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Electrophysiological markers of skill-related neuroplasticity

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ABSTRACT

Neuroplasticity involved in acquiring a new cognitive skill was investigated with standard time domain event-related potentials (ERPs) of scalp-recorded electroencephalographic (EEG) activity and frequency domain analysis of EEG oscillations looking at the event-related synchronization (ERS) and desynchronization (ERD) of neural activity. Electroencephalographic activity was recorded before and after practice, while participants performed alphabet addition (i.e., E + 3 = G, true or false?). Participant's performance became automated with practice through a switch in cognitive strategy from mentally counting-up in the alphabet to retrieving the answer from memory. Time domain analysis of the ERPs revealed a prominent positive peak at ~300 ms that was not reactive to problem attributes but was reduced with practice. A second prominent positive peak observed at ~500 ms was found to be larger after practice, mainly for problems presented with correct answers. Frequency domain spectral analyses yielded two distinct findings: (1) a frontal midline ERS of theta activity that was greater after practice, and (2) a beta band ERD that increased with problem difficulty before, but not after practice. Because the EEG oscillations were not phase locked to the stimulus, they were viewed as being independent of the time domain results. Consequently, use of time and frequency domain analyses provides a more comprehensive account of the underlying electrophysiological data than either method alone. When used in combination with a well-defined cognitive/behavioral paradigm, this approach serves to constrain the interpretations of EEG data and sets a new standard for studying the neuroplasticity involved in skill acquisition.

Response times (RTs) decrease and accuracy increases with practice across a wide range of tasks, from cigar rolling to memory retrieval (Crossman, 1959). In tasks where problem solving relies on a single cognitive strategy, the RT speed-up with practice can be characterized by a power function fitted with a single parameter (Newell and Rosenbloom, 1981). In tasks that can be solved by more than one cognitive strategy (Logan, 1988; Rickard, 1997, 1999), however, a power function is not always the best fit to these data (Heathcote et al., 2000).

From the early work of pioneers in the area of cognitive science (Bryan and Harter, 1899; Fitts, 1964) to modern theories of skill acquisition, RT speed-up and concomitant improvements in response accuracy has been described in terms of a progression through different stages of learning. While most theories provide accounts for various practice-related phenomena, they differ with respect to the stages of learning that underlie these effects. The adapted control of thought theory of skill acquisition (ACT; Anderson, 1983, 1992; Anderson et al., 2004) proposes a transition from a declarative "what" form of knowledge to a procedural "how to" form of knowledge. In the declarative stage, knowledge consists of facts that must be rehearsed, including situational characteristics and instructions. During practice, the learner develops task-specific procedures that do not require the active maintenance of declarative knowledge. Task performance is thought to be subsumed by a single strategy that improves continuously as these procedures are refined or tuned to a specific context. In contrast, the instance theory of automatization (Logan, 1988) and the component power-law theory of automatization (Rickard, 1997) suggest that the acquisition of some skills involves a strategic switch from one type of processing to another. Both of these theories suggest that initially, a multi-step algorithm is used to perform a task. With practice, direct links to memory are developed and eventually, asymptotic performance is attained primarily through a memory retrieval process. Both Logan and Rickard take the position that there is no memory representation initially and that the longer algorithm determines the perfor-

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mance. As the memory representation strengthens with practice, both theories speculate that performance relies mainly on the faster memory retrieval process. The purpose of the present study is to investigate the changes in EEG associated with learning a new cognitive skill.

Pseudo-arithmetic tasks are well suited for assessing skill acquisition because they allow for the study of a new cognitive skill that participants have had no prior knowledge of, or experience in performing. These paradigms are also used because much is known about the cognitive processing necessary for performance, and this allows for certainty regarding which processes are affected by specific experimental manipulations. In one such pseudo-arithmetic task, known as alphabet addition, participants are challenged with learning a new cognitive skill similar to simple addition. With alphabet addition, instead of presenting typical arithmetic problems that ask participants to add two numbers (e.g., 5 + 5 = ?), participants are presented with a problem such as L + 7 = ? To arrive at the correct answer "S", one needs to count up seven letters in the alphabet, starting from the letter "L". As mentioned previously, studies have shown that this task can become automated with practice, such that RTs decrease and accuracy increases (e.g., Logan, 1988; Rickard, 1997). Similar to when a child is first learning the solution to 5 + 5, improvements in performance have been demonstrated to be a product of participant's shift from using a problem-solving algorithm (mental counting) to relying on the retrieval of the answer from memory (e.g., Logan, 1988; Logan and Klapp, 1991; Rickard, 1997).

