Building Object Representations: Mechanisms of Perceptual Learning in Human Visual Cortex

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Building Object Representations:  
Mechanisms of Perceptual Learning in Human Visual Cortex

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**Introduction**

Human experience is dominated by the sense of vision. Our cognition of the world and interactions within it rely so heavily on visual representations, that it is no surprise that nearly 60 percent of the human brain is involved in processing visual information (Kandel, et al., 2013). Following the conversion (transduction) of visual stimuli into neural codes by the retina of the eye, the subsequent organization of vision in the human brain is hierarchical (Hirsch & Spinelli, 1970) such that early visual areas, low in the hierarchy (i.e. V1, V2), contain neural representations of simple features of the environment, such as edges of particular orientation (Hubel & Wiesel, 1962). These lower visual brain areas feed into higher areas of the hierarchy (V3, V4) where simple features are combined into increasingly complex and segregated neural representations of objects in the environment (Felleman & Van Essen, 1991; Martin, 2007).

Neuroimaging research has made great strides in mapping these high-level brain regions for object representations (Ishai et al., 1999; Martin, 2007) as well as how the visual representations within those regions change as object categories are learned (Seger & Miller, 2010). However, the field of cognitive neuroscience has not yet been able to adequately explain how the visual system comes to create such a complex high-level representation of a visual object from beginning experience.

The brain encounters new objects every day in the environment and encodes these objects as representations to call upon for later recognition. While neuroscientists know that these representations of categorized information must be formed, little is known about how the brain accomplishes this mechanistically. Though our subjective visual experience as experts segregating objects may make this problem seem trivial, consider the complexity of representing and recognizing any everyday objects, such as a pencil. A pencil can take many forms; it can be a true three-dimensional object or a two-dimensional drawing, it can have different shading,
different sizes, or it could be mixed with several pens. Despite these incredible variations in low-level features, the visual system is readily able to extract the high-level object pattern of the pencil from the clutter and noise of the visual environment.

A further example of the complexity required by the brain to create categorical object representations are the challenges found in artificial neural networks designed to recognize objects. Computer scientists researching artificial intelligence have developed such computational neural networks to allow computers to recognize objects (Egmont-Petersen et al., 2001). These networks function similarly to the human visual system in that they have inputs of images, have layers like the visual cortex to process the pieces of the image to form the whole object, and then have an output that correctly categorizes the image. These networks are trained on thousands and thousands of image sets and generate more and more accurate outputs with training. Yet, these computer networks can generate more errors than that of a specialized human brain. Computer neural networks can produce 99% accurate outputs that are completely incorrect (Nguyen et al., 2015).

How does the human visual system allow for such incredible and flexible object pattern recognition? The human brain does not have an innate or preprogrammed knowledge of objects; it uses training and experience to develop its expertise in object recognition (Hirsch & Spinelli, 1970). Without adequate exposure to particular visual patterns, the visual system will not learn to represent these patterns, rendering the perception and identification of such a pattern impossible despite otherwise normal brain anatomy (Hirsch & Spinelli, 1970). Though much prior research has established that object representations are a result of extensive visual perceptual learning, little is known about the brain mechanisms through which object representations begin to develop and come to be shaped by experience.
Perceptual and Category Learning

Perceptual learning refers to changes in perceptual performance resulting from extensive experience, training, or feedback in the discrimination of stimuli. Perceptual learning provides a unique model for examining how sensory regions of the brain functionally reorganizes and adapts (neuroplasticity) as a function of experience and training. Much of the perceptual learning literature has focused on how early primary sensory areas (i.e., V1) reorganize during training on discriminating tilt of visual stimuli and motion coherence and show how the brain begins to represent objects starting at V1 (Bao, et al., 2010). These studies have revealed robust but incredibly specific effects of training on neural representations as such early effects of training in V1 fail to generalize to other stimuli or locations in the visual field (Bao, et al., 2010; Ramachandran & Braddick, 1973).

