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# Dissociating electrophysiological correlates of contextual and perceptual learning in a visual search task

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**Perceptual learning and contextual learning are two types of implicit visual learning that can co-occur in the same tasks. For example, to find an animal in the woods, you need to know where to look in the environment (contextual learning) and you must be able to discriminate its features (perceptual learning). However, contextual and perceptual learning are typically studied using distinct experimental paradigms, and little is known regarding their comparative neural mechanisms. In this study, we investigated contextual and perceptual learning in 12 healthy adult humans as they performed the same visual search task, and we examined psychophysical and electrophysiological (event-related potentials) measures of learning. Participants were trained to look for a visual stimulus, a small line with a specific orientation, presented among distractors. We found better performance for the trained target orientation as compared to an untrained control orientation, reflecting specificity of perceptual learning for the orientation of trained elements. This orientation specificity effect was associated with changes in the C1 component. We also found better performance for repeated spatial configurations as compared to novel ones, reflecting contextual learning. This context-specific effect was associated with the N2pc component. Taken together, these results suggest that contextual and perceptual learning are distinct visual learning phenomena that have different behavioral and electrophysiological characteristics.**

## Introduction

Visual learning is typically divided into conceptually distinct subtypes (e.g., perceptual learning, contextual learning, statistical learning, reinforcement learning, priming), each with different researchers studying them and each being explored with distinct paradigms. However, this overspecialization limits our understanding, as multiple types of learning commonly co-occur in all but the simplest tasks (Maniglia &

Seitz, 2018). For example, finding our car keys in the morning involves learning the spatial context of where the keys may have been placed in each room, referred to as contextual learning (Chun & Jiang, 1998), as well as learning the distinguishing features of the keys and improving sensitivity to recognize them when searching the correct location; these sensitivity improvements are referred to as perceptual learning (Fahle, 2004).

Although conceptually perceptual learning and contextual learning must operate together in a complementary fashion to help us perform search tasks, little is known of the mechanisms by which they work together to influence task performance. Contextual learning is believed to be high level, involving associations between spatially distributed objects, and develops with only few trials (Chun & Jiang, 1998). Electrophysiological studies suggest that contextual learning is related to late event-related potentials (ERPs) occurring 200 ms or more after stimulus onset, such as the N2pc component (Johnson, Woodman, Braun, & Luck, 2007; Le Dantec & Seitz, 2010; Olson & Chun, 2001; Schankin & Schubö, 2009; Schankin & Schubö, 2010; Schankin, Hagemann, & Schubö, 2011). Perceptual learning is thought to be a lower level form of learning, as it can be very specific to stimulus orientation or retinotopic location and can take many days of training to show robust effects (Ahamadi, McDevitt, Silver, & Mednick, 2018; Bao, Yang, Rios, He, & Engel, 2010; Crist, Kapadia, Westheimer, & Gilbert, 1997; Le Dantec & Seitz, 2012; Schoups, Vogels, Qian, & Orban, 2001; Zhang, Zhang, Xiao, Klein, Levi, & Yu, 2010).

Unlike contextual learning, perceptual learning has been associated with earlier electrophysiological components, such as the posterior C1 component (Bao et al., 2010; Ding, Song, Fan, & Chen, 2003; Pourtois, Rauss, Vuilleumer, & Schwartz, 2008; Reinke, He, Wang, & Alain, 2003; Seppänen, Hämäläinen, Pesonen, & Tervaniemi, 2012; Shoji & Skrandies, 2006; Song, Ding, Fan, Qu, Xu, Lu, & Peng, 2005; Song et al., 2007). The polarity of the C1 component varies as a function

of the visual field location of the stimulus (Ahamadi et al., 2018; Di Russo, Martínez, & Hillyard, 2003; Rauss, Pourtois, Vuilleumer, & Schwartz, 2009; Zhang et al., 2015) and generally appears positive when the stimulus is presented in the lower visual field (LVF) and negative when it appears in the upper visual field (UVF). This difference of polarity reported for the C1 component is consistent with potential neural generators located on either side of the calcarine sulcus in the cortical area V1 (Di Russo et al, 2003). Furthermore, fMRI studies in humans (Jehee, Ling, Swisher, van Bergen, & Tong, 2012; Li, Piëch, & Gilbert, 2008; Shibata, Watanabe, Sasaki, & Kawato, 2011), single unit recording studies in animals (Adab & Vogels, 2011; Schoups et al., 2001), and computational studies (Poggio, Fahle, & Edelman, 1992; Wenliang & Seitz, 2018) provide complementary evidence that perceptual learning can involve plasticity in V1, although later brain regions are also implicated in perceptual learning (Dosher & Lu, 1998; Law & Gold, 2008; Maniglia & Seitz, 2018).

Although behavioral evidence suggests that perceptual learning and contextual learning are dissociated (Le Dantec et al., 2012), to date no study has examined, within the same experimental setting, the extent to which they rely upon the same or different neural processes. Here, we address this directly by measuring ERPs while perceptual learning and contextual learning take place in concert during learning of a single visual search task. In this task, participants trained for eight sessions to improve their ability to find a specific target orientation within a target array of similarly oriented distractors (typical of perceptual learning tasks), where some stimulus contexts (spatial distribution of stimuli) were repeated within and across sessions and other contexts were novel (typical of contextual learning tasks).

We evaluated contextual learning by examining differences in performance between repeated and novel contexts, both within the training sessions (days 3–10) and within testing sessions (days 2, 11, 12). Electrophysiological correlates of contextual learning were evaluated by examining differences in ERPs before learning (day 2, as a control) and after learning (day 11). To facilitate a fair comparison between repeated and novel contexts, we employed a yoked design that ensured that orientation differences were equated between these conditions. In our analyses, we address the extent to which performance and electrophysiological changes were specific to the trained contexts.

We evaluated perceptual learning by examining the extent to which changes in performance were specific to the trained orientation. This orientation-specific learning was evaluated by comparing behavioral differences (day 12) and electrophysiological differences (day 11) between trained and untrained target orientations with a baseline session (day 2) prior to

training. We also conducted a passive exposure session (C1 protocol, on day 11) after training, which involved the presentation of stimulus arrays containing only the trained or untrained target orientations (on different trials) at all possible stimulus locations used in the training protocol, in either the upper or lower visual field (again in different trials). See Figure 1, upper right section, for an example of this stimulus array for an upper visual field presentation. We used this protocol to examine whether effects of perceptual learning were retained outside of the trained task context, an important measure of whether measures of learning for the trained orientation are evident without top-down attention to that orientation (Adab & Vogels, 2011).

Given prior evidence that perceptual learning and contextual learning are behaviorally dissociated (Le Dantec & Seitz, 2010), we hypothesized that ERP components previously shown to reflect perceptual learning (such as the C1 component; Bao et al., 2010) and contextual learning (such as the N2pc component; Schankin & Schubö, 2009) would also be dissociated. To the best of our knowledge, this study is the first to examine how these ERP components may show independent measures of learning within the same task.

## Method

Twelve (six females and six males; age range, 19–25 years; mean, 22.33 years; SD = 2.18 years) undergraduate students at the University of California–Riverside participated in the study and were paid $10 an hour. They all had normal or corrected-to-normal vision during the sessions. Participants provided written informed consent at the beginning of the experiment, and they were all tested according to the guidelines of the Human Research Board of the University of California–Riverside. Four additional participants were excluded at the beginning of the experiment because they were unable to perform with the eye-tracker (glare problems with their glasses or uncontrollable ocular saccades). Also, during the C1 protocol on day 11 (at the end of electroencephalography [EEG] session 2; see below), one participant aborted the session due to a migraine.