This shift from a counting strategy to a memory retrieval strategy represents a qualitative change in cognitive processing. Based on previous research we hypothesize that skill-related changes in cognitive strategy should be detectable in electrophysiological activity recorded from the scalp; either from averaged event-related potentials (ERPs) or assessing changes in the oscillatory dynamics of electroencephalogram (EEG) activity at various frequencies. Consider the fact that while these two approaches have properties in common, they are fundamentally different in terms of how they can potentially extract the electrophysiological correlates of cognitive events. The approach that uses averaged ERPs falls under the rubric of the additive model. With this model, linear signal averaging in the time domain is used to improve signal-to-noise ratio and extract the response over trials. With this approach, only EEG activity that is phase locked to the stimulus is extracted from the background; all other neural activity is considered random noise and is eliminated from the average by phase cancellation. Nevertheless, ERPs are valuable in studying sensory and cognitive events because they are non-invasive, have excellent temporal resolution, can be measured during the actual presentation of the stimuli, and provide a record of cognitive processing based on post-synaptic activation of populations of neurons in the cerebral cortex (Garnsey, 1993; Coles and Rugg, 1994). These EEG measures are in contrast to imaging techniques such as functional magnetic resonance imaging (*f*MRI) and positron emission tomography (PET) that have good spatial but poorer temporal resolution, because they are based on a hemodynamic response with inherent delays in the range of hundreds of milliseconds to seconds.

1. Dynamic changes in EEG rhymicities: assessment of locked and unlocked activity

Because the dynamic underpinnings of event-related changes in brain activity are inherently complex, other sophisticated analysis paradigms are required to provide a more comprehensive account of the underlying neural activity (e.g., Pfurtscheller and Lopes da Silva, 1999). Accordingly, stimulus or cognitive related changes in EEG oscillations can be quantified as event-related synchronizations (ERSs; increases in EEG power) and event-related desynchronizations (ERDs; decreases in EEG power) at specific frequencies. Event-related synchronizations and ERDs are quantified in the frequency domain by spectral analysis and custom-designed signal processing algorithms. These types of data are not captured by signal averaging in the time domain (i.e., standard ERP analysis) because they are oscillatory in nature and do not have a fixed phase.

Moreover, it is also known that there is EEG activity that is reactive to the stimulus but not phase locked to the event. This type of neural activity has been termed induced, emergent, or unlocked (Başar and Bullock, 1992; Ohl et al., 2003; Kalcher and Pfurtscheller, 1995; McFarland and Cacace, 2004). Başar and Bullock (1992) and Cacace and McFarland (2007) have suggested that event-related changes in the unlocked component are a rich source of brain activity that has virtually gone untapped in many previous investigations. Kalcher and Pfurtscheller (1995) showed that by subtracting the averaged time-domain ERP (i.e., the composite average) from individual trials prior to spectral analysis, it was possible to distinguish time-locked and unlocked neural activity. McFarland and Cacace (2004) confirmed and extended this approach by using a moving regression analysis prior to subtraction, which allows for a better account of amplitude and phase jitter on individual trials. Thus, the contention of the present study is that using both time and frequency domain analyses allow for a more comprehensive account of stimulus-related changes in EEG activity during cognitive processing.

There have been relatively few studies documenting electrophysiological markers associated with strategy shifts during skill acquisition. Pauli et al. (1994) examined the relationship between averaged ERPs and practice using simple multiplication (e.g., 4×7 = ?). In this study, participants were trained over a period of four sessions and ERPs were measured during each session. The initial ERP demonstrated a fronto-central positivity at ~300 ms after stimulus onset. Following training, this response diminished and was replaced by a more focused positivity centered over centro-parietal regions. The authors suggest that the 300 ms frontal–central positivity reflects frontal lobe processing during the acquisition stage of skill learning. A shift to a more parietal focus with practice was interpreted as the neural correlate of automatization (Pauli et al., 1994). Smith et al. (1999) compared practice-related changes in EEG oscillations between a verbal working memory task, a spatial working memory task, and a video game task. The results showed greater practice-related EEG synchronization in a posterior fast alpha band for the verbal memory tasks, but not the other two tasks. Alpha synchronizations are thought to be intermittent idling rhythms between drowsiness and intense alertness, and therefore provide evidence for differing levels of alertness associated with different practice-related neurocognitive strategies being manifest between the verbal and spatial tasks. Smith et al. (1999) also found greater practice-related EEG synchronizations in the theta frequency band. These theta-related changes were found over middle frontal regions with all tasks and were interpreted as indicating increased concentration with practice (also see Fairclough et al., 2005, for a similar finding).