Looking beyond low-level perceptual of V1’s preliminary visual representations, adaptations can be found in higher-order visual areas through training in visual object expertise and category learning. The examination of visual object expertise and category learning provides a window into the neural mechanisms through which high-level, spatially invariant object representations are formed in the visual system. Numerous stimuli and paradigms have been used to study how such representations come to be formed. Stimuli range from training of real-world objects such as birds (Scott et al., 2006) to artificial experimental objects such as dot patterns (Posner & Keele, 1968) and object expertise is developed through a variety of paradigms including prototype learning, information integration, morphed continuum, arbitrary categorization, and rule-based categorization (Seger & Miller, 2010). In prototype learning tasks, participants distinguish amongst a prototype pattern that has been distorted and randomly distorted dots. In information integration, participants are required to integrate two or more
stimulus components information in order to correctly categorize the stimuli (e.g. weight of lines as well as tilt). Morphed continuum tasks involve distinguishing between stimuli that are continuous morphs between distinct prototype categories (e.g. morphs created between the prototype dog vs. the prototype cat). Arbitrary categorization uses stimuli that are categorized probabilistically with no shared features. Lastly, rule-based categorization requires participants to distinguish between categories based on explicitly set rules (e.g. “same-different” rule task).

The prototype distortion is of particular importance to the current study. Prototype distortion tasks involve learning to group dot patterns into a prototype category and distinguishing between patterns that are simply a distortion of the prototype (Homa et al., 1981; Posner and Keele, 1968). These tasks can be presented in two forms (A, B) or (A, not A). In (A, B) tasks, subjects categorize distorted dot prototypes into either category A or category B. Contrastingly, in (A, not A) tasks, subjects categorize distorted prototype patterns as category A and other random patterns as category not A. This type of paradigm is important to the research of novel object representations, as participants do not have previous experience with the prototype before experimentation. This paradigm is also useful in developing an implicit reinforcement task since participants can learn to group the stimuli by feedback (Ashby 1998).

Whole-brain neuroimaging research (functional magnetic resonance imaging) has shown that as subjects learned to categorize random dot patterns, neuronal changes take place in the visual cortex and these activations decrease as learning progresses and subjects become more proficient (Little et al., 2004). This is suggestive of high-level neuroplasticity involved in perceptual learning as the brain learns to categorize objects and more experience leads to a more efficient visual network with expertise. However, little research has been done to understand the temporal mechanisms of how this categorization takes place in the brain as participants gain
increasing experience with distinguishing this prototype category implicitly and how the neuronal networks change over a short period of time as learning progresses.

An effective method for investigating the temporal dynamics of high-level category learning is the event-related potential (ERP). ERP is a method of analyzing electroencephalography (EEG) data to provide a stimulus-locked neural response, which provides a metric of cortical activity with millisecond resolution. This allows for research of changes in the brain that are in direct correlation with changes in the visual field. These event-related potentials are extracted from EEG data by analyzing the EEG recording of potentials during the time period immediately following stimulus presentation for several hundred milliseconds. This electrical activity at the cortex follows standard patterns of positive and negative fluctuation and creates waveforms of activity that have been well studied. ERP waveforms provide scientists time-course data of neural processing and show the robustness of neural recruitment related to stimulus processing by the cortex. ERPs can be broken up into component parts, which are distinguished by polarity (negative or positive) and latency relative to stimulus presentation. These components have been studied in a variety of different situations and are thought to reflect different types of cognitive processing and can therefore give insight into the mechanisms and dynamics of neural processing. This time course data is particularly important in studying the millisecond changes in neuroplasticity taking place over the course of perceptual learning.

Several ERP studies have previously investigated category learning in the brain (Grossman et al., 2009; Krigolson et al., 2009; Rossion et al., 2007). These studies have described one primary visual electric component of the ERP to be associated with object recognition – the N250. The N250 is a negative deflection that onsets about 250 milliseconds
(ms) after a stimulus is presented, which co-occurs with the development of perceptual expertise in object recognition (Scott et al., 2006; Tanaka et al., 2006). An additional ERP component that has been well studied in categorical and perceptual learning is the P3 (or P300) component, which is a positive evoked potential that occurs about 300 milliseconds post-stimulus. P3 is a wide-ranging component that has several different associations within ERP research however, it is most commonly seen in relation to stimulus processing. Most importantly for category learning, P3 has shown to increase in amplitude as learning progresses and participants are more familiar with the goal of the task (Barceló et al., 2000; Luu et al., 2007). In the brain, P3 has been proposed to reflect the release of norepinephrine broadly throughout the cerebral cortex from the primary norepinephrine nucleus of the brainstem, the locus coeruleus (Nieuwenhuis, Aston-Jones & Cohen, 2005). As norepinephrine has been strongly linked to the induction of neuroplasticity (Sara, 2009), the P3 may provide a robust index of the occurrence of neuroplasticity during the acquisition of visual object perceptual representations.

