# Alpha-band EEG activity in perceptual learning

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

## Introduction

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

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

(Ahissar & Hochstein, 2004; Byers & Serences, 2012; Dosher & Lu, 1998; Fahle, 2005; Hung & Seitz, 2014; Jeter, Dosher, Liu, & Lu, 2010; Petrov, Dosher, & Lu, 2005; Pilly, Grossberg, & Seitz, 2010; Xiao et al., 2008; Zhang et al., 2010).

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

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

The alpha bandwidth found within EEG refers to the set of frequencies ranging approximately from 8–12 Hz. This bandwidth was first observed and studied by Berger (1929), who noted that the amplitude of activity in these frequencies increased significantly when human subjects sat quietly with their eyes closed. A large body of evidence points towards thalamo-cortico connections as the source of alpha oscillations (for a review, see Hughes & Crunelli, 2005) although evidence also exists for intracortical sources (Bollimunta, Chen, Schroeder, & Ding, 2008; Jones, Pritchett, Stufflebeam, Hämäläinen, & Moore, 2007; Lopes da Silva, van Lierop, Schrijer, & Storm van Leeuwen, 1973;

Ronnqvist, McAllister, Woodhall, Stanford, & Hall, 2013; Silva, Amitai, & Connors, 1991). Alpha power is most prominent in occipital channels of the EEG but can also be found across other areas of the scalp (e.g., Rolandic alpha rhythms found over sensory-motor areas). These alpha oscillations have been shown to vary significantly based on a participant's cognitive state (Berger, 1929; Klimesch, 2012), and level of alpha power during a range of tasks can predict performance (Hanslmayr, Gross, Klimesch, & Shapiro, 2011; Payne & Sekuler, 2014).

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

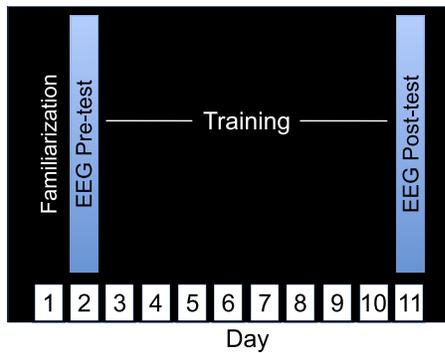In the present study, we examine how psychophysical and electrophysiological measures change as

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

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

## Methods

### Participants

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

### Display apparatus

An Apple Mac Mini (Apple, Inc., Cupertino, CA) running OSX 10.5.6 controlled the experiment. The stimuli were displayed on a 24-in. wide Sony Trinitron (Sony Corp., Tokyo, Japan) CRT monitor with a resolution of 1600 × 1200 pixels and a refresh rate of 100 Hz. Participants sat 50–55-in. from the screen with their heads restrained by a chinrest. The range in distance is due to individual differences in posture because a chinrest was used without a forehead restraint. An EyeLink 1000 eyetracking system (SR Research, Ltd., Mississauga, ON, Canada) was used with custom software to ensure that stimuli were only displayed while participants fixated on the center of the screen. Stimuli were created and controlled by custom code written in Matlab (The Mathworks, Inc., Natick, MA), using the Psychophysics Toolbox (Brainard, 1997; Kleiner, Brainard, & Pelli, 2007). Mediating the connection between the monitor, the computer, and the EEG system was a Datapixx processor (Vpixx Technologies, Inc., Saint-Bruno, QC, Canada) which enables a 16-bit digital-to-analog conversion (DAC), allowing for a 256-fold increase in the display's possible contrast values, and which provides monitor-refresh–locked stimulus presentations for accurate timing of stimuli and response triggers.

### PL training

The PL training took place over 8 days and began 1 day after the pre-test (Figure 1). On each day, participants performed a visual search task for approximately 1 hr (Figure 2). The stimuli in the task comprised white or black lines (0.1° × 1°; 95 cd/m² and 5.5 cd/m², respectively) that were presented on a gray background (40 cd/m²). On each trial, participants first fixated on a centrally presented red dot for 1100–2000 ms (determined pseudorandomly). The trial only proceeded if the participant maintained fixation for this period of time. After fixation, a search display was presented for 100 ms, followed by a blank gray response screen that was presented for up to 2000 ms during which the participant made a response, and a further 500-ms intertrial interval (ITI).