In general, available studies have either evaluated practice-related changes in averaged ERPs (Pauli et al., 1994) or practice-related changes in EEG oscillations (Fairclough et al., 2005; Gevins et al., 1997; Smith et al., 1999). To our knowledge, no study has combined both types of EEG analyses nor have they evaluated the locked and unlocked components during skill acquisition. Furthermore, it is also the case that previous studies have used tasks that were already known to the participants (simple arithmetic) or where little was known about the neurocognitive strategies involved. The present investigation sought to improve and expand on these earlier observations by using an alphabet-addition task and by analyzing the electrophysiologic data in both the time and frequency domains for both locked and unlocked EEG activity. Therefore, one contention of the present study is that when investigating neuroplasticity due to cognitive skill acquisition, having a novel well-understood behavioral paradigm is an imperative core issue in helping to constrain the interpretations of the electrophysiological data. A second contention is that the combination the two different types of analysis of scalp-recorded electrical signals (i.e., the analysis of ERPs and the analysis of EEG oscillations) provide for a more comprehensive understanding of the underlying brain processes.

2. Method

2.1. Participants

Ten undergraduate students from Union College (five males, five females ranging in age from 19 to 22 years) participated in this study. None of the individuals reported a history of medical or neurological problems and all reported normal visual acuity. Some individuals were paid forty dollars for their participation, while others volunteered for the experiment in order to obtain out-of-class credit for an introductory psychology course. In the latter case, participants were compensated with 2 h of credit and were paid twenty dollars. The Institutional Review Boards (IRBs) of Albany Medical College and Union College approved this study. All participants provided signed informed consent.

2.2. Task and materials

The alphabet-addition task was designed within a verification format. That is, participants were presented with equations of the form *letter* + *number* = *letter* and their task was to indicate whether the given answer was correct or incorrect by responding either true or false for a given problem. For example, in the equation A + 2 = C, the correct response was true; whereas in the equation A + 2 = E, the correct response was false.

Electrophysiological recordings were made on two separate sessions while participants performed the alphabet-addition task. During the first EEG recording session, the participants were naïve with respect to the task; the second EEG recording session followed 6 days of practice with the alphabet-addition task. Stimuli consisted of a total of 40 problems, presented 4 times each across 4 blocks in EEG session. The 40 problems were equally divided across difficulty. Two presentations of the problem were with a true answer and two presentations included one of two possible false answers. In the practice sessions (days 1–6), participants were presented with the same 160 problems, 4 times over a total of 16 blocks per day (totaling 96 blocks of practice). Based on previous research with the alphabet-addition task (Logan and Klapp, 1991; Zbrodoff, 1995), problem difficulty was defined by the size of the number addend. Specifically, large addends (i.e., where the number addend was between 6 and 9) were defined as difficult; addends of 4–5 were defined as medium difficulty, and addends of 1–3 were defined as easy. In this context, a difficult problem would be F + 8 = N, a medium difficulty problem be S + 6 = Y, and an easy problem would be K + 3 = N. Each of the 40 problems was presented twice with an incorrect answer being either one letter or five letters away from the true answer and roughly balanced with regard to whether the presented (false) answer was above or below the correct answer in the alphabet. If the incorrect answer for the 1 away instance were up 1 character in the alphabet, then the incorrect answer for the 5 away instance would be down 5 characters in the alphabet. Conversely, if the incorrect answer for the 1 away instance of the problem were down 1 character in the alphabet from the correct answer, then the incorrect answer for the 5 away instance would be up 5 characters in the alphabet. For example, given the problem H + 7 = O, the two incorrect answers that were derived were H + 7 = P and H + 7 = J.