The experiment was controlled with a Mac Mini (Apple, Inc., Cuppertino, CA) running MATLAB (MathWorks, Natick, MA) and Psychtoolbox 3 (Brainard, 1997; Pelli, 1997). Participants sat on a height-adjustable chair 50 to 55 inches away from a 19.5-inch-wide Trinitron CRT monitor (Sony Corp., Tokyo, Japan) set to a resolution of 1024 × 768 pixels and a refresh rate of 100 Hz. An eye-tracker (EyeLink 1000; SR Research, Ltd., Kanata, ON, Canada) and custom software were used to implement a gaze-enabled display so stimuli were only presented when participants kept their gaze at the center of the
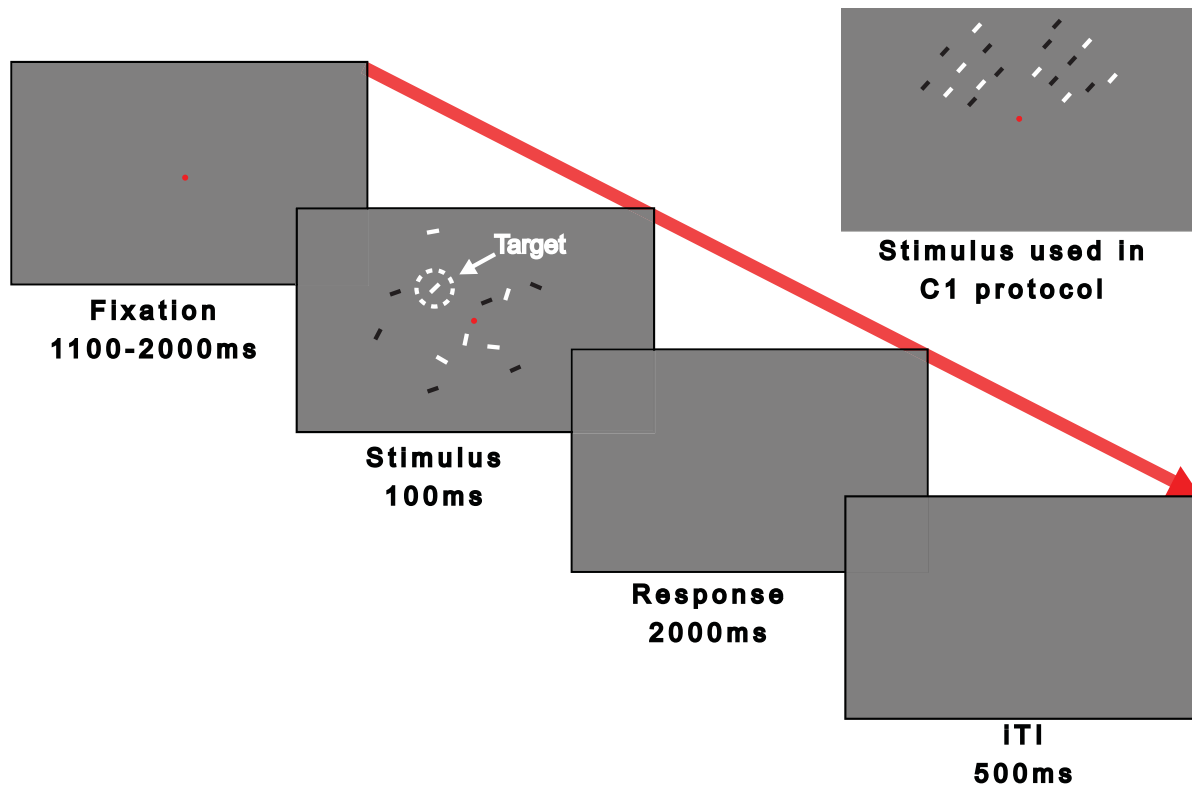
Figure 1. Illustration of the protocol used in the training and testing sessions. Additionally, an illustration of the stimulus used during the C1 protocol is presented in the top right of the panel.

monitor. Accurate timing of stimuli and response triggers was ensured by using a DATAPixx visual stimulator (VPixx Technologies Inc., Saint-Bruno, QC, Canada).

Participants performed a visual search task using stimuli (Figure 1) composed of white (95 cd/m$^2$) or black (5.5 cd/m$^2$) lines (0.1° × 1°) presented on a gray (40 cd/m$^2$) background. In this task, participants first fixated a centrally presented red dot for 500 ms, then the search display was presented for 100 ms followed by a gray-screen response window for 2000 ms. The participants were trained to find a target with a specific orientation—trained target of 45° (Figure 1) or 135°, counterbalanced across subjects—among a set of distractors (ranging from 316° to 44° and from 46° to 134°) and to report the color of the target (pressing 1 for white or 2 for black), which was randomized across trials. The target orientation was cued at the beginning of each block with an instructional screen showing an example line of the target orientation.

The spatial locations of targets and distractors were presented on a grid such that the eccentricity (3°, 5°, 8°) and placement in the left/right and upper/lower visual quadrants were balanced across repeated and novel contexts. Each line could be presented in one of nine locations in each quadrant (three at each eccentricity of 16.875°, 45°, or 73.125° from the cardinal axis), and three lines were presented in each visual quadrant

for a set size of 12 items. To manipulate context, we pre-calculated all possible configurations of the 12 items within the grid given the above constraints. To prevent the occurrence of displays where all items were presented at the same eccentricity, we added the further constraint that all displays must contain at least three items in each eccentricity. From this set of possible search displays, some contexts were selected to be repeated on each day (the target location of each of these contexts were fixed for each subject) and others were selected for use as novel contexts. The configurations used for repeated contexts were held constant throughout the training and testing sessions.

The experiment was divided into different phases (Figure 2). In the familiarization phase (day 1), participants were instructed on the task, and 20 practice trials were conducted. After each response, based on the subject's accuracy, the word "correct" or "wrong" was presented at the center of the screen for 1 second. The next trial then began with presentation of the red fixation dot.

In phase 2 (EEG session 1 on day 2) and phase 4 (EEG session 2 on day 11), participants conducted the same task but also with untrained target orientations. In this session, trained and untrained target orientations were presented in separate, interleaved blocks with separate staircases for each orientation. EEG recordings were conducted during these sessions. Each session

Figure 2. Presentation of the different phases of the experiment and the number of corresponding days. Phases 1 to 5 correspond, respectively, to familiarization on day 1, first EEG session on day 2, training on days 3 to 10, second EEG session on day 11 (as well as C1 protocol on day 11), and final behavioral transfer test on day 12.

consisted of 1200 trials that were split into eight blocks, with a short break between blocks. These sessions each lasted approximately 3 hours, with approximately 1 hour devoted to the EEG recording and time on task. During the two EEG sessions, we used a fixed orientation difference between target and distractors of 30° for EEG session 1 and 15° for EEG session 2, which corresponded closely to the threshold values found at the beginning and end of training, respectively.