The participant's task in each trial was to find a target line within a set of distractor lines in the search display and report with a keypress ("1" for white and "2" for black) during the response period whether the line was white or black. The target line was defined by its orientation, which could be either 45° or 135° (counterbalanced across participants), and was randomly assigned its color for each trial. The orientations of the distractors were determined by a staircase wherein the distractor lines were offset from the target line by a number of degrees between 0°–90°, which we refer to as $\theta$. After every 24 trials, $\theta$ was adjusted according to the participant's performance such that if the average performance for the previous 24 trials was above 80% correct then $\theta$ was decreased, making the task more difficult, and if the average performance was lower than 70% correct then $\theta$ was increased, making the task easier (Le Dantec, Melton, & Seitz, 2012). Each training session took place on a separate day, consisted of 1,200 trials, and lasted approximately 1 hr. The 1,200 trials of each session were split into eight blocks with a short participant-controlled break between each block. In addition, on the first day of the experiment, there was a familiarization session in which
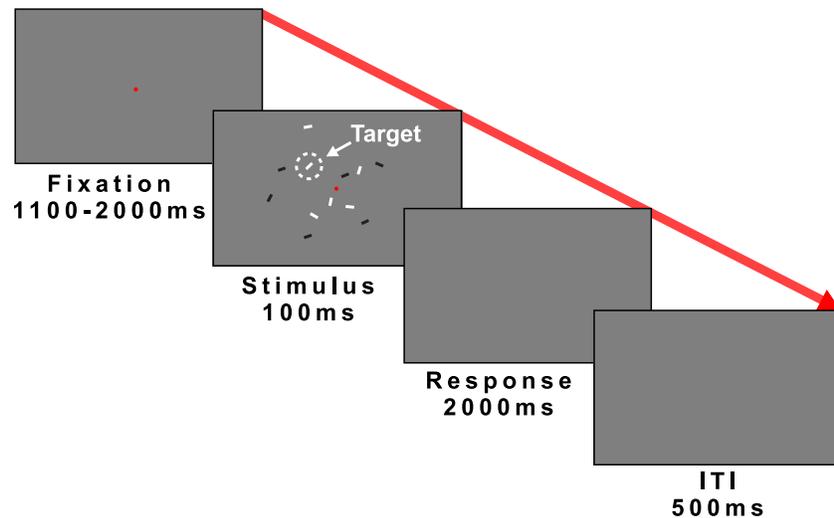
Figure 2. Diagram of a single trial. After a fixation period the stimulus array appeared for 100 ms. (The target is marked for illustrative purposes here but was distinguishable only by its orientation during actual presentations.) This was followed by a blank screen while the response was made and a 500-ms intertrial interval after the response.

participants were instructed on the task and ran 20 practice trials with visual feedback.

## Pre- and post-testing

One day before training and 1 day after training, pre- and post-test sessions were conducted. These sessions were similar to the training sessions with three main differences. First, EEG recordings were collected during these test sessions. Second, the target line could either be of the trained orientation or untrained orientation, run in separate, interleaved blocks so that the participants knew which orientation to search for in each block of trials. Third, instead of a staircase determining $\theta$, the offset of the distractor lines was set to 30° for all pre-test trials and 15° for all post-test trials. This was done to avoid stimulus-driven differences in processing between orientations while keeping stimuli close to threshold. An examination of the average beginning and ending $\theta$ thresholds in the training sessions (Figure 4, in Results below) confirm that 30° and 15° were very near the obtained average thresholds.