2.3. Procedure

Electroencephalographic (EEG) activity was recorded from 17 electrodes sampling areas from central, left and right frontal, temporal, and occipital regions on the scalp (F3, F4, F7, F8, C3, C4, P3, P4, T3, T4, T5, T6, O1, O2, Fz, Cz, Pz), based on the 10–20 system of the International Federation (Jasper, 1958). For ease of application, an electrode cap was used (Quick Cap, NeuroMedical Supplies). Individual channels of EEG were referenced to linked mastoids and the left forearm served as ground. Two additional bipolar channels were used to monitor vertical and horizontal electro-ocular (EOC) activity. The vertical EOC channel had electrodes placed over the superior and inferior orbicularis occuli muscles and was used to detect eye blinks; the horizontal EOC channel had electrodes placed over the outer canthus of each eye and was used to detect low frequency lateral eye movements. Raw EEG activity was collected and stored in digital form on a trial-by-trial basis using commercially available hardware and software configurations (SCAN and STIM systems, NeuroScan, El Paso, TX, USA). Signal processing (spectral analysis, time domain averaging, generation of scalp topographies, etc.) was performed off-line on raw epoched data.

During EEG data collection, individuals were tested in a lighted, sound attenuated test booth (Tracoustics, RE 145) and were seated on a padded reclining chair having head, leg, and arm support. Participants were instructed to focus on a computer screen that was situated approximately one meter to the front and center of the individual. The computer screen was positioned atop an adjustable table that could be raised or lowered to accommodate the participant's height. Participants were also advised to minimize any unnecessary eye movements or muscle contractions during testing.

Electroencephalographic activity was recorded over a 2000 ms time epoch (1000 ms pre-stimulus silent baseline interval; 1000 ms post-stimulus response interval), amplified $\times$20,000, filtered between 0.1 and 300 Hz (12 dB/octave slope) using a Grass model 12 NeuroData acquisition system, and digitized at a rate of 1000 Hz with 16 bit resolution. Triggering for EEG data acquisition, control of analog-to-digital conversion, and stimulus presentation was performed by the aforementioned STIM and SCAN systems. Individual trials of EEG that exceeded 50 μV were rejected as artifacts and not included in the data analysis.

The experimental task consisted of presenting alphabet-addition problems visually on a computer monitor situated directly in front of the individual using the StimGen software provided with the NeuroScan instrumentation. Stimuli were presented at eye level and centered on the computer screen using a 3-cm text size and an Arial type font. Individuals were instructed to respond as quickly and accurately as possible to each individual stimulus presentation by pressing a button on a response device (STIM system response pad, P/N 1141) situated on the right side of the participant and positioned on the arm of the chair. This response selection device provided a mechanism to measure RT and to record the accuracy of the response. For each trial and for every individual, RT and performance data were saved in a computer file for off-line analysis. Response time in milliseconds (ms) was measured from the onset of the stimulus presentation to the time of button press selection indicating a true or false answer. Participants were not given feedback regarding the correctness of their response. Each problem remained visible on the computer screen until the participant responded. An interstimulus interval of 3000 ms was used, during which time a simple cross-appeared on the center of the screen. The cross on the computer screen was included as a visual cue to minimize eye movement contamination during testing.

2.3.1. Practice sessions

All individuals took part in 6 practice sessions between the two EEG recording sessions. The first practice session was on day one and was performed after the first EEG recording. Consecutive practice sessions 2–6 were carried out on days 2–6, prior to the final EEG recording on day seven of the study. These practice sessions were performed in a different room than that used for the EEG recording. Participants were seated in front of a desktop computer and were run through a separate practice program controlled by commercially available software used in psychological research (E-Prime, Psychology Software Tools, www.pstnet.com). The E-Prime software was programmed to present alphabet-addition problems one at a time on the center of the computer screen. Similar to the EEG recording, participants were instructed to respond to the alphabet-addition problem as quickly and as accurately as possible by pressing a button on a keyboard that indicated their response (either true or false). All problems remained visible on the computer screen until the participant responded. Again, participants were not given feedback regarding the correctness of their response.