**Reinforcement Learning**

Although perceptual and category learning demonstrate the occurrence of plasticity and adaptation within the visual system, how learning within visual networks is mediated is not known. Reinforcement learning may play a key part in mediating the visual system as it adapts to perceptual changes through feedback. Feedback mechanisms have shown to affect sensory and decision neurons in the brains of monkeys and, in turn, their performance in low-level perceptual learning (Law & Gold, 2009). In humans, psychophysical work has indicated that reinforcement learning plays a role in low-level perceptual learning (Seitz & Watanabe, 2003) as well as high-level object category learning (Homa & Cultice, 1984; Krigolson et al., 2009). Many of the brain’s experiences with the environment are learned through trial and error and maximizing on
correct choices and decreasing incorrect choices. As individuals perform goal-directed tasks and they receive feedback on their performance, the brain then uses this feedback (usually in the form of errors) to adapt its actions for the future. It is well known that learning through reward feedback affects the midbrain dopaminergic system (DA; Schultz et al., 1992). One target of the tegmental DA system of particular importance for reinforcement learning, are the dorsal portions of the anterior cingulate cortex (dACC) of the medial prefrontal cortex (Holroyd & Coles, 2002; Nieuwenhuis et al., 2004; Shenhav et al., 2013). Reliable neural signatures of this dopaminergic-dACC circuit have been described with both fMRI and ERP (Barch et al., 2000; Carter et al., 1998; Falkenstein, et al., 1990; Holroyd & Krigolson, 2007; Yeung, Botvinick, & Cohen, 2004). Using ERP, two well-established frontal components have been thoroughly described: the error-related negativity (ERN) (Falkenstein, et al., 1990) and the feedback-related negativity (FRN). Both the ERN and FRN represent activity within the dACC in response to motor errors or stimulus feedback, respectively. The ERN is a large negative potential that occurs around 50-100 milliseconds after an erroneous motor response is given during a task. This ERP component was first discovered during stimulus-response motor tasks where participants had to respond as quickly as possible and researchers notice that this negativity corresponded to the brain’s response to the understanding that a response error had been made (Falkenstein et al., 1990). The FRN is an increased negative potential that occurs 200-300 milliseconds after corrective feedback has been presented following a motor response (Holroyd et al., 2003). In correspondence with learning, as participants understand the goal of the task they rely on feedback less to make goal-directed actions and the amplitude of the FRN decreases as learning progresses (Luft, 2014). The ERN and FRN have been reliably localized to the dACC using
fMRI and ERP source analysis (Dehaene, Posner, & Tucker, 1994; Hauser et al., 2014; Herrmann et al., 2004; Holroyd et al., 2004; Miltner et al., 1997; Nieuwenhuis et al., 2004).

Previous ERP and neuroimaging literature have investigated how the visual system becomes an expert at categorizing objects. Krigolson, et al. (2009) looked at the changes in FRNs, since they saw that reinforcement learning plays a part in implicit categorization in perceptual learning (implicit categorical learning is dependent upon learning through feedback) (Ashby et al., 1998). This study by Krigolson, et al. (2009) showed that participants implicitly (without explicitly explained rules) learned to categorize computer generated “blob” stimuli through feedback. In addition, as participants gained expertise in categorizing these stimuli, they found a linear decrease in FRN throughout the experiment. This study suggests that reinforcement learning mechanisms in the medial-frontal cortex may be involved in the development of implicit categories. It would seem that these electrophysiological mechanisms could also modulate the visual system in perceptual learning. A neuroimaging study by Kahnt et al. (2011) demonstrated reinforcement learning and perceptual learning both involve the ACC network mentioned earlier, which implies that this network influences high-level visual category learning. This research reveals the importance in understanding how reinforcement influences perceptual expertise, however, little to no research has been done to advance our knowledge of how this is accomplished in the brain.