In phase 3 (days 3–10), participants were trained on the visual search task with the trained orientation for 9 days. Each session consisted of 1200 trials and lasted approximately 1 hour. Sessions were split into eight blocks, with a self-timed break between each block, and blocks were further subdivided into miniblocks consisting of 24 trials (12 repeated contexts and 12 novel contexts, each different). During these training sessions, the distractor range (an orientation wedge centered on 0° or 90°, with orientations of distractors evenly distributed across the wedge) was determined by means of a staircase procedure where, after each miniblock, the orientation range of the distractors was adjusted such that the orientation of the closest distractor (and thus also the distractor range) was increased if average performance of the previous miniblock was greater than 80% correct; otherwise, the range was decreased if the previous miniblock performance was lower than 70% correct (Le Dantec, Melton, & Seitz, 2012). The value for the new block was set to the current threshold value (orientation difference between the target and closest distractor) plus that value multiplied by the difference between the proportion of correct responses for that block and 0.75, with no change made when proportion correct was between 0.7 and 0.8. Thus,

the threshold reported in the results is the orientation difference between the target and the closest distractor to the target.

In phase 4 (on day 11), the C1 protocol was also run to elicit an inversion of polarity generally reported for the C1 component (Ahamadi et al., 2018; Di Russo et al., 2003; Rauss et al., 2009; Zhang, Li, Song, & Yu, 2015). The C1 component is generally clearer when stimuli are presented in a specific quadrant (Zhang et al., 2015) or hemifield (Ahamadi et al., 2018) and not mixed with other stimuli in four quadrants at the same time, as found in the main procedure. Thus, the stimuli used for the C1 protocol were composed of randomly white or black lines simultaneously presented for 100 ms in all of the 18 possible locations in either the UVF or LVF. A 2 × 2 design was used such that, on a given trial, stimuli were presented in the UVF versus LVF at the trained versus untrained orientation (see Figure 1, upper right section, for an example of an UVF trial). Participants were asked to keep their gaze on the red fixation dot at the center of the screen and avoid blinking. Trials were aborted and replaced with new trials if eye movements were made. A total of 400 stimuli were presented during the C1 protocol, taking approximately 20 minutes. The C1 protocol was conducted at the end of the experiment so we could explore the effect of perceptual learning on the C1 component and test our hypothesis that early differences in EEG activity would be found between the trained and untrained orientations outside of the trained task context. Of note, this protocol also controlled for feature-based attention, as there was no task, and the stimulus configuration was different (e.g., with no orientation outlier) than employed during training.

In phase 5 (day 12), participants ran a final behavioral test session with the same task including both the trained and untrained target orientations. Here, we used a fixed orientation difference between the target and distractors of 15°, which approximated the final threshold value found in the training sessions.

The EEG was recorded using 128 active electrodes (ActiveTwo; BioSemi BV, Amsterdam, Netherlands) (Figure 3) relative to two central electrodes (Common Mode Sense and Driven Right Leg) with a sampling rate of 1024 Hz. All silver–silver chloride electrodes were mounted in an elastic ActiveTwo cap according to the 10-5 electrode placement (Oostenveld & Praamstra, 2001).

Horizontal electrooculograms (HEOGs) and vertical electrooculograms (VEOGs) were recorded using additional electrodes affixed with double-sided adhesive tape at the outer right and left canthi (HEOG) and above the right and left eye (VEOG). To maintain contact between the electrode and the scalp, we used conductive gel (Signa Gel, Parker Laboratories, Inc., Fairfield, NJ).
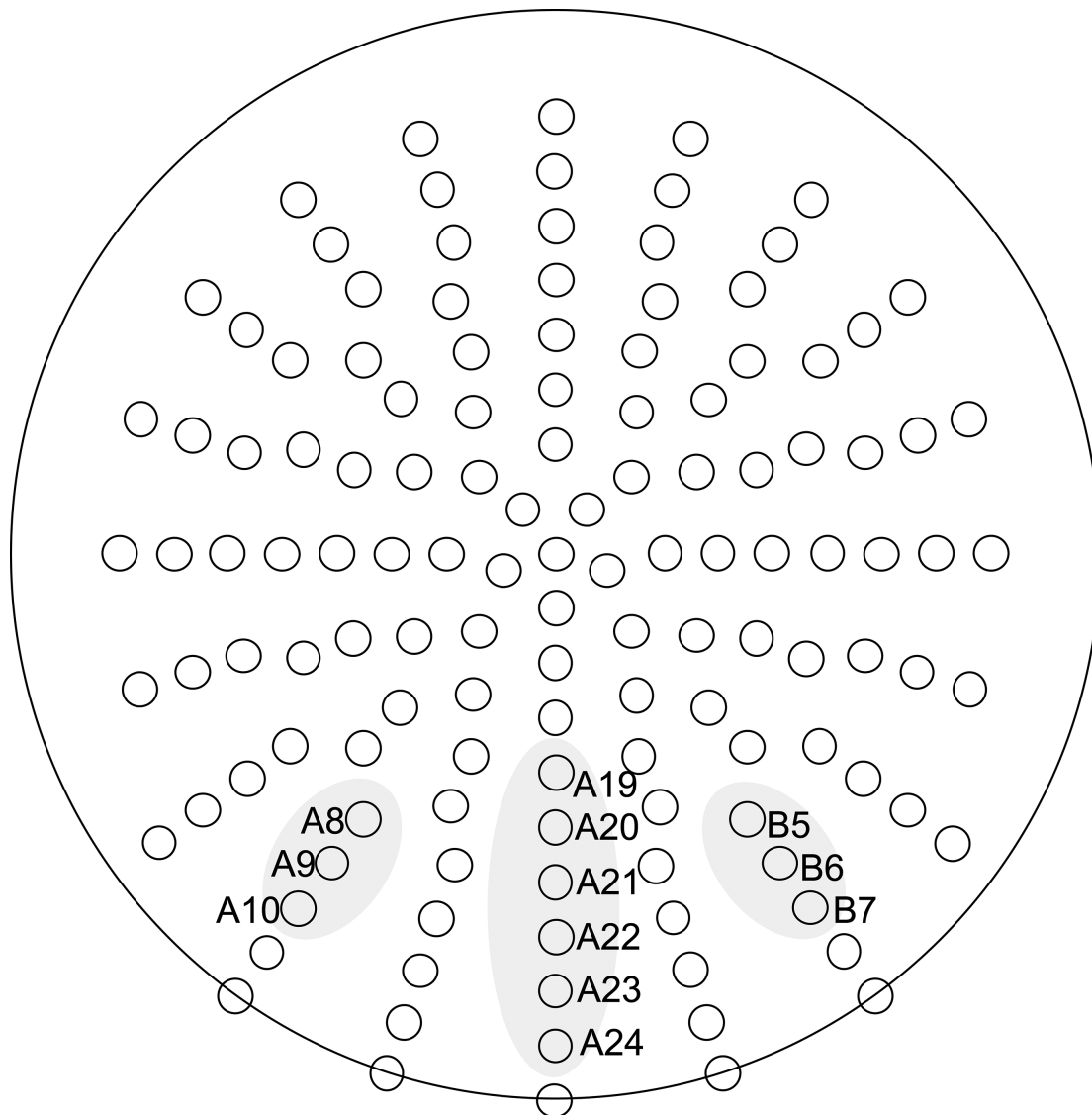
Figure 3. Schematic representation of the electrode (128-electrode BioSemi system) clusters used to explore activities recorded in the middle parieto-occipital area (electrodes A19, A20, A21, A22, and A23) and parieto-occipital area (electrodes A8, A9 and A10 for the left hemisphere and electrodes B5, B6, and B7 for the right hemisphere).