Additionally, during the practice sessions, the participants were prompted to report the cognitive strategy that they used immediately after responding to a true/false problem. These "strategy probes" occurred randomly after one quarter of the trials (i.e., 10 in each block) and were accomplished by having individuals press one of three buttons. Button 1 was used to indicate counting-up in the alphabet, button 2 was used to indicate retrieval of the correct answer from memory, and button 3 was used to indicate that they did something other than counting or memory retrieval (e.g., guessing). This technique has been demonstrated to be a valid and reliable way to assess processing strategies in previous studies using the alphabet-addition task (e.g., Rickard, 1997).

2.3.2. Time domain analysis of EEG activity

The data were first smoothed with a 10 point running average. Effects of eye movements were then eliminated by computing the regression of the two eye movement channels on each EEG channel and then removing the regressed effect (Croft et al., 2005). Since earlier components generally have shorter time-courses, averages for topographies were computed at 50 ms intervals for the first 200 ms and 100 ms intervals thereafter.

2.3.3. Spectral analysis of EEG activity

To assess for underlying changes in EEG oscillations, each 1000 ms segment of data (pre-stimulus baseline or post-stimulus interval) was detrended by removing the mean and linear component. Autoregressive spectral analysis (maximum entropy method, 40th order Berg model) was used to quantify the frequency composition of each pre- and post-stimulus epoch over the bandwidth from 1.0 to 80.0 Hz (Marple, 1987). By comparing pre-stimulus baseline vs. stimulus-related intervals, event-related changes in EEG spectra were ascertained. Event-related synchronizations, and ERDs were assessed by computing Pearson's product moment correlations (Pearson's r) for each 3 Hz spectral bin for all alphabet-addition conditions. In this computation, the stimulus condition was a dummy variable with 0 representing the baseline and 1 representing the stimulus interval. The Pearson's r statistic was selected because correlation coefficients represent a normalized difference metric that is signed (i.e., the coefficients had both positive and negative values). Positive correlations represent synchronization of EEG activity and negative correlations represent desynchronization of EEG at various frequencies. Given the properties of the Pearson's r, the magnitudes of this measure range from 0 (no correlation) to ± 1 (where +1 represents the greatest synchronization value; -1 represents the greatest desynchronization value). In the figures event-related synchronizations and ERDs were plotted as spectra (Pearson's r vs. frequency) at specific electrode locations and as topographic maps for specific frequencies, to allow for the spatial distribution of the correlation indices to be evaluated in a comprehensive manner.

Different authors have divided the EEG spectrum into bands according to varying criterion. For example, Mantini et al. (2007) defined theta as 4–8 Hz activity while Freeman (2006) defined it as 3–7 Hz activity. Generally higher frequency bands such as gamma are afforded much broader ranges. These divisions are somewhat arbitrary however, and the identification of frequency ranges at which functional effects occur should have priority. Accordingly we examined the lower frequency range into 3 Hz wide bins and the higher frequency ranges into 6 Hz bins.

3. Results

3.1. Behavioral data

The data are summarized in two sections: section one provides an analysis from the practice sessions and section two provides an analysis from the EEG recordings. With respect to the behavioral data, changes in RT, accuracy, and strategy showed clear effects of practice (Fig. 1a–c). As mentioned previously, RT speed-up with practice is well characterized by a power function. In log–log coordinates the power function becomes a linear function, which allows for easier assessment of deviations from a power function (Newell and Rosenbloom, 1981). In Fig. 1a, there was a monotonic relationship between RT and practice, when data were plotted on log–log coordinates. Based on regression analysis and confirmed by the proportion reduction of error observed [PRE(1,94) = 0.64, $p < 0.001$; Judd and McClelland, 1989], a quadratic regression model ($r^2 = 0.97$) produced a better fit to the data than a linear regression ($r^2 = 0.91$). Higher order polynomials did not improve the fit. These findings are similar to those reported by Rickard (1997) for the alphabet-addition task. Rickard (1997) interpreted the deviation from linearity to be a function of the strategy shift from counting-up in the alphabet to direct retrieval of the answer from memory. As shown in Fig. 1b, the proportion of correct responses increased reliably across practice blocks ($r^2 = 0.34$, $p < 0.001$). Furthermore, when data were analyzed by strategy (Fig. 1c), the proportion of trials that participants reported counting-up in the alphabet decreased with practice ($r^2 = 0.83$), while the proportion of trials that participants reported using memory retrieval increased with practice ($r^2 = 0.87$).