Thesis Experiment

It is clear in the vision sciences that the visual system learns to see objects by creating representations of these objects through experience and these representations are built through a hierarchy (from low-level to high-level representations) in the brain. Perceptual learning studies have demonstrated that the network changes during training (neuroplasticity) involved in
building these representations are hierarchical as well. In category learning studies the brain has shown to gain expertise by performance monitoring and the reinforcement networks involved most likely play a role in the visual system’s categorical representations of objects. However, little research has been done to extrapolate the temporal mechanisms of how reinforcement mediates the formation of novel visual object representations over the course of short-term training. Here, I used EEG to identify the mechanisms in the cortex involved in short-term plasticity changes as the brain learned to represent (through category learning) a novel prototype pattern by reinforcement training.

**Materials & Methods**

*Participants.* All procedures described here have been approved by the University of Arkansas International Review Board. Forty-two undergraduate participants were recruited from the University of Arkansas (twenty-two females, mean age 20.8, SD = 2.52 years, age range 18-29 years). All participants were naïve to the purpose of the study and filled out demographic information where they self-reported having normal or corrected-to-normal vision; twenty participants reported nearsightedness and two reported farsightedness (seven reported astigmatism). Twenty-one participants were excluded from analysis for one of two reasons. First, because this study required participants to learn implicitly (i.e. without explicit instruction given) some participants did not learn to identify a pattern. These participants were identified by calculating their $d'$; participants with a $d' < 0.5$ did not have a high enough accuracy or correct rejection rate to indicate they learned the pattern. This data is not useful in my analysis since my interest was in changes as participants learned to detect the pattern. Secondly, other participants were also excluded because they learned to detect the pattern too quickly (reaching the threshold $d'$ in under 20 trials) and therefore their data did not contain enough trials to use when
comparing early learning trials to later learning trials. In addition to receiving credit toward their Psychology course requirements as compensation, subjects received a monetary reward for task accuracy (one cent added for every correct trial response and one cent subtracted for every incorrect trial response, for an average total of $5.48 in bonus money).

Stimuli. This experiment was conducted in a laboratory under low levels of ambient illumination. The 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. Subjects placed their heads in a chinrest to maintain a viewing distance of 57 cm.

Subjects performed a hybrid of an object category learning and visual search task. In this hybrid task, subjects maintained fixation on a central yellow fixation dot (0.2° diameter) while four peripheral arrays of small white squares were briefly flashed. Each array consisted of 48 small white squares (0.12° × 0.12° each) positioned within a 2.3° × 2.3° area. The four 48-square arrays were positioned in the upper left, upper right, lower left, and lower right visual quadrants, each at an eccentricity of 6.4° from the central fixation point. In a target-present condition, one of the four arrays contained a distorted prototype object pattern. The prototype pattern was roughly an “X” shape (Figure 1). Importantly, the prototype pattern itself was never shown, only a statistically distorted version of the prototype. These distorted versions of the prototype were formed by starting with the element positions of the prototype pattern shifting the x- and y-coordinate of each element by a pseudo-randomly generated number drawn from a normal distribution (M = 0°, SD = 0.25°). No distorted element position was permitted to exceed the 2.3° × 2.3° dimensions of the array (see examples in Figure 1). The elements in each of the three remaining arrays in the target-present condition were randomly positioned by first drawing x- and y-coordinates from a uniform distribution and then applying the same normally-distributed
distortion procedure to these randomly positioned white square elements. In a target-absent condition, the elements of each of the four arrays were positioned in this manner (see examples in Figure 1).

Figure 1. A prototype stimulus was generated for the target stimulus and then distorted slightly in every target present trial, while the rest of the locations contained random noise patterns.

Procedure. Each trial began with yellow fixation point, which was displayed for a random interval between 1500 and 2500 milliseconds (ms), after which the four 48-square visual arrays were flashed for 200 ms (Figure 2). Participants then responded whether or not a pattern was present. Following the participants’ response, a random period between 300 and 500 ms passed after which a feedback stimulus (red or green square) appeared at fixation for a duration of 2000 ms. A green or red feedback stimulus indicated correct and incorrect responses, respectively. Subjects viewed and responded to a total of 1792 trials, and in 896 (50%) of the
trials, one position (of the four) of the peripheral array contained a distortion of a prototype dot pattern (target-present condition). In the other 50% of trials the visual array consisted entirely of randomly generated dot patterns (target-absent condition). Therefore, participants performed a version of the prototype distortion task “A, not A” by learning to categorize the distorted pattern as a version of the prototype (A) and categorize the rest of the dot patterns as random (not A; Ashby et al., 1998). Therefore, participants respond “Yes” if the stimuli is part of category “A” and “No” if the stimuli is part of category “not A.” However, this task presented trials that had both “A” and “not A” categories as well as trials that contained only “not A” patterns so this task also required participants to perform a visual search to locate if the “A” pattern was present within one of the four locations or not. Therefore, participants indicated “Yes” if the pattern was present within one of the four locations and this represented category “A” and conversely participants indicated “No” if the pattern was absent which represented category “not A.”