Data preparation was performed using EMSE Suite 5.4. (Source Signal Imaging, Inc., San Diego, CA). Signal was re-referenced to the average of the active electrodes (Picton et al., 2000). Data were high- and low-pass filtered offline using zero phase-shift Butterworth filters with half-amplitude cutoffs at 0.01 Hz and 100 Hz, respectively. Each epoch of EEG ranged from 200 ms before stimulus onset to 500 ms after stimulus onset for phases 2 and 4, and each epoch was 400 ms after stimulus onset for the C1 protocol. Baseline correction was then performed by normalizing waveforms relative to a baseline occurring within a 200-ms pre-stimulus period.

Correction of eye blinks was performed according to the procedure described by Pflieger (2001). Importantly, prior to the EEG sessions, subjects were shown the

impact of eye blinks or eye movement artifacts on their own EEG signals, and we urged them to do their best to avoid them. Furthermore, only correct response trials without eye movements were included in the analysis of the electrophysiological components. Globally, we ended up removing 35.45% of the trials for EEG session 1 on day 2 and 31.4% for EEG session 2 on day 11. This is relatively high according to the standard proposed by Picton et al. (2000) but was necessary not only to remove the wrong trials but also to fulfill the necessity to study only the trials where the subjects were efficiently stimulated in the different locations of their visual field. In the C1 protocol on day 11, we removed only 1.07% of the trials, which is very low but expected, considering that the subjects were not required to perform a task other than maintaining fixation.
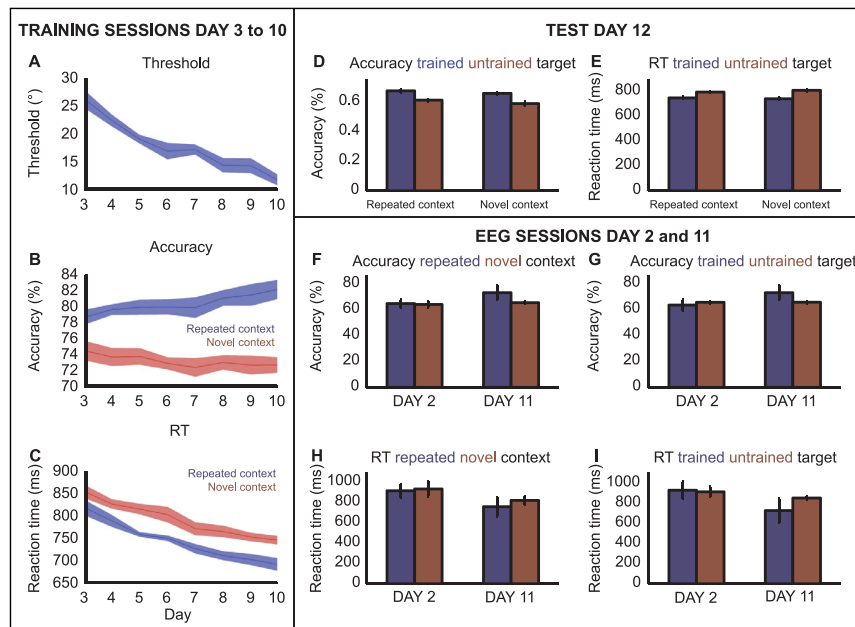
Figure 4. Behavioral performance. (A) Average thresholds, (B) accuracy, and (C) reaction times for training sessions on days 3 to 10. (D) Average accuracy and (E) reaction times recorded during behavioral tests on day 12. (F, G) Average accuracy for (F) repeated versus novel contexts and (G) trained versus untrained orientations for EEG session 1 on day 2 and EEG session 2 on day 11. (H, I) Average reaction time accuracy for (H) repeated versus novel contexts and (I) trained versus untrained orientations for EEG session 1 on day 2 and EEG session 2 on day 11. Error bars are reflected within subject standard error.

ERP components were identified on the basis of their polarity, latency, and distinctive topographical properties. The C1 component is generally recorded in midline parieto-occipital electrodes (Slotnick, 2018), so we identified a cluster of electrodes (electrodes A19, A20, A21, A22, and A23; Figure 3) in this area and averaged their activities before the average amplitude of the C1 component was extracted and analyzed. Similarly, the N2pc component is commonly recorded in parieto-occipital areas, so we identified two clusters (electrodes A8, A9, and A10 for the left hemisphere and B5, B6, and B7 for the right hemisphere; Figure 3) to analyze it, and activities were averaged per cluster. The amplitude of each component was calculated as the mean potential in the following time windows: C1, 20 to 80 ms (in phases 2 and 4) and 30 to 100 ms (in the C1 protocol); N2pc, 250 to 350 ms. These temporal windows were also used to produce the mapping of the corresponding activities in the figures. The N2pc component, which has been consistently shown to be involved in visual search tasks, was obtained as the difference between posterior electrodes ipsilateral and contralateral to the target position in the search array (Kiss, Van Velzen, & Elmer, 2008; Luck & Hillyard, 1994). To analyze the difference between N2pc components contralateral versus ipsilateral in EEG session 2 on day 11, we created a composite of the signals recorded when the stimulus was presented contralaterally (regardless of presentation on the right or left part of the visual field) and another ipsilaterally (same way). After that, we compared the contralateral versus ipsilateral activity. For statistical analysis, mean amplitudes were averaged across trained and untrained targets, as well as repeated and novel contexts.

## Results

### Behavioral data

We first examined data from the training sessions to confirm whether standard measures of perceptual learning and contextual learning could be observed. For perceptual learning, consistent with previous reports (Le Dantec et al., 2012), we found that orientation discrimination thresholds (as defined by the distractor with the closest orientation to the target) improved as a function of training day; for the effect of day, $F(7, 184) = 5.02$, $p < 0.0001$, and $\eta^2 = 0.160$ (Figure 4A). For contextual learning (e.g., difference in performance between novel configurations and those repeated across all of the training sessions), we found that performance on the repeated contexts in the training sessions (days 3–10) was more accurate compared with the novel contexts; for the effect of context, $F(1, 10) = 6.755$, $p = 0.0019$, and $\eta^2 = 0.403$ (Figure 4B). Performance

also showed faster reaction times compared with the novel contexts; for the effect of context, $F(1, 10) = 15.067$, $p = 0.0026$, and $\eta^2 = 0.601$ (Figure 4C). These data show that both perceptual and contextual learning arose through the training and that this learning was maintained across sessions (Le Dantec et al., 2012).

To better understand these learning effects, we analyzed data from the behavioral testing session (day 12). These data (Figure 4D, 4E) show that perceptual learning was orientation specific, with better accuracy for trained versus untrained target orientations; for the effect of target, $F(1, 11) = 24.953$, $p = 0.0004$, and $\eta^2 = 0.694$) (Figure 4D). Also, the data reflect faster reaction times; for the effect of target, $F(1, 11) = 31.267$, $p = 0.0002$, and $\eta^2 = 0.739$ (Figure 4E). Further, there was an effect of contextual learning on accuracy; for the effect of context, $F(1, 10) = 10.278$, $p = 0.0084$, and $\eta^2 = 0.506$) (Figure 4D). The same was not true for reaction time; for the effect of context, $F(1, 10) = 1.085$, $p = 0.3199$, and $\eta^2 = 0.097$ (Figure 4E). No interaction was found between the context and target factors, suggesting that, at least at the behavioral level, perceptual learning and contextual learning represent independent aspects of learning.