Response times and accuracy during EEG recordings were analyzed by two separate $2 \times 3 \times 2$ repeated measures analyses-of-variance (ANOVA), using session (pre- or post-practice), level-of-difficulty (easy, medium, or difficult), and answer type (true or false) as factors. Logarithmic transformations (base_{10}) of RTs were performed to normalize the distributions and reduce any effects of outliers. All RT means for this analysis were reported as anti-logs of the mean logarithmic values. There were no significant findings in the analysis of participants' proportion correct responses (accuracy). Overall, participants were slower to respond during the pre-practice EEG recording (mean = 3802 ms) than in the post-practice recording (mean = 1413 ms), $F(1,9) = 56.43$, $p < 0.01$. RTs also increased monotonically across easy, medium, and difficult

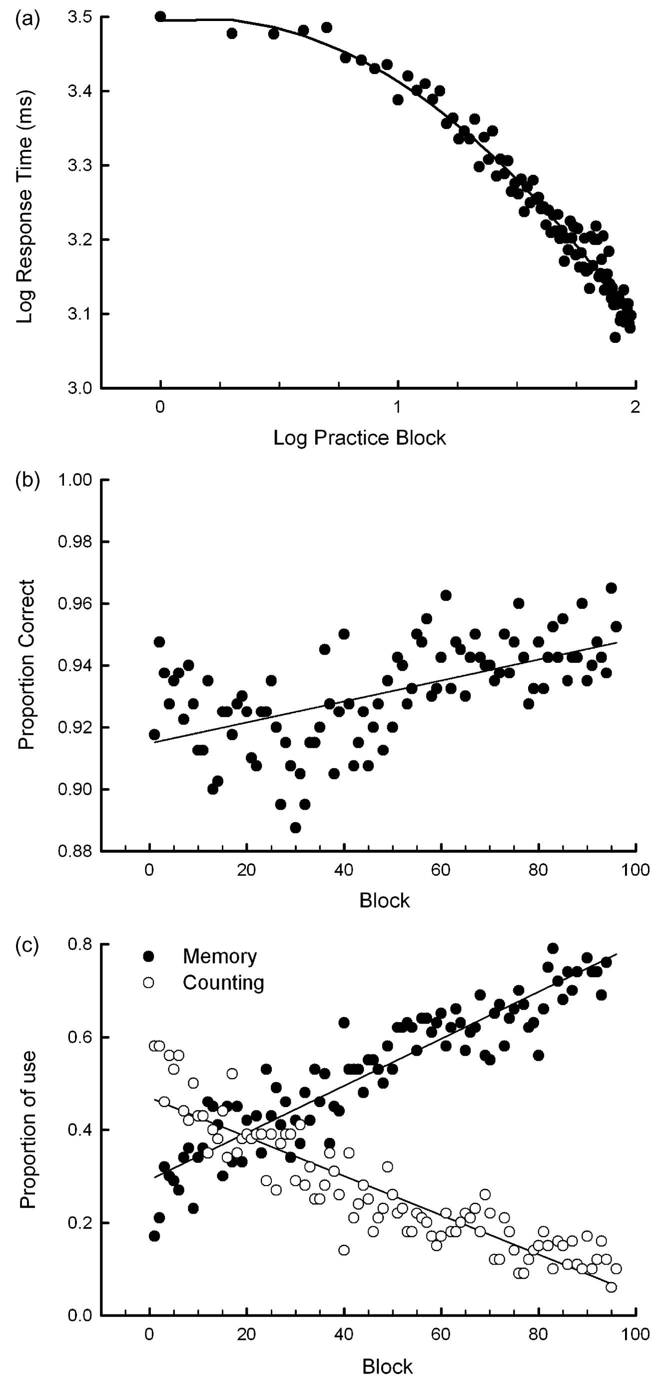

Fig. 1. (a) The relationship between RT and practice (filled circles) on the alphabet arithmetic task, when data were plotted on log–log coordinates. The y-axis depicts logarithm (base_{10}) RTs for correct trials; x-axis is represents the logarithm (base_{10}) of practice block. (b) The average proportion of correct responses (y-axis) as a function of practice block (x-axis). (c) The average proportion of trials in each block that either cognitive strategy is used (y-axis) as a function of practice block (x-axis).