At the beginning of the experiment, subjects were instructed that a visual dot pattern would be present on half of the trials and absent on the other half. This prototype pattern was not described to the subjects in any way. They were simply instructed to look for a “pattern.” Participants indicated whether the display contained the prototype pattern or not by pressing ‘1’ or ‘2’ respectively, on a keyboard number pad. Following their response, feedback was displayed based on subjects’ accuracy; a green square was displayed over the fixation if the response was correct and a red square was displayed if the response was incorrect. Participants learned to discriminate the stimulus only through the feedback they received. Over the course of many trials subjects learned to detect the prototype and reached at least 80% accuracy or more within a block (with an overall average accuracy of 71% across all blocks for all subjects). Their accuracy was displayed after every block (total of 16 blocks). At the end of the experiment, subjects filled
out a survey indicated whether or not they learned to distinguish the pattern and drew what it looked like.

Figure 2. The trials began at fixation and then were either target present trials (50%) or target absent trials (50%) where participants responded on the keyboard whether the target was present or absent and then given corrective feedback.

**EEG Recording and Analysis.** Participants were placed in a 64-channel BrainAmp DC ActiCap active EEG system. Electrodes were placed according to the standard 10-10 system at 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. Electrooculogram (EOG) was acquired using four electrodes placed on the left and right canthi and above and below the left eye. Continuous EEG data was referenced to a common reference electrode (FCz) during recording and was digitally sampled at 1000 Hz and low-pass filtered at 250 Hz. The scalp-recorded EEG channels were processed offline and re-referenced to the average of the left and right mastoid channels (M1 and M2). Horizontal EOG (HEOG) and vertical EOG (VEOG) were obtained by averaging the left and right canthi channels and the channels above and below the left eye, respectively. While processing the data, a bandpass filter of 0.1-30 Hz was applied to the EEG and EOG data (24 decibels/octave). VEOG and HEOG ocular artifacts were corrected using standard regression procedures as outlined by Gratton, Coles, & Donchin (1983). General artifact rejection excluded trials that had peak amplitudes of ±150 µV or 100 ms segments with less than 0.5 µV. All target locations were collapsed across left and right visual fields in target present trials. Segmentation extracted 600 ms epochs, -100 to 500 ms relative to stimulus presentation. Separate sets of segments were formed time-locked to the onset of visual dot arrays as well as the onset of feedback stimuli. All segments were baseline corrected according to 100 ms prior to stimulus onset (-100-0 ms). These sets of segments were then used to calculate ERPs for visual object arrays (visual evoked potentials, or VEPs) and feedback stimuli (FRNs).

**Psychophysical Data.** To examine the progression of perceptual learning, each participant’s behavioral and electrophysiological data was windowed into five performance phases: baseline, early learning, and three post-learning phases. To determine these phases for each participant, a moving average of accuracy was calculated in the target-present and target-absent conditions using a 16 trial window. From these moving averages of target-present and
target-present accuracy, a continuous aggregate measure of perceptual sensitivity was then calculated using $d'$ (Wickens, 2002). Then this $d'$ data was scaled (0 to 1) and a Weibull function was fit to these data (five parameter fit) to determine performance thresholds and asymptote for each participant. Each participant’s behavioral and ERP data was then windowed relative to calculate threshold performance levels such that “baseline” window was determined as those trials less than or equal to a 10% performance threshold, and the three post-learning phases (post-1, post-2, post-3) were set as three equivalent sized trial intervals that surpassing a 90% performance threshold. The “early learning” window was the trials between 10% and 90% of the threshold. In order to analyze learning progression across the experiment, a repeated measures analysis of variance (ANOVA) was conducted on the $d'$ values across a factor of learning window (baseline, early learning, post-1 learning, post-2 learning, and post-3 learning). This statistical test used an alpha level of 0.05.