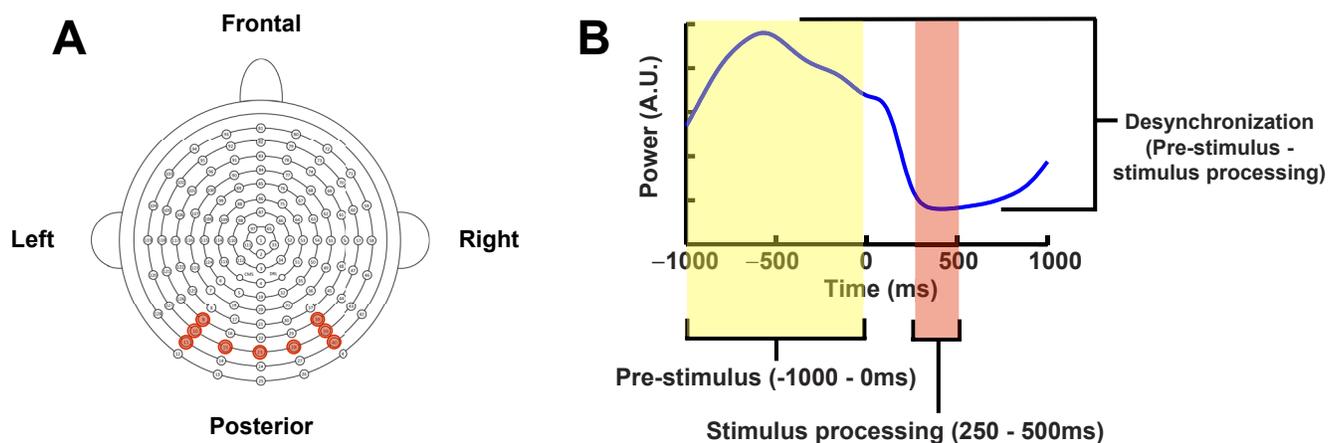Each session consisted of 1,200 trials, lasted approximately 1.5 hr (plus additional time for EEG set-



Figure 3. (A) Overhead view of the placement of 128 electrodes using the BioSemi ActiveTwo system. Red highlighted regions denote electrodes used in the alpha power analyses, corresponding approximately to sites Oz, O1, O2, PO7, PO8, PO9, PO10, P3, and P4. (B) Diagram of the pre-stimulus period (yellow shaded region), the stimulus processing period (red shaded region), and desynchronization (the difference between the mean pre-stimulus period and mean stimulus processing period) used in the alpha power analyses. The pre-stimulus period consists of the 1000 ms before the stimulus onset (0 ms). The stimulus processing period consists of the 250–500 ms after the stimulus onset.

up), and was split into eight blocks with a 30-s break between each block and a 3-min break half-way through the session in which participants were required to get up and stretch. Each of the eight blocks consisted of 150 trials and each block alternated between containing targets of a trained orientation or targets of an untrained orientation, for a total of 600 trials in each condition.

## Electroencephalography

EEG was recorded using 128-active Ag/AgCl electrodes (ActiveTwo system, BioSemi, Inc., Amsterdam, Netherlands) at a rate of 1024 Hz. All electrodes were mounted in an elastic ActiveTwo cap according to the BioSemi layout and labeled according to the 10/20 system (Oostenveld & Praamstra, 2001; Figure 3A). Given that alpha power is most prominent in occipital channels, and that we were analyzing a visual task, a bilateral selection of nine occipital and parietal electrodes was analyzed, corresponding approximately to sites Oz, O1, O2, PO7, PO8, PO9, PO10, P3, and P4 (Figure 3A, highlighted regions). The selection of electrode sites to analyze was based on post hoc analyses of where the greatest overall areas of alpha power occurred in the recorded EEGs. Horizontal and vertical electrooculograms (HEOG and VEOG, respectively) were recorded, using additional electrodes affixed with adhesive disks at, respectively, the outer right and left canthi (HEOG) and below the right and left eye (VEOG). Conductive gel was applied to maintain the contact between the electrodes and the scalp (Signa Gel, Parker Laboratories, Inc., Fairfield, NJ).

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

After processing using EMSE Suite software, time-frequency analysis was conducted using Matlab and the FieldTrip toolbox (Oostenveld, Fries, Maris, & Schoffelen, 2011). The data were segmented into 6-s periods centered on each stimulus presentation and convolved with a Morlet wavelet. The frequencies of interest extracted were 2–20 Hz, and each wavelet had a width of seven cycles.