To confirm that the behavioral data recorded in EEG sessions showed the effects of perceptual learning and contextual learning, we analyzed the behavioral results from both EEG sessions (days 2 and 11). Consistent with the day 12 measures of perceptual learning, we found significant interactions between the target orientation and session factors (T × S): For accuracy, $F(1, 11) = 47.134$, $p = 0.0001$, and $\eta^2 = 0.810$ (Figure 4G); for reaction times, $F(1, 11) = 16.191$, $p = 0.002$, and $\eta^2 = 0.595$ (Figure 4I). Likewise for contextual learning, we found significant interactions between context and session factors (C × S) for both accuracy and reaction times: For accuracy, $F(1, 11) = 28.906$, $p = 0.0002$, and $\eta^2 = 0.724$ (Figure 4F); for reaction times, $F(1, 11) = 7.941$, $p = 0.0167$, and $\eta^2 = 0.419$ (Figure 4H).

These interactions indicate that the effects of context and target vary as a function of session (Figure 4). Consistent with these interactions, the pre-test (day 2) did not show an effect (based on *t*-test) of either context or target orientation on accuracy (C: $p = 0.6789$, $d = 0.10$; T: $p = 0.1521$, $d = -0.31$) or reaction times (C: $p = 0.1108$, $d = -0.11$; T: $p = 0.4772$, $d = 0.22$). However, in the post-test (day 11), context and target orientation significantly improved (based on *t*-test) in both accuracy (C: $p = 0.00021$, $d = 1.67$; T: $p = 0.00095$, $d = 1.50$) and reaction times (C: $p = 0.00025$, $d = -0.34$; T: $p = 0.0011$, $d = -65.9$), eliciting higher accuracy and faster reaction times for repeated contexts and the trained target. These results confirm that behavioral measures of both perceptual learning and contextual learning were observable in the EEG post-test.

## Electroencephalographic data

To understand the electrophysiological correlates of perceptual learning and contextual learning, we examined data recorded on days 2 and 11. We first report activity differences between trained and untrained orientations, as well as the effect of repeated and novel contexts on early visual ERPs. We then report lateralized potentials to estimate the N2pc component and, finally, discuss relationships between the behavioral and EEG signatures of learning.

### *Early ERPs for trained versus untrained conditions*

To address whether training gains may be mediated by early visual processes, we focused on the C1 component (although the full time courses of the ERPs are shown in Figure 5). During the first EEG session on day 2 (Figures 5A, 5B) and second EEG session on day 11 (Figures 5D, 5E), we identified the C1 component in the midline parieto-occipital part of the scalp as visible on the mapping of the activities recorded during the respective time windows (Figures 5C, 5F).

For perceptual learning, we compared the activity for trained versus untrained target orientations in the EEG sessions. As a control, we verified that the ERPs recorded during the first EEG session (day 2) did not show any significant difference between the C1 components (Figures 5A, 5B) recorded for trained and untrained orientations, where, for T, $F(1, 11) = 1.392$, $p = 0.2630$, and $\eta^2 = 0.11$, and those recorded independently of the visual field, where, for T × F, $F(1, 11) = 1.224$, $p = 0.2922$, and $\eta^2 = 0.10$. However, after training, we can see that activity differed between the trained and untrained target orientations (Figures 5D, 5E), particularly when the target was presented in the LVF. The ANOVA for target orientation and hemifield factors (T × H) revealed a significant interaction, where $F(1, 11) = 9.664$, $p = 0.0099$, and $\eta^2 = 0.467$, for the C1 component recorded in midline parieto-occipital areas during the second EEG session (day 11). Significant differences were found when targets were presented in the LVF ($t = -2.2834$, $p = 0.0433$, $d = -1.93$) (Figure 5F, lower row) but not in the UVF ($t = -0.8211$, $p = 0.4290$, $d = -0.18$) (Figure 5F, upper row).

To further characterize these changes in the C1 component, we examined data from the C1 protocol (day 11), where we presented stimuli only in either the UVF (Figure 6A) or the LVF (Figure 6B). As is typical of the C1 component, we observed differences of polarity according to the position of the stimuli in the visual field. An ANOVA involving the target orientation and hemifield factors (T × H) revealed a significant interaction with the C1 components, where $F(1, 11) = 9.231$, $p = 0.01$, and $\eta^2 = 0.456$. This reflects
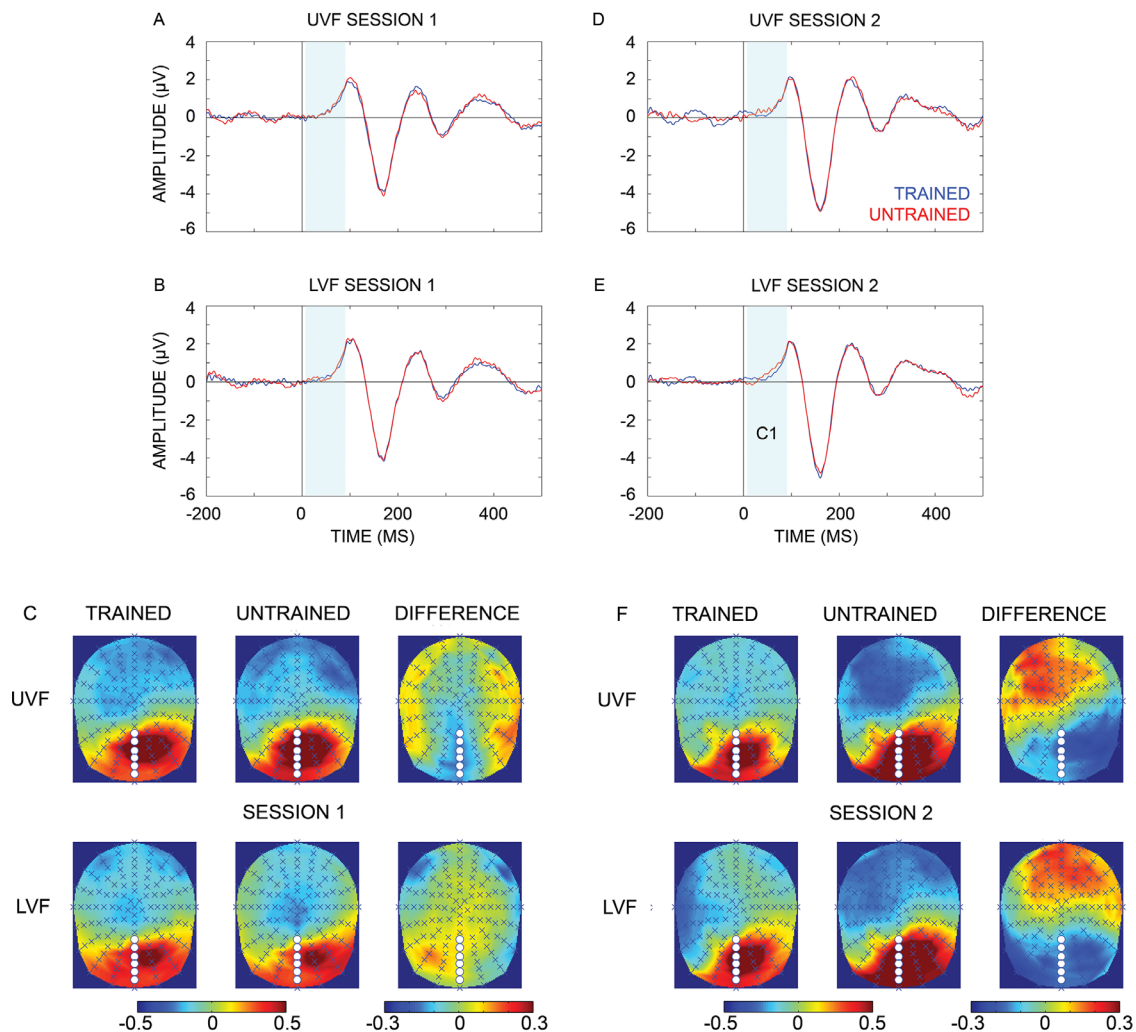
Figure 5. (A) ERPs recorded during EEG session 1 (day 2) from posterior electrodes with a trained (blue) or untrained (red) target orientation presented in the UVF. (B) ERPs recorded during EEG session 1 (day 2) from posterior electrodes with a trained (blue) or untrained (red) target orientation presented in the LVF. (C) C1 component topographical map (average activity from 20 to 80 ms after stimulus onset) during EEG session 1 for trained target orientation (left) or untrained target orientation (middle) and their difference (right). The top row represents the UVF, and the bottom one represents the LVF. (D) ERPs recorded during EEG session 2 (day 11) from posterior electrodes, with a trained (blue) or untrained (red) target orientation presented in the UVF. (E) ERPs recorded during EEG session 2 (day 11) from posterior electrodes, with a trained target orientation (blue) or untrained target orientation (red) presented in the LVF. (C) C1 component topographical map (average activity from 20 to 80 ms after stimulus onset) for EEG session 1 with trained target orientation (left) or untrained target orientation (middle) and their difference (right). The white dots indicate electrode clusters used to obtain the trained and untrained average amplitudes for the C1 component. The top row represents the UVF and the bottom one the LVF.