**ERP Data.** An alpha level of 0.05 was used for all statistical tests with Bonferroni corrections for multiple comparisons. N250 and P3 components of VEPs were quantified as the average voltage within a specific time window and collapsed across electrodes PO7 and PO8 for N250 and only electrode Pz for P3. Time windows for these components were determined from grand average ERPs collapsed across experimental manipulations. N250 was found to peak from 250 – 410 ms and P3 was found to peak from 400 – 500 ms. Experimental analysis of the VEPs was performed as a 2 x 5 repeated measures analysis of variance (ANOVA) with factors of target condition (present vs. absent) and time windows of learning (baseline, early learning, post-1 learning, post-2 learning, and post-3 learning). Paired t-tests were performed comparing mean amplitudes of both N250 and P3 for target condition at each time window.
The FRN peak amplitude was quantified as the average voltage within a specific time window collapsed across electrode (FCz). Time windows for these components were determined from grand average ERPs and found to be 180 – 290 ms following the presentation of feedback stimuli. Experimental analysis of FRNs was performed as a 2 x 5 ANOVA with factors of target (present and absent) and window (baseline, early learning, post-1 learning, post-2 learning, and post-3 learning) on the difference of the correct amplitudes from the incorrect. Pairwise t-tests were conducted to analyze differences in these FRN mean peak differences across time windows and across target conditions.

**Results**

*Psychophysical Data.* A repeated measures analysis of variance (ANOVA) was conducted on $d'$ values with a single factor of learning window (baseline, early learning, post-1, post-2, and post-3). This ANOVA revealed a significant effect of learning window, $F(4, 80) = 58.143, p<0.001$. Post-hoc pairwise comparisons were then calculated to identify which windows were significantly different and the windows, baseline, early learning, post-1 learning, post-2 learning, and post-3 learning were all significantly different ($p<0.001$), except post-3 learning was not significantly different from post-2 learning with $p>0.05$ (See Figure 3).
Figure 3. Mean $d'$ across time windows. Shows mean $d'$ of baseline (dark blue), early learning (red), post-1 learning (green), post-2 learning (purple), post-3 learning (light blue). Baseline, early learning, post-1, post-2, and post-3 were significantly different as marked by an asterisk (*).

**ERP Analysis.** From the grand averaged ERP component waveforms, peak amplitudes were determined across subjects such that N250 had a peak amplitude from 250 – 310 ms, P3 had a peak amplitude from 400 – 500 ms, and FRN had a peak amplitude from 180 – 290 ms (See Figure 9). These component amplitudes were averaged to yield mean peak amplitudes for each time window in the target present and target absent conditions (Figure 4-6).

A $2 \times 5$ repeated measures ANOVA was calculated for N250 amplitudes with factors of target conditions (present or absent) and trial window (baseline, early, post-1, post-2, post-3). Significantly main effects were found for target condition, $F(1, 20) = 15.062, p<0.001$, and trial window, $F(4, 80) = 4.168, p<0.005$. No interaction was found between the two factors, $p>0.05$. Post-hoc comparisons were performed to identify which time windows were significantly
different in the target conditions. The mean N250 amplitudes between the absent and present condition of the post-1 learning window were significant $t(20) = 2.599, p<.017$, the post-2 learning window $t(20) = 4.058, p<0.001$, and the post-3 learning window $t(20) = 4.382, p<0.001$ (see Figure 4). The time windows baseline and early learning were not significantly different between target conditions, $p>0.05$ (see Figure 4).

![N250 (250-310ms) Mean Peak Amplitudes](image)

**Figure 4.** Mean component amplitude for the N250 across time windows for the conditions target absent (gray) and target present (red). Significance is marked with an asterisk (*) and error bars indicate standard error of the mean.

To examine changes in the P3 component as a function of learning, an additional $2 \times 5$ repeated measures ANOVA was conducted, again with factors of target condition (present or absent) and trial window (baseline, early, post-1, post-2, post-3). The P3 ANOVA revealed a main effect of target condition, $F(1, 20) = 38.854, p<0.001$, but no significant effect of trial window and no interaction between the target condition and window ($p>0.05$). Post-hoc t-tests
were performed to identify which time windows were significantly different in the target conditions. The mean P3 amplitudes were significantly different between the target conditions (present and absent) for early learning $t(20) = -3.444$, $p<0.003$, post-1 learning $t(20) = -2.970$, $p<0.008$, post-2 learning $t(20) = -2.970$, $p<0.001$, and post-3 learning $t(20) = -5.764$, $p<0.001$ (see Figure 5). The baseline window was not significantly different between target conditions, $p>0.05$ (see Figure 5).