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

EEG data were analyzed primarily by comparing pre-test alpha power versus post-test alpha power. Within the pre- and post-tests, two time periods of interest were defined—a pre-stimulus period, 1000 ms preceding the stimulus onset in each trial for each participant, and the stimulus processing period, 250–500 ms following the stimulus onset in each trial for each participant (Figure 3B). These two periods were defined post hoc based on the length of pre-stimulus fixation and on the average timing of alpha desynchronization (desynchronization, in this usage, describing a decrease in overall alpha power following stimulus presentation). Statistical tests to determine differences between the pre-test and post-test values within these periods were performed by calculating the mean power during the period of interest in the pre- and post-tests for each participant and conducting either repeated measures factorial ANOVA or paired-samples $t$ tests between those mean values, depending on the analysis of interest.

## Results

### Behavioral results

Behavioral results, in the form of orientation thresholds, response accuracy, and reaction times (RTs), all demonstrate classical evidence of PL. Orientation thresholds ($\theta$) decreased as a function of training (Figure 4; effect of day: $F[7, 56] = 5.88$, $p = 0.000038$, $\eta^2 = 0.42$) and a planned $t$ test between $\theta$ on
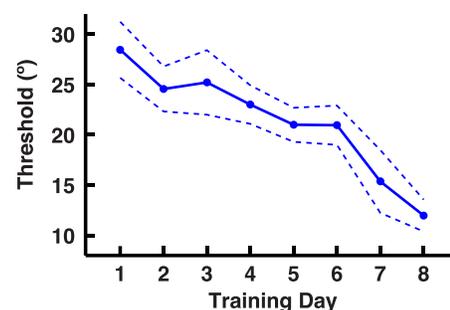


Figure 4. Orientation offset ($\theta$) threshold as a function of training day. Dashed lines denote ±1 SEM.
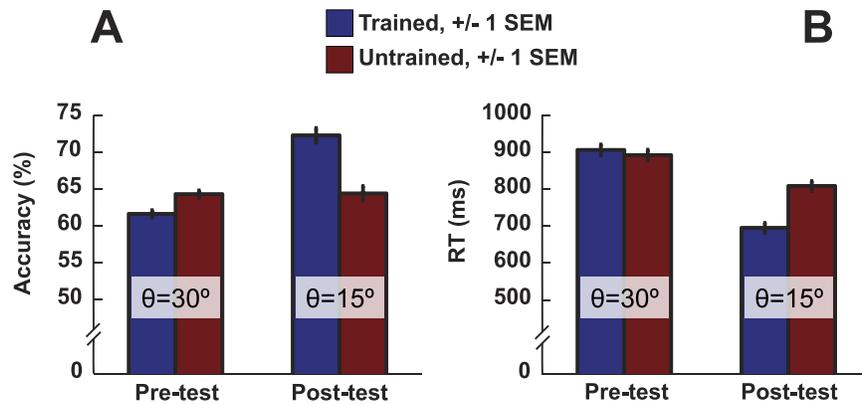
Figure 5. Accuracy (A) and RTs (B) for trained targets (blue bars) and untrained targets (red bars) during the pre-test and post-test. Error bars denote $\pm 1$ *SEM*. $\theta$ denotes the orientation offset, in degrees, between the target and the distractors in the pre- and post-test.
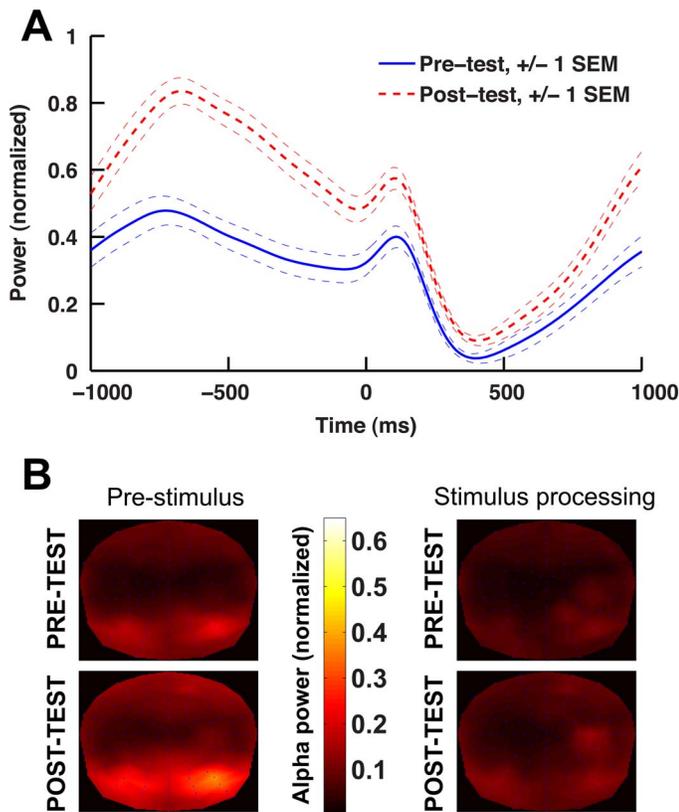


