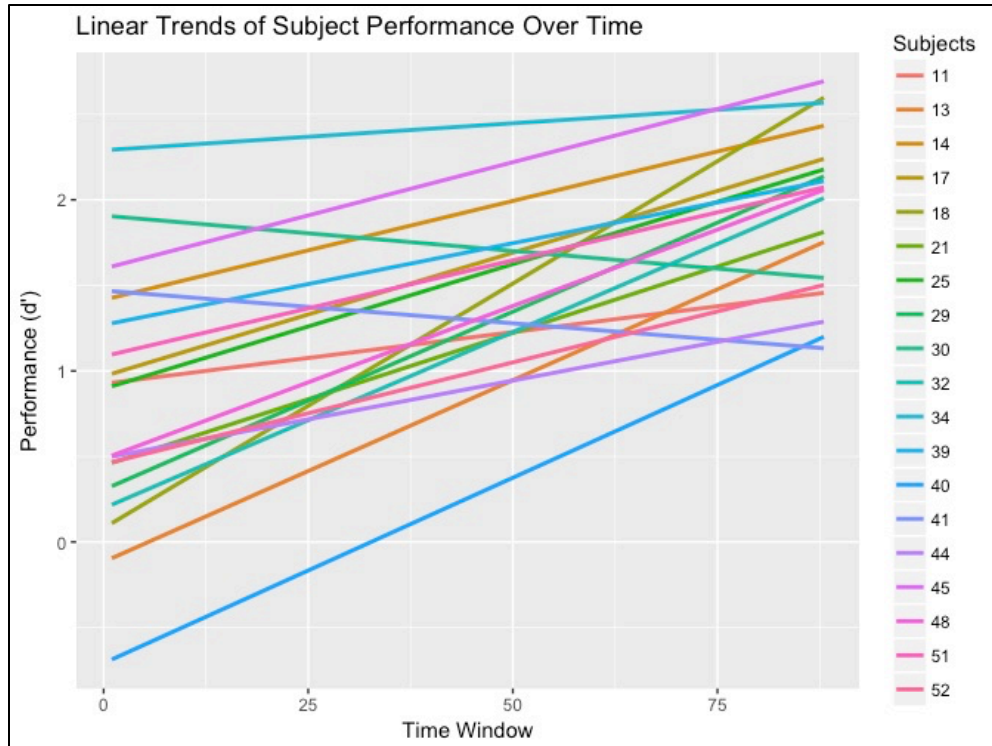


Figure 4. Linear fit lines presented for each subject's performance across each time window. The lines all have an average positive linear trend, however their intercepts with the y-axis differ widely. All subjects generally improved in performance over the course of the study however, they had different learning rates at the very beginning of the study.

There was a significant fixed effect of time window on predicting behavioral performance (d'), $\beta = 0.015$, $SE = 0.002$, $t(1647) = 6.704$, $p < .0001$, for each participant's average value of the predictors N1 and N250. The average performance across all participants improved from the first time window ($M = 0.009$, $SD = 0.314$) to the last time window ($M = 1.755$, $SD = 0.703$).

There was no significant interaction between N1 and time window as a fixed effect predictor of performance, $\beta = 0.0002$, $SE = 0.0002$, $t(1647) = 1.139$, $p = 0.255$. However, there was a significant fixed effect of the N1 on predicting behavioral performance during the last time window (at the end of learning), $\beta = 0.018$, $SE = 0.009$, $t(1647) = 2.014$, $p < .05$. In contrast,

during the first time window (at the beginning of learning) there was no predictive effect of N1 on performance, $\beta = -0.001$, $SE = 0.002$, $t(1647) = -0.050$, $p = 0.960$.

Although there was no fixed effect of N250 on predicting behavioral performance during the first time window, $\beta = 0.016$, $SE = 0.016$, $t(1647) = 1.495$, $p = 0.135$, there was a trending effect of N250 in the last time window, $\beta = -0.020$, $SE = 0.002$, $t(1647) = -1.953$, $p = 0.051$.

More importantly, there was a significant interaction between N250 across time window as a fixed effect predictor of performance, $\beta = 0.0004$, $SE = 0.0002$, $t(1647) = -1.967$, $p < .05$. This indicates that the predictive power of the N250 component on performance increases over time. The average N250 component grew larger in negative amplitude from the first time window ($M = -0.479$, $SD = 3.774$), to the last time window ($M = -1.867$, $SD = 4.776$). Therefore, as the N250 component became more negative over time this also predicted the increased behavioral performance over time. To investigate this interaction further, I calculated the average participant's Spearman correlation between performance (d') and N250 for each time window (Figure 5). In Figure 5, a LOESS curve has been plotted to show the trend line of these correlations over time; the correlations became more strongly negative later in time, reflecting the nature of this interaction was this change in the strength of relationship between the predictor N250 and the behavioral outcome later in time. All analyzed fixed effects can be found in Figure 6.