a significant difference in the 30- to 100-ms period in the midline parieto-occipital electrodes between the trained and untrained orientations ($t = 2.5988$, $p = 0.0247$, $d = -0.94$) for stimuli presented in the LVF (Figures 6B, 6C, lower row). Of note, the C1 component for the LVF showed a significant difference between the trained and untrained orientations even for the earliest period (30–60 ms), consistent with an early locus of perceptual learning. On the other hand, for the UVF, we failed to find an effect of target orientation during the 30- to 60-ms period; however,

we did observe a significant difference during the 100- to 160-ms period ($t = -2.5020$, $p = 0.0294$, $d = -0.66$), perhaps consistent with an effect on the P1 potential.

For contextual learning, we compared activity related to the repeated and novel contexts recorded during EEG session 2 (day 11). Here, we found no significant differences in the C1 component on any midline parieto-occipital electrodes ($t = -0.8474$, $p = 0.4148$, $d = -0.20$). Together, these results suggest a possible dissociation between perceptual learning and
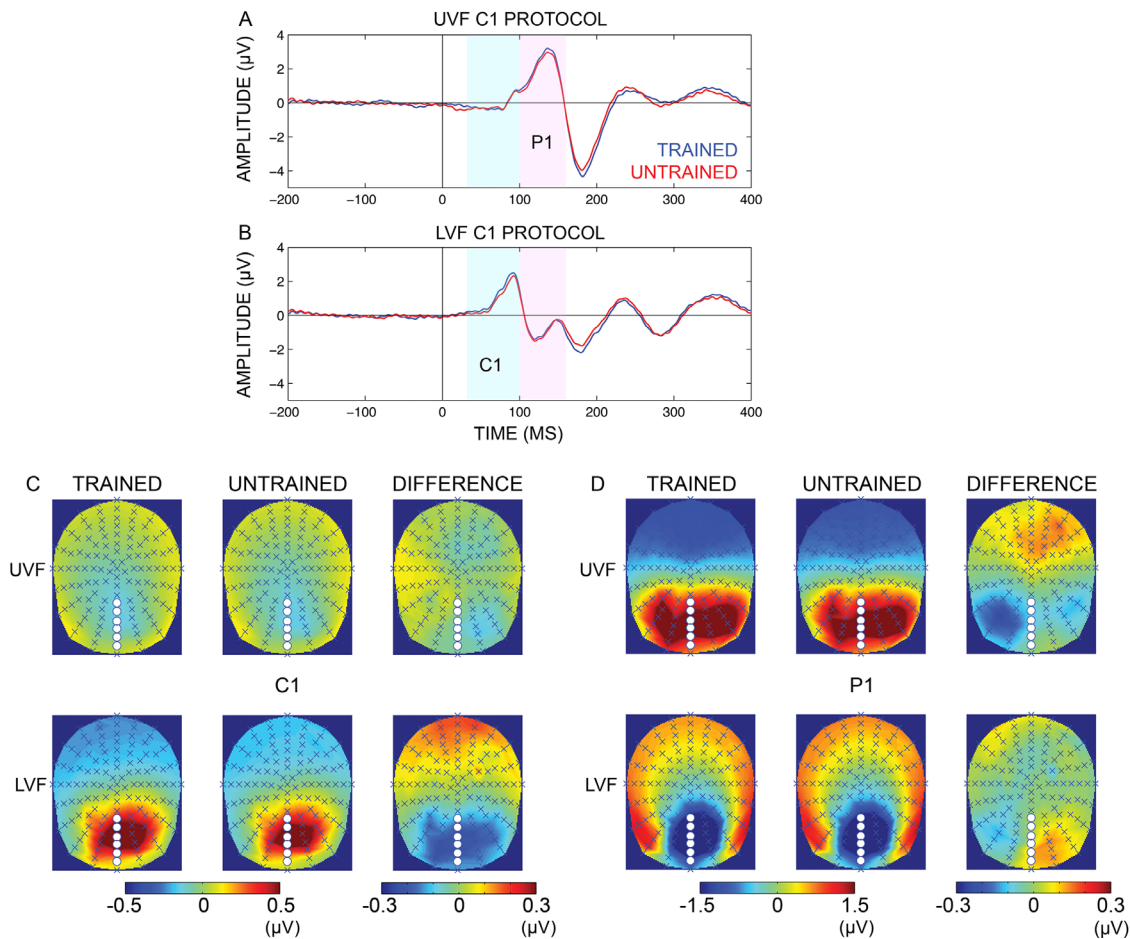
Figure 6. (A) ERPs recorded during EEG session 2 (day 11) from posterior electrodes with a trained (blue) or untrained (red) target orientation presented in the UVF. (B) ERPs recorded during EEG session 2 (day 11) from posterior electrodes with a trained (blue) or untrained (red) target orientation presented in the LVF. (C) C1 component topographical map (average activity from 30 to 100 ms after stimulus onset) for C1 protocol with trained target orientation (left) or untrained target orientation (middle) and their difference (right). The white dots indicate the corresponding electrodes included in the clusters for C1 component. (D) P1 component topographical map (average activity from 100 to 160 ms after stimulus onset) for C1 protocol with trained target orientation (left) or untrained target orientation (middle) and their difference (right). The white dots indicate electrode clusters used to obtain the P1 component. The top row represents the UVF and the bottom one the LVF. (E) ERPs recorded during EEG session 2 (day 11) from posterior electrodes (bold blue, trained target; bold red, untrained target) and frontal electrodes (same color code but with dashed lines), with target orientation presented in the LVF.

contextual learning with evidence for an early locus of perceptual learning, but perhaps a later locus of contextual learning as examined in the next section.

### Lateralized potentials

We next examined lateralized potentials to examine changes specific to the hemisphere in response to the target location. Here, we focused on the N2pc component (although the full time course of the lateralized responses is shown in Figures 7A and 7B) and examined differences in ERPs contralateral versus ipsilateral to the hemifield in which the target was presented.