problems ($M = 1820$ ms, $M = 2344$ ms, and $M = 2951$ ms for easy, medium, and difficult problems, respectively), $F(1,9) = 48.77$, $p < 0.01$. Similarly, participants were faster overall to respond to true ($M = 776$ ms) than false problems ($M = 2291$ ms), $F(1,9) = 5.1$, $p = 0.05$. These findings are further qualified by two interactions involving the session variable. The first was a two-way interaction between session and difficulty such that the increase in RTs across levels-of-difficulty was greater in the pre-practice EEG than in the post-practice EEG recording session, $F(2,18) = 22.11$, $p < 0.01$

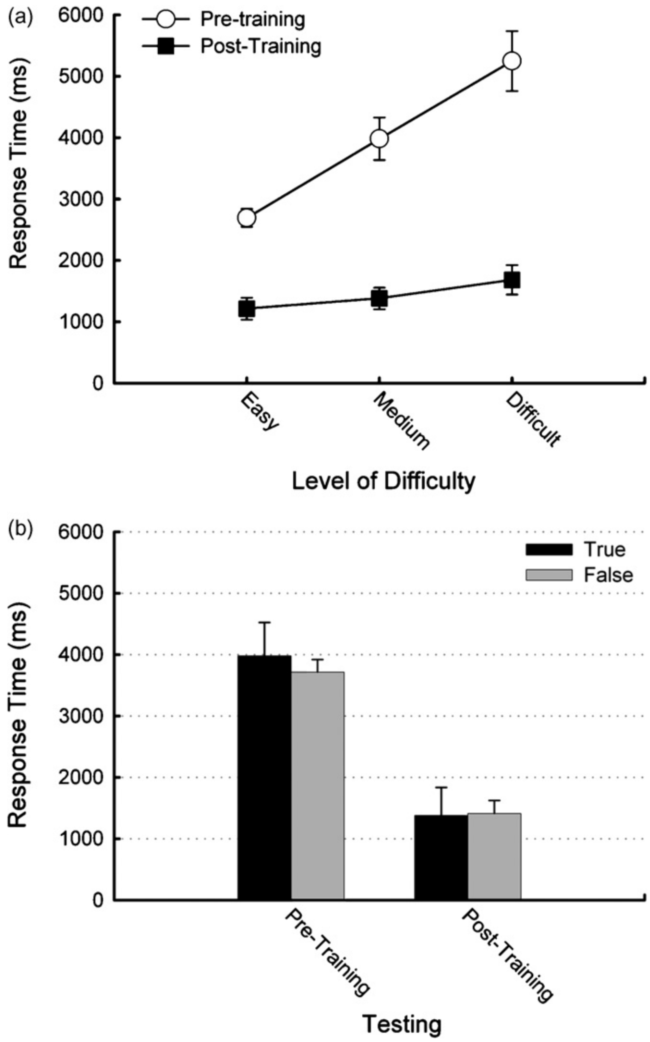

Fig. 2. (a) Line graph depicting average differences in RTs (*y*-axis) as a function difficulty (*x*-axis) for pre- and post-practice sessions. (b) Bar graphs showing average response times (*y*-axis), for true and false problems in the pre- and post-practice EEG session (*x*-axis). Error bars depict standard error of the means for each condition.

(Fig. 2a). The second two-way interaction (Fig. 2b) was a effect between session and problem type, such that the RT difference between true and false problems was only found in the pre-practice EEG recording but not in the post-practice recording, $F(1,9) = 5.3$, $p = 0.05$. These two interactions suggested that attributes of the problems that make them more difficult when performance relied on the counting strategy were not factors once the participants switched to the memory retrieval strategy.

3.2. Electrophysiological data

3.2.1. Event-related potential (ERP) analysis

A $2 \times 3 \times 17 \times 15 \times 2$ repeated measures ANOVA was performed on the amplitude of the ERP, with session (pre- or post-practice), level-of-difficulty (easy, medium, or difficult), electrode location (17 locations), time (0, 50, 101, 152, 203, 300, 351, 402, 453, 500, 601, 703, 800, 902, and 996 ms), and problem type (true or false) used as factors Effect sizes are reported as proportion of explained variance (partial eta squared [η^2]).