Figure 6. (A) Peristimulus period of normalized alpha power as a function of pre-test (thick solid blue line) and post-test (thick dashed red line) with all trial conditions contributing. Thin dashed lines denote $\pm 1$ *SEM*. (B) Scalp distributions showing normalized alpha power during the pre-stimulus period ($-1000$–0 ms) as a function of pre-test and post-test (left side) and normalized alpha power during the stimulus processing period (250–500 ms) as a function of pre-test and post-test (right side). Lighter regions denote more relative alpha power, darker regions denote less relative alpha power. Nose is up, left on left.

the first and last day of training (mean of 28.44° and 11.96°, respectively) revealed a significant learning effect, $t(14) = 5.59$, $p = 0.000067$, Cohen's $d = 2.98$. Accuracy improved overall as a function of training from the pre-test to the post-test (Figure 5A; main effect of test session: $F[1, 7] = 11.02$, $p = 0.013$, $\eta^2 = 0.18$); however, this was largely due to the greater increase in accuracy for trained targets as compared to untrained targets (Target × Session interaction: $F[1, 7] = 76.37$, $p = 0.0001$, $\eta^2 = 0.17$). Similarly, RTs show an overall decrease in latency as a function of training from the pre-test to the post-test (Figure 5B; main effect of test session: $F[1, 7] = 10.78$, $p = 0.013$, $\eta^2 = 0.13$), and also showed a significant interaction between trained/untrained targets and testing session, where the trained targets showed a greater decrease in RT than the untrained targets (Target × Session interaction: $F[1, 7] = 13.29$, $p = 0.0082$, $\eta^2 = 0.024$). These data show that learning is, at least in part, specific to the trained orientation.

## EEG data

To evaluate how alpha changed with PL, we analyzed alpha power across all trials of the pre- versus the post-test. Our first observation is that during the pre-stimulus period (1000 ms prior to stimulus onset; see Figure 3B), there is significantly more alpha power in the post-test than in the pre-test, $t(7) = 3.97$, $p = 0.0054$, Cohen's $d = 1.40$, mean normalized alpha power values of 0.67 and 0.39, respectively (Figure 6A). Topographic maps for the pre-stimulus periods in the pre- and post-test can be seen in Figure 6B. Lighter regions represent more alpha power and darker regions represent less alpha power.

Once the stimulus appears, there is a notable reduction of alpha (often referred to as alpha desynchronization) with a greater desynchronization of alpha
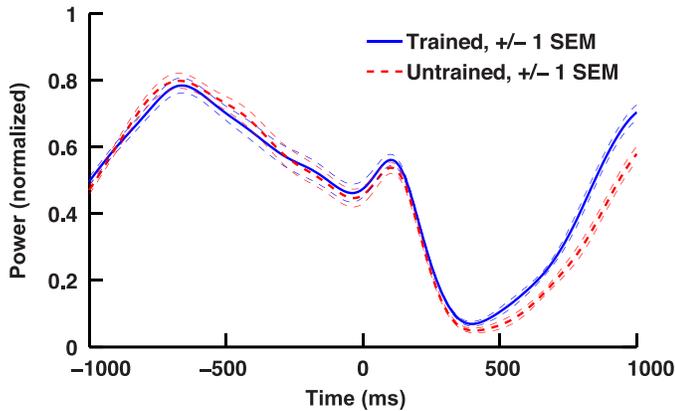
Figure 7. Peristimulus period of normalized alpha power as a function of trained targets (thick solid blue line) and untrained targets (thick dashed red line) within the post-test only. Thin dashed lines denote ±1 *SEM*. The pre-stimulus period is −1000–0 ms and the stimulus processing period is 250–500 ms.