![P3 (400-500ms) Mean Peak Amplitudes](image)

Figure 5. Mean component amplitude for the P3 across time windows for the conditions target absent (gray) and target present (red). Significance is marked with an asterisk (*) and error bars indicate standard error of the mean.

Because the FRN is dependent upon accuracy (incorrect or correct feedback), the mean amplitudes across the time windows for each target present and absent condition were calculated by subtracting the correct condition from the incorrect condition (Figure 6). A repeated measures ANOVA was conducted to compare the mean amplitude differences (incorrect-correct) across target conditions and time windows. Here, a significant effect of target was found $F(1, 20) =$
4.487, p<0.047 (Figure 8) and a significant effect of window was found $F(4, 80) = 51.797$, p<0.004 (Figure 7). However, no significant interaction was found between target and window p>0.05 (Figure 6). Then a set of pairwise t-tests was run to determine any windows in which target conditions differed. These comparisons revealed no significant effects (ps >0.05; Figure 7). To examine why there was a greater effect of absent over present (Figure 8), differences in accuracy due to target condition were analyzed. A paired samples t-test was performed to identify differences in accuracy over the learning period (all windows) for each target condition (present and absent) and the target present condition (M=0.668) was found to be significantly higher in accuracy $t(20) = 2.296$, p<0.033 than the target absent condition (M=0.615).

![FRN Mean Peak Amplitude Difference (Incorrect-Correct)](image)

Figure 6. The difference between incorrect and correct amplitudes across windows for each target condition: present (red) and absent (gray). Error bars indicate standard error of the mean.
Figure 7. Mean amplitude of component FRN collapsed across target condition showing change across time windows (blue). Error bars indicate standard error of the mean.
Figure 8. Mean amplitude of component FRN collapsed across time windows across showing change across target condition, present (red) and absent (gray). Significance is marked with an asterisk (*) and error bars indicate standard error of the mean.
Discussion

The goal of this study was to better understand the neural mechanisms that underlie the processes of the brain learning to represent a novel object through known categorical learning mechanisms and how they are mediated by reinforcement. The hybrid visual search-prototype distortion task allowed for the observation of short-term changes in the brain as participants learned to differentiate the target present object category from the target absent category.

In my analysis of the behavioral changes due to learning, $d'$ accurately portrayed participants gaining expertise of the target pattern over the course of the trials. This $d'$ showed that participants had no expertise with the target pattern in the baseline time window and as they gained expertise their accuracy and correct rejections, which is what $d'$ shows, increased as learning progressed over the other time windows (early, post-1, post-2, and post-3).
In my ERP analysis, I was interested in changes of two components of the visual evoked potential, P3 and the N250. The development of the P3 component has been correlated with the development of learning during a task (Luu et al., 2007). The results revealed a P3 component that was not different between the target conditions in the baseline of learning but as learning progressed through the windows, the P3 increased more in peak amplitude in the target present condition following learning than in the target absent condition. An additional VEP component, the N250 component, has been proposed as an index of the development of object representation (Scott et al., 2006; Tanaka et al., 2006). The results revealed that the N250 component did not have a difference in peak amplitude between the target conditions in the baseline or the early learning windows but because the N250 is associated with object representations, this indicates that participants have not yet created an object representation and this follows the d’ behavioral data at this point in learning where participants have not yet developed expertise with the target pattern. However, there was a bigger difference in N250 peak amplitudes for target absent than target present in the post-1, post-2, and post-3 learning time windows. This suggests that the target absent is the object category that is being developed during learning.