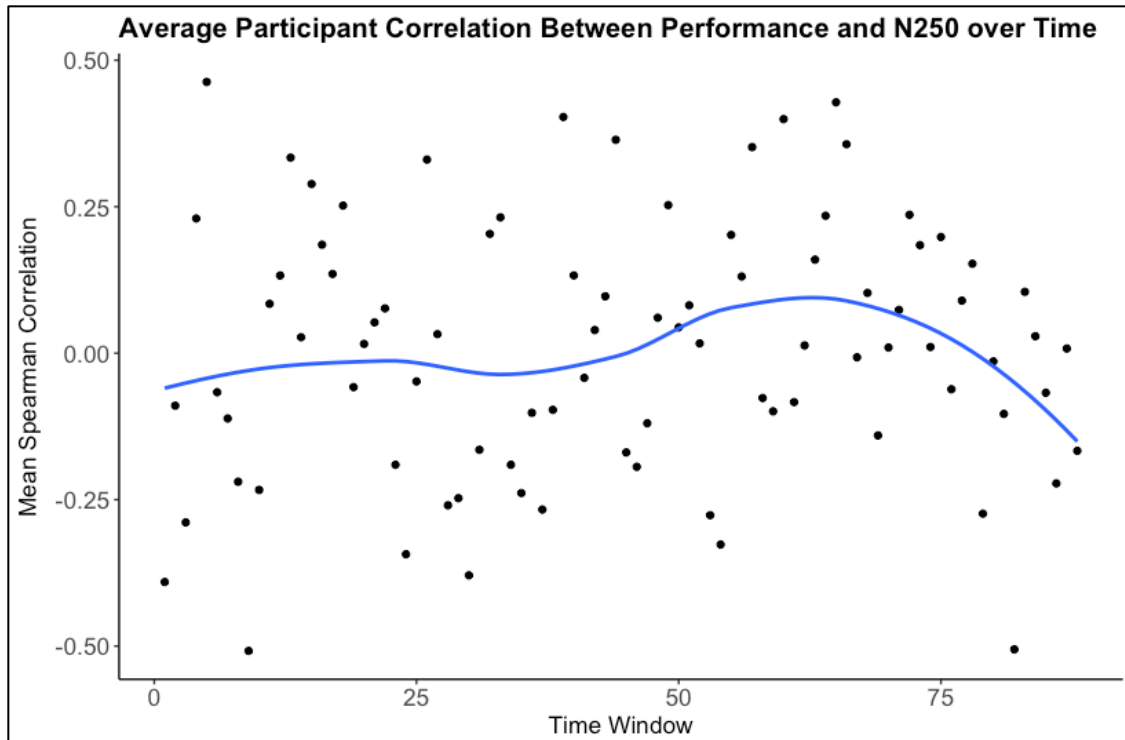


Figure 5. A participant's average spearman correlation between N250 and behavioral performance (d') plotted for each time window. The correlations tend to be very randomly distributed positive and negative until the end of learning where they begin to cluster into a negative linear trend.