in the post-test compared to in the pre-test. (Note here there are actually two phases of alpha desynchronization—one occurring around 500 ms before stimulus onset that corresponds with the onset of the fixation period and another at 0 ms when the stimulus array appeared. We refer to the post-stimulus desynchronization in subsequent usage.) Clarifying this effect, we examined whether the extent of alpha desynchronization (1000-ms pre-stimulus period minus stimulus processing period—250–500 ms) significantly differed between the pre-/post-test. Here a 2 (Test session) × 2 (Trial period) ANOVA showed a significant Session × Period interaction, $F(1, 7) = 13.36$, $p = 0.0081$, $\eta^2 = 0.044$, signifying that the amount of alpha desynchronization at the time of stimulus processing was greater after PL. Notably, alpha was also slightly, but significantly, greater during the stimulus processing period (250–500 ms after stimulus onset; see Figure 3B) in the post-test than in the pre-test, $t(7) = 2.53$, $p = 0.039$, Cohen's $d = 0.90$; mean normalized alpha power values of 0.13 and 0.066, respectively. Topographic maps for the stimulus processing periods of the pre- and post-test can be seen in Figure 6B.

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

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

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

## Discussion

Here we examined alpha power in EEG recordings and its relationship to PL. Behavioral results (Figures 4 and 5) show that PL occurred over the training period with improved orientation discrimination thresholds and superior accuracy and lower response latencies for the trained compared to the untrained target orientations. After training, EEG alpha power during the prestimulus period increased, and desynchronization

during the stimulus processing period also increased. However, while the change in alpha power with PL was dramatic and strongly significant, these changes did not appear to reflect a stimulus-specific component of learning in this task. We suggest that these results are consistent with the hypothesis of an increase of automaticity with learning, and that this increase is at least partially stimulus independent.

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

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

While it is natural to assume that changes in alpha should be related to task performance, there are a number of reasons to expect that direct correlations may not be in evidence. First off, there were only eight participants and numerous factors (differences in wakefulness, use of caffeine or other drugs, differences in impedance between the sessions, etc.) could impact how individual magnitudes of change of alpha may not be linearly related to changes in performance levels,

especially across sessions. There are also possible cognitive explanations that could have given rise to a lack of correlations. For example, if participants actively regulate (whether implicitly or explicitly) task-related resources, then changes in alpha power with training would reflect how much alpha power the system can tolerate during task performance. This would mean that accuracy, RT, or threshold would be kept relatively constant while alpha fluctuates, leading to no expected correlation. A lack of correlations of alpha power with performance and learning may be consistent with a subject's being able to regulate the amount of alpha that can be tolerated based upon their skill at the task. Further research will be required to substantiate this postulate, but in any event, the lack of correlations found between alpha power and performance is not evidence for or against our interpretation.

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

However, there is also the possibility the changes in alpha are epiphenomenal and are unrelated to PL. The issue of causality is one that is difficult to address, and in fact, even if significant correlations with behavior had

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

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

As a whole, our results enrich the current discussion in the literature regarding the mechanisms that underlie PL. Instead of the classic view that PL is a unitary process reflecting changes in processing in low-level perceptual areas (Fahle, 2004; Fiorentini & Berardi, 1980; Gilbert et al., 2001), the field is increasingly recognizing that PL involves plasticity in myriad brain processes related to the trained task and stimuli (Watanabe & Sasaki, 2015).

For example, PL has been observed in both early (Schoups et al., 2001) and late processing stages (Law & Gold, 2008) and can be at least partially explained by changes in decision processes (Dosher, Jeter, Liu, & Lu, 2013). In fact, small changes in training procedures can give rise to substantial changes in the behavioral characteristics of PL and likely the underlying distribution of learning across the brain (Hung & Seitz, 2014). Our results add to this literature and are consistent with models of PL that posit that attention is a contributing factor (Byers & Serences, 2012) and suggest that a component of transfer found in studies of PL may depend on an individual's brain state at the time of stimulus processing. While more research will be required to clarify the links between alpha EEG, automaticity, and PL, the present results suggest that alpha EEG is a useful window into an individual's level of attention during task performance and may help us better understand what is learned during PL.

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