Main effects are not reported because there were significant interactions among all variables: session × time × channel $F(210,1890) = 2.58$, $p < 0.01$, $\eta^2 = 0.223$); session × time × problem type $F(14,126) = 2.54$, $p < 0.01$, $\eta^2 = 0.220$; session × channel × problem type $F(15,270) = 2.05$, $p < 0.01$, $\eta^2 = 0.186$; level-of-difficulty × time × channel $F(420,3780) = 1.27$, $p < 0.01$, $\eta^2 = 0.124$; level-of-difficulty × time × problem type $F(28,252) = 1.67$, $p < 0.02$, $\eta^2 = 0.157$; session × level-of-difficulty × time × problem type $F(28,252) = 1.64$, $p < 0.02$, $\eta^2 = 0.154$; and session × time × channel × problem type $F(210, 1890) = 1.42$, $p < 0.01$, $\eta^2 = 0.136$. To determine the temporal locus of this latter four-way interaction, separate four-way ANOVAs at each time point were performed. These analyses resulted in significant session × channel × problem type interactions at six time points: 300 ms, $F(15,135) = 2.07$, $p < 0.01$; 453 ms, $F(15,135) = 1.99$, $p < 0.02$; 500 ms, $F(15,135) = 2.96$, $p < 0.01$; 601 ms, $F(15,135) = 2.69$, $p < 0.01$; 902 ms, $F = (15,135)$ 1.88, $p < 0.01$, and 996 ms, $F(15,135) = 2.44$, $p < 0.01$. As seen in Fig. 3a, these significant three-way interactions correspond to a positive peak at 300 ms and a second peak at 500.

Scalp topographies for pre- vs. post-training and true vs. false problems are presented in Fig. 3b at 300 ms and 500 ms, respectively. Based on the spatial distribution of the voltages, the positive 300 ms peak had a distinct focus in right anterior central regions that was largest in both pre-training true and false problems (Fig. 3b). In contrast, the positive 500 ms peak showed problem specific scalp distributions demonstrated by a distinct focus mainly over central regions for the post-training true problems. Thus, the early 300 ms peak was found to be prominent prior to training and was *not* problem specific; while the later 500 ms peak was enhanced by training and *was* problem specific.

3.2.2. EEG oscillations

The data were next analyzed for spectral content by means of a 40th order autoregressive model (see Cacace and McFarland, 2003 for details). For the initial analysis, spectra were computed separately for the pre-stimulus baseline and post-stimulus interval. These data were then analyzed with a six-way $8 \times 2 \times 3 \times 17 \times 2 \times 2$ ANOVA using frequency (3 Hz, 6 Hz, 9 Hz, 12 Hz, 15 Hz, 18 Hz, 21 Hz, or 24 Hz, in 3 Hz wide bins), session (pre- vs. post-training), level-of-difficulty (easy, medium, or difficult), electrode location, presence of stimulus (baseline vs. post-stimulus), and problem type (true vs. false), as repeated measures. Effect sizes are reported as proportion of explained variance (partial eta squared [η^2]). Although the resulting analysis involved 61 main effects and interactions, we restricted consideration to effects involving interactions including session, frequency, and stimulus, since these were factors of interest. The interaction of session × frequen-frequency × channel × stimulus × problem type was highly significant $F(112,1008) = 1.96$, $p < 0.01$, $\eta^2 = 0.179$. Subsequent analysis of "simple" interactions at each level of frequency indicated that the session × channel × stimulus × problem type interaction was significant for the 3 Hz (theta) frequency. This effect is illustrated in Fig. 4, which shows the correlation topographies between the pre-stimulus baseline vs. the post-stimulus interval. As can be seen in this figure, there is a frontal–central focus in the theta synchronization to stimulus presentation. According to traditional nomenclature this effect is at the border of the theta and delta bands, but is referred to as theta throughout because of the somewhat arbitrary nature of the traditional labels. Of most importance this synchronization was greatest in the post-training recording, but was particularly weak for the pre-training false problems.

In order to gain additional insight to the nature of the post-stimulus theta effect, we removed the phase-locked component and focused on unlocked EEG activity (see McFarland and Cacace, 2004). Interactions involving training, EEG frequency, and stimulus were observed for both the raw data and for the data with the time-locked component removed. Of particular interest was the fact that