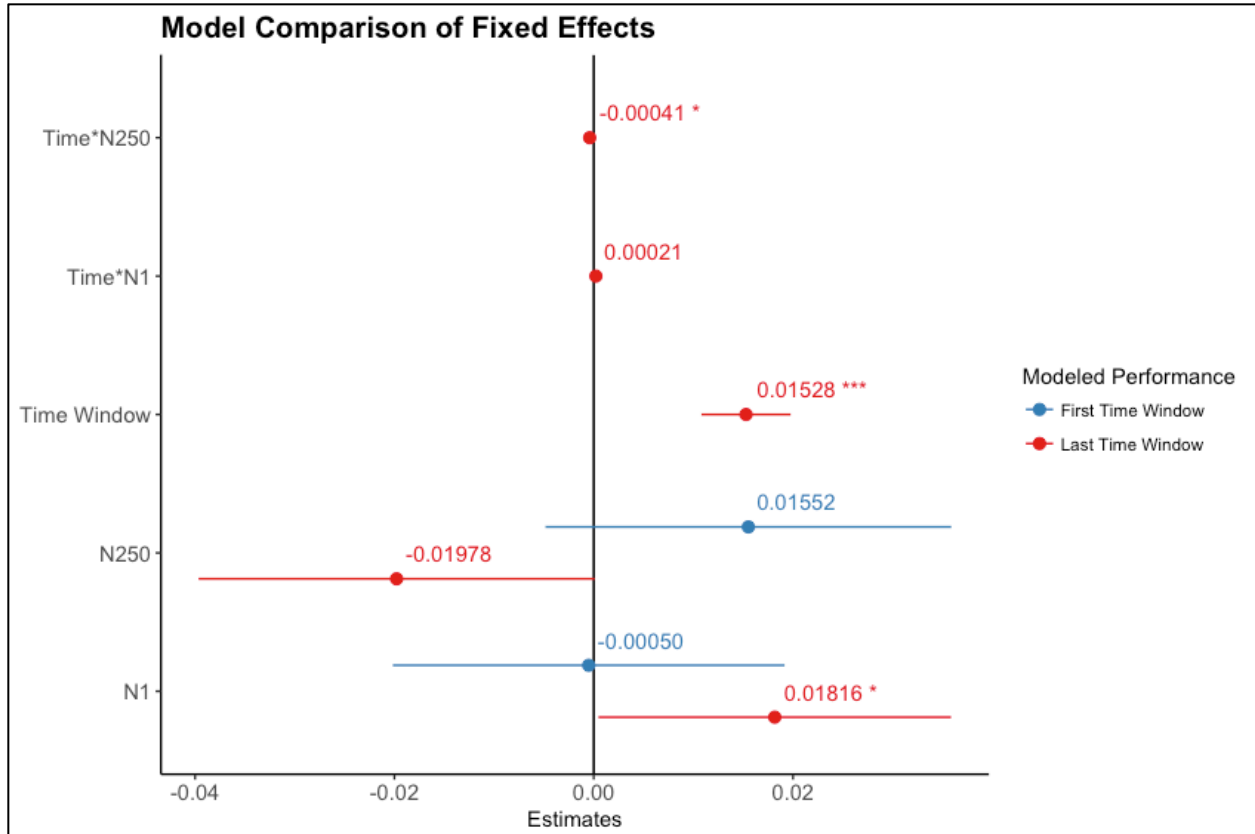


Figure 6. Fixed-effect parameter estimates and corresponding 95% confidence intervals from two models. The blue estimates indicate the model with time window centered on the first time window (beginning of learning) and the red estimates indicate the model with time window centered on the last time window (end of learning). N1 and N250 both reflect difference waveforms (present – absent). Asterisks indicate significance level, $p < .05$ (*), and $p < .0001$ (***).

Discussion

The central objective of this study was to investigate the temporal neural mechanisms involved in the development of a novel visual object representation in the human visual system. I used a novel paradigm combining visual search with a prototype distortion category task to study short-term changes in the brain’s visual system as participants learned to recognize a target object and identify trials that contained that object using only corrective feedback. Using MLM, I modeled behavioral performance (measured by d') by including predictors of time (to model learning over time), N1 (to investigate visual processes early in the visual hierarchy that may be

involved in developing object representations), and N250 (to investigate later object category formation).

As predicted, behavioral performance improved over the course of learning, with time serving as a significant predictor of increasing performance. This confirms that early in time participants did not have a representation of the target visual object and as they gained expertise with the target this coincided with an increase in d' .

The ERP component effects both did and did not support my predictions. First, focusing on the N1 difference amplitude predictor, there was no predictability of behavioral performance over time by the difference in N1 (Target Present – Target Absent trials). Because there was no interaction with the time predictor, the N1 component does not appear to be associated with learning over time. Therefore, the lack of an N1 effect as learning progressed did not add any new information to our understanding of any short-term changes in the visual system during object representation formation as indexed by the component N1. This could be due to subject to subject differences in learning rate, baseline learning or different cognitive or behavioral strategies in learning, causing the relationship with N1 to be inconsistent from subject to subject. This is why I modeled this relationship using MLM because if the N1 predictor is truly involved in the development of object representations then it should be consistent across subjects. MLM allowed for the testing of these effects as true within-subjects effects.

In contrast, as predicted, the N250 change over time did significantly predict changes in behavioral performance, such that as participants gained more experience with the target object the N250 amplitude became more negative in the target present condition than the target absent condition and this predicted an increase in behavioral performance. This result indicated that, similar to previous studies (Scott et al., 2006; Tanaka et al., 2006), the N250 component might

be indexing the development of an object representation over time. Unique to my study, however, was that this N250 component was also involved in the development of a *novel* object representation in the visual system from first exposure. Instead of a pre vs. posttest measure, here the N250 was used as a predictive measure of the development of an object representation as evidenced by improved performance in identification of the object from very beginning exposure to end using a continuous measure of time. Although these results are not causal in nature, they provide correlational evidence that the N250 component is reflective of an underlying neural mechanism involved in object representation formation in visual cortex.