For contextual learning, we found a significant difference between repeated and novel contexts (Figure 7A) for targets presented contralaterally versus ipsilaterally in the N2pc component. An ANOVA for context and lateralization factors (C × L) revealed a significant interaction with the N2pc component, where $F(1, 11) = 12.784$, $p = 0.0061$, and $\eta^2 = 0.537$. Following up on this effect, we found a significant difference between contralateral and ipsilateral target presentations in parieto-occipital electrodes ($p < 0.05$, $t$-test) (Figure 7C, upper row).

Notably for perceptual learning, during EEG session 2 (day 11), we also found a significant, but smaller, effect on the N2pc component between trained targets presented contralaterally and ipsilaterally ($p < 0.05$,
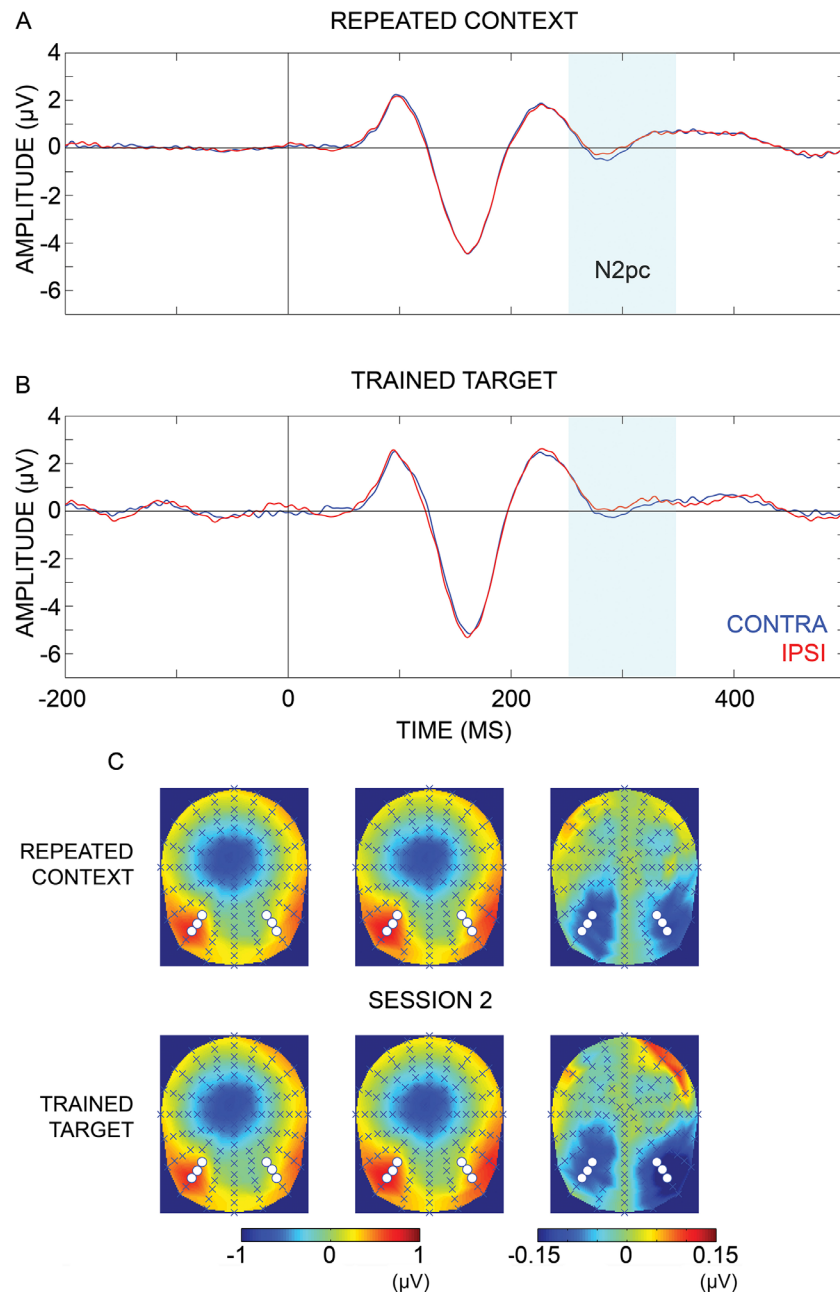
Figure 7. (A) ERPs recorded during EEG session 2 (day 11) from posterior electrodes with a repeated context and target presented contralaterally (blue) and ipsilaterally (red). (B) ERPs recorded during EEG session 2 (day 11) from posterior electrodes with a trained target and target presented contralaterally (blue) and ipsilaterally (red). (C) N2pc component topographical map (average activity from 250 to 350 ms after stimulus onset) for session 1 with target presented contralaterally (left) or ipsilaterally (middle) and their difference (right). The white dots indicate electrode clusters used to obtain the average amplitudes for the N2pc component elicited in the different conditions. The top row represents the repeated contexts and the bottom one trained targets.

*t*-test) (Figures 7B, 7C, lower row). We also found a significant interation for the factors of target and lateralization (T × L), for which $F(1,11) = 5.250$ and $\eta^2 = 0.323$.

To address the extent to which perceptual learning and contextual learning may interact to influence the N2pc component, we performed an ANOVA involving the context and target factors to examine differences between the N2pc component recorded with a stimulus presented on the ipsilateral field of the subjects versus being presented on the contralateral field. Interestingly, we found an effect of the context factor, where $F(1, 11) = 17.620$, $p = 0.001$, and $\eta^2 = 0.615$, and the target factor, where $F(1, 11) = 8.371$, $p = 0.09$, and
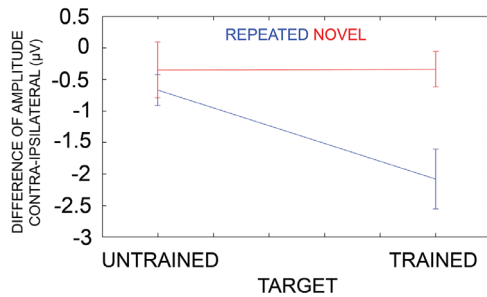
Figure 8. N2pc component (contralateral–ipsilateral) as a function of the factors context and target factors. Error bars reflect within-subject standard error.

$\eta^2 = 0.615$, as well as an interaction between context and target (C × T), where $F(1, 11) = 5.06$, $p = 0.046$, and $\eta^2 = 0.315$) (Figure 8). This result supports the idea that the N2pc component is largely mediated by contextual learning, as no N2pc component was evident for the novel context even when presented with the trained target. However, the interaction suggests that perceptual learning and contextual learning may jointly influence the N2pc component. Further research will be required to determine whether this represents a process that is sensitive to both the context and trained orientation or whether a nonlinearity exists in how the effects of context and trained target are combined in the ERP signal.

### Relationships between EEG and behavior

An important question in addressing the relationship between behavioral and electrophysiological signatures of learning is the extent to which measures of performance and electrophysiology covary. To address this, we examined correlations between the C1 and N2pc components and the primary behavioral learning outcome measures for perceptual learning and contextual learning.

For the C1 component, we found a trend in the correlation between the change in accuracy between the test sessions for the trained versus untrained target orientations ($r = 0.32$, $p = 0.053$) for stimuli presented in the lower visual field in the 30- to 100-ms time window measured during the C1 protocol. As a control, we found no correlation between the C1 component and accuracy differences for repeated versus novel contexts ($r = –0.10$, $p = 0.92$). Whereas the correlation between perceptual learning and the C1 component is only a trend, it is notable that the C1 component recorded during the C1 protocol correlates with the perceptual learning effect on behavior as measured in the training sessions.