Further ERP analysis was conducted to evaluate how reinforcement could mediate the learning of object categories by looking at the changes in the FRN component. The FRN component did not differ for the target conditions over the learning windows. However, when the FRN peak amplitudes were analyzed across the learning windows (collapsed across target condition) the FRN amplitudes were greater for baseline and early learning windows and then decreased in amplitude as learning progressed into the post-learning windows. This follows other research of the FRN, which shows that as the brain develops an understanding of the goal throughout learning the FRN amplitude decreases (Luft, 2014). How the FRN peak amplitude
differed between the target conditions (collapsed across the learning windows) was of interest and greater FRN amplitudes were found in the target absent condition than in the target present condition. When this difference is compared to the increase in target present accuracy over the target absent accuracy, it is apparent that participants developed higher expertise for the target pattern and used the feedback less. In contrast, participants still relied on feedback (creating a greater FRN amplitude) in the absent condition by the end of learning. These FRN results indicate that although the FRN is not necessarily a direct mediator of this visual object category learning, the FRN still followed a general reinforcement mechanism for the learning process. This generalized reinforcement mechanism may have contributed to an overall increase in excitability that facilitated the changes in the brain during categorical learning.

As a whole, these three components follow the learning framework as the brain gained expertise with the target object pattern. First, the FRN component began with greater amplitudes in the baseline and early learning stages; the FRN has been tied to tegmental DA system in the dACC. Then the P3 component began increasing in amplitude in the target present condition in the early learning stage. Since P3 has shown to reflect the release of norepinephrine from the locus coeruleus (Nieuwenhuis, Aston-Jones & Cohen, 2005), this amplitude increase may reflect this same norepinephrine release due to the visual category learning. Finally, the N250 component began increasing in amplitude in the target absent condition in the post-1 learning stage; this component is reflective of perceptual expertise (Scott et al., 2006; Tanaka et al., 2006). These changes in component amplitudes that correlate with learning stages in the development of this object expertise are an important development in the research of object representations.
The sequential order arising in differences found between FRN, P3, and N250 components may indicate the inter-network neural mechanisms that underlie the development of an object representation. Because the FRN effects that were found are consistent with other FRN research and these effects were due to visual feedback, this suggests that visual feedback engages the mesencephalic dopamine system in the dACC. This network has been well researched and found to be reflected by the FRN and therefore this study implies that the visual feedback engaged this network as seen by changes in the FRN (Dehaene, Posner, & Tucker, 1994; Hauser et al., 2014; Herrmann et al., 2004; Holroyd et al., 2004; Miltner et al., 1997; Nieuwenhuis et al., 2004). Following the FRN effects, the P3 effects suggest that the dACC then modulates the output of norepinephrine from the locus coeruleus. Finally, following the P3 effect, the N250 effect appears and suggests this norepinephrine release from the locus coeruleus increases plasticity susceptibility in the visual cortices as an object representation is formed. Although there is not strong causal evidence, this sequence of components and the evidence of their strong correlations with neuronal networks allow for the development of a theory on the neural mechanisms that are at work during the formation of novel object representations.

These results are very promising in their correlational implications of the neural networks involved in object representations. However, to establish stronger relationships between the FRN, P3, and N250, I will conduct several additional analyses of these data. First, the trial windows I selected may be inhibiting the resolution of learning effects, as some data could fall in between these windows or my window selection may not be precise enough. To establish an improved temporal resolution of learning effects I will construct and analyze moving averages of $d'$, N250, P3, and FRN data in order to better establish the progression of these component effects throughout learning. The disadvantage to using a moving average for trial windows is the
decrease in signal to noise ratio, which is why I started out with the windows that I did to search for effects. I also looked at incorrect and correct trials together because when I was investigating for effects I wanted to keep a high signal to noise ratio. However in further analysis, I will examine the FRN effects in correct and incorrect trials separately to better understand the extent of this effect. Additionally, I would also investigate the possible differences in VEP effects in correct vs. incorrect feedback trials. This would allow me to better understand the sequential effects of the FRN on the VEPs, especially early on in learning.

Further developments in the basic research of the neural underpinnings of object representation formation, like those found in this study, contribute to visual neuroscience’s understanding of the human visual system as a whole. Understanding the neural networks within the visual system, and how they change, allows us to understand how the brain “learns to see.” These findings advance neuroscience’s attempts to create artificial retinas; the more that is known about the brain’s visual system, the better these artificial retinas will be able to replicate the human eye. Advances that neuroscience research makes in the human visual system also contributes to advances in computer vision as well as artificial intelligence. An enhanced understanding of neuroplasticity in the human visual system, through studies such as this, will contribute to continued improvements in both public health and technology.
References