One caveat to these results was that the effect size for the interaction of N250 with time was quite small, semi-partial $R^2 = 0.002$. However, this study could have become underpowered once participants were excluded due to differences in learning rate or for no evidence of learning, decreasing the sample from 42 to 19. Collecting more participant data could help clarify these results by potentially improving the effect size. Additionally, this data could be further underpowered from the use of a linear model to examine potentially non-linear data. Upon further investigation, the relationship between behavioral performance and time appeared to be more logarithmic than linear; however, for simplicity of interpretation I retained the use of a linear model. An improved analysis could provide a better model fit to the data if this relationship was modeled non-linearly.

Although the analyses detailed in this thesis were designed specifically to understand the short-term plasticity changes in the visual system during object representation formation, further investigation could be made into how visual feedback influences the reinforcement systems in the frontal cortex. Since participants learned to detect the visual target object through corrective feedback, my preliminary findings in Long (2016) analyzed the feedback-related negativity

(FRN) component and its development with learning. The FRN has been shown to begin as a large negative deflection following corrective feedback (200-300 ms) (Holroyd, Nieuwenhuis, Yeung, & Cohen, 2003). As learning progresses, performance improves, and participants do not require the feedback to assess whether they were correct, the FRN decreases in amplitude (Luft, 2014). In Long (2016), I found mixed results with the FRN amplitudes but found a general decline in the difference (Incorrect trials – Correct trials) over the course of learning. An improved analysis could create an additional predictor of FRN difference amplitude to the current model. This may explain some of the unexplained variance in the model as well as explore the potential network connections between the visual and reinforcement systems of the brain involved in visual object representations.

Conclusion

Using multilevel modeling, I showed correlational evidence of changes in the VEP component, the N250, which developed over time with improvement in behavioral performance. This finding indicates that the N250 component developed as participants formed an object representation in the visual cortex. Although we did not see changes over time in the N1 component, this could be due to subject-level differences in learning. Further analyses are required to investigate these effects with improved power as well as improved causal experimental evidence of the N250 component indexing object representation formation. This study contributes to the basic research of the neural mechanisms underlying visual object representation formation, research that is vital to understanding the short-term plasticity changes in human visual cortex. Further understanding the mechanisms of this system in typical humans

contributes to the creation of artificial retinas as well as adds to our understanding of what happens when the mechanism is impaired in cases such as visual agnosia.

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Appendix



Office of Research Compliance
Institutional Review Board

November 10, 2014

MEMORANDUM

TO: Stephanie Long
Hayden Pacl
Matt Gannon
Nathan Parks

FROM: Ro Windwalker
IRB Coordinator

RE: New Protocol Approval

IRB Protocol #: 14-10-206

Protocol Title: *Brain Mechanisms of Perceptual and Cognitive Learning*

Review Type: EXEMPT EXPEDITED FULL IRB

Approved Project Period: Start Date: 11/10/2014 Expiration Date: 11/09/2015

Your protocol has been approved by the IRB. Protocols are approved for a maximum period of one year. If you wish to continue the project past the approved project period (see above), you must submit a request, using the form *Continuing Review for IRB Approved Projects*, prior to the expiration date. This form is available from the IRB Coordinator or on the Research Compliance website (<https://vpred.uark.edu/units/rscp/index.php>). As a courtesy, you will be sent a reminder two months in advance of that date. However, failure to receive a reminder does not negate your obligation to make the request in sufficient time for review and approval. Federal regulations prohibit retroactive approval of continuation. Failure to receive approval to continue the project prior to the expiration date will result in Termination of the protocol approval. The IRB Coordinator can give you guidance on submission times.

This protocol has been approved for 80 participants. If you wish to make any modifications in the approved protocol, including enrolling more than this number, you must seek approval *prior* to implementing those changes. All modifications should be requested in writing (email is acceptable) and must provide sufficient detail to assess the impact of the change.

If you have questions or need any assistance from the IRB, please contact me at 210 Administration Building, 5-2208, or irb@uark.edu.

210 Administration Building • 1 University of Arkansas • Fayetteville, AR 72701
Voice (479) 575-2208 • Fax (479) 575-3846 • Email irb@uark.edu

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