For the N2pc component, we examined correlations for both contextual and target orientation effects. In the case of contextual learning, we found a significant

correlation between the difference in magnitude of repeated and novel N2pcs and reaction time ($r = –0.48$, $p = 0.0001$) and a trend for accuracy differences ($r = 0.34$, $p = 0.13$) for the repeated versus novel contexts in the post-test analysis. As a control, we found no correlations between the N2pc component for differences in the repeated and novel contexts and accuracy ($r = 0.11$, $p = 0.126$), nor for differences in reaction time ($r = –0.18$, $p = 0.4$) between the trained and untrained orientations. In the case of target orientation, we found a significant correlation between the amplitude differences between the N2pc component for the trained versus untrained orientations (Figure 8) and accuracy differences for trained versus untrained orientations (Figure 4) in the post-test ($r = –0.59$, $p = 0.034$), but no such correlation between differences in the N2pc component and reaction time ($r = –0.06$, $p = 0.625$) as a function of trained orientation.

Overall, these results provide further evidence that the perceptual learning effect may be mediated by early processes related to the C1 and that contextual learning may be related to later processes related to the N2pc component. Importantly, because our hypothesis is that perceptual learning has bottom-up effects on later processes, there are also interesting relationships between perceptual learning and the N2pc component. Notably, the correlations for perceptual learning and contextual learning with N2pc component are of opposite polarity. A possible explanation for this would be that participants with greater perceptual learning showed pop-out for the trained orientation and thus had a smaller N2pc component. This would be consistent with our hypothesis that contextual learning may represent more of a top-down effect compared to perceptual learning, which shows more of a bottom-up effect.

## Discussion

Here we described two types of implicit visual learning (perceptual learning and contextual learning) that arise together through training on a visual search task. Behavioral measures corroborate previous findings that perceptual learning and contextual learning give rise to dissociated performance benefits (Le Dantec et al., 2012). Electrophysiological measures show that benefits of perceptual learning are associated with the early C1 ERP potential and that contextual learning is better reflected in the later N2pc component.

The ERPs indicate that the earliest visual component, the C1 component, is associated with perceptual learning. Because of its early latency, the polarity inversion between the upper and lower visual fields (Clark, Fan, & Hillyard, 1994; Jeffreys & Axford, 1972a; Jeffreys & Axford, 1972b; Rauss et al., 2009), the retinotopic specificity of its distribution on the scalp

(Clark et al., 1994; Jeffreys & Axford, 1972a; Jeffreys & Axford, 1972b), and localization approaches (Pitts, Martinez, & Hillyard, 2010; Proverbio, Del Zotto, & Zani, 2010), the C1 component has been considered an index of initial afferent activity in the primary visual cortex (V1).

However, the locus of the C1 component in the primary visual cortex has been challenged by Ales, Yates, and Norcia (2010), who showed that polarity reversal observed for event-related potentials could be generated by activities located in V2 and V3 (although see Kelly, Schroeder, & Lalor, 2013). Of note, the effects that we observed for the C1 component differed such that stimuli in the upper visual field presented more differences in the period of the classical P1 potential (Cobb & Dawson, 1960; Luck & Hillyard, 1994; Spehlmann, 1965), which is thought to be generated in the extrastriate visual cortex (Di Russo et al., 2003; Mangun, Hopfinger, Kussmaul, Fletcher, & Heinze, 1997; Martínez et al., 1999; Woldorff et al., 1998). Together these studies are consistent with a locus of the observed perceptual learning effect in the early occipital visual cortex; however, the use of other techniques, such as fMRI, would be needed to determine a more precise localization of this perceptual learning effect.

We also note that we found evidence of a relationship between perceptual learning and contextual learning both within the trained task context and also during a passive viewing condition using a stimulus array that contained no orientation differences to search for. This is consistent with similar approaches showing electrophysiological effects of perceptual learning in the early visual cortex in monkeys (Adab & Vogels, 2011) for orientation discrimination that are evident in both active and passive viewing. This provides some evidence that the observation of an early locus may not be simply explained by the effects of top-down attention and is consistent with the hypothesis that the perceptual learning effect is at least partially mediated by bottom-up processes.

The results demonstrating a relationship between perceptual learning and the C1 component show similarities and differences with other studies of learning. Pourtois et al. (2008) trained subjects on the texture discrimination task (Karni & Sagi, 1991) and found a change in the C1 component in the upper visual field but not in the lower visual field, in contrast to what we found. However, they only trained participants for a single session, and behavioral effects were also limited to the upper visual field. Bao et al. (2010) trained participants for 24 or more days on an orientation discrimination task and found changes in the C1 in both the upper and lower visual fields. However, the effect found in the C1 component was not location specific to the trained stimulus location (unlike the behavioral results), and the authors suggested that there could be an attentional factor to the observed C1 effect (e.g.,

Rauss, Schwartz, & Pourtois, 2011). Thus, although these different studies consistently demonstrate an early locus to perceptual learning, inconsistencies among studies indicate that there is more to be understood about the mechanistic relationship between the C1 component and perceptual learning. An important issue that needs to be addressed in future studies is to examine the extent to which differences between the training and testing approaches in these studies may explain the differences in findings. For example, across these studies there are numerous differences in the details of the trained task and also the conditions of how the C1 component was measured (e.g., active vs. passive, in a trained context or outside of a trained context). Further, as we collected data with the C1 protocol only on day 11, there is the possibility that baseline differences could have increased or reduced our observed effects. Our work and that of others show that these details of training and how learning effects are estimated can have an immense impact on measured outcomes (Hung & Seitz, 2014; Kattner, Cochrane, Cox, Gorman, & Green, 2017).

For contextual learning, we found a significant effect on the N2pc component; however, we did not observe any significant differences between repeated and novel contexts earlier than ∼200 ms. These results are consistent with the hypothesis that contextual learning is a relatively higher level type of learning (e.g., Olson & Chun, 2001; Schankin et al., 2011).

Although our results are consistent with extant findings of effects of perceptual learning on the C1 component and effects of contextual learning on the N2pc component, they are novel in the demonstration of a dissociation between the two forms of learning that co-occur in the same task. This is an important step in addressing the observation that perceptual learning is a whole brain phenomenon involving many subcomponents (Maniglia & Seitz, 2018). To date, a key difficulty in the field of perceptual learning has been in attributing behavioral changes due to learning to their neural correlates. For example, although some authors argue that perceptual learning has an early locus, potentially involving V1 (Karni & Sagi, 1991; Schoups et al., 2001) or even the lateral geniculate nucleus (Yu, Zhang, Qiu, & Fang, 2016), other research suggests that specificity can arise from learning read-out in decision areas (Dosher & Lu, 1998; Law & Gold, 2008) or through top-down processes (Li, Piëch, & Gilbert, 2004). Across studies there is evidence showing that perceptual training can give rise to learning in very different stages of processing, including representation changes, attentional learning (Byers & Serences, 2012), and new decision rules (Zhang et al., 2010). Although it is most typical for research in the field to attempt to identify a single locus or a new or understudied locus of learning, research such as the current study and others demonstrates that a typical learning process

likely involves more than just a single one of these components of learning (Frankó, Seitz, & Vogels, 2010; Le Dantec et al., 2012; Maniglia & Seitz, 2018). We suggest that our study helps point the way toward dissociating the various components of behavioral learning and relating them to the various components of neural processing.

*Keywords: perceptual learning, contextual learning, visual search task, specificity of learning, psychophysics, event-related potentials, C1, N2pc*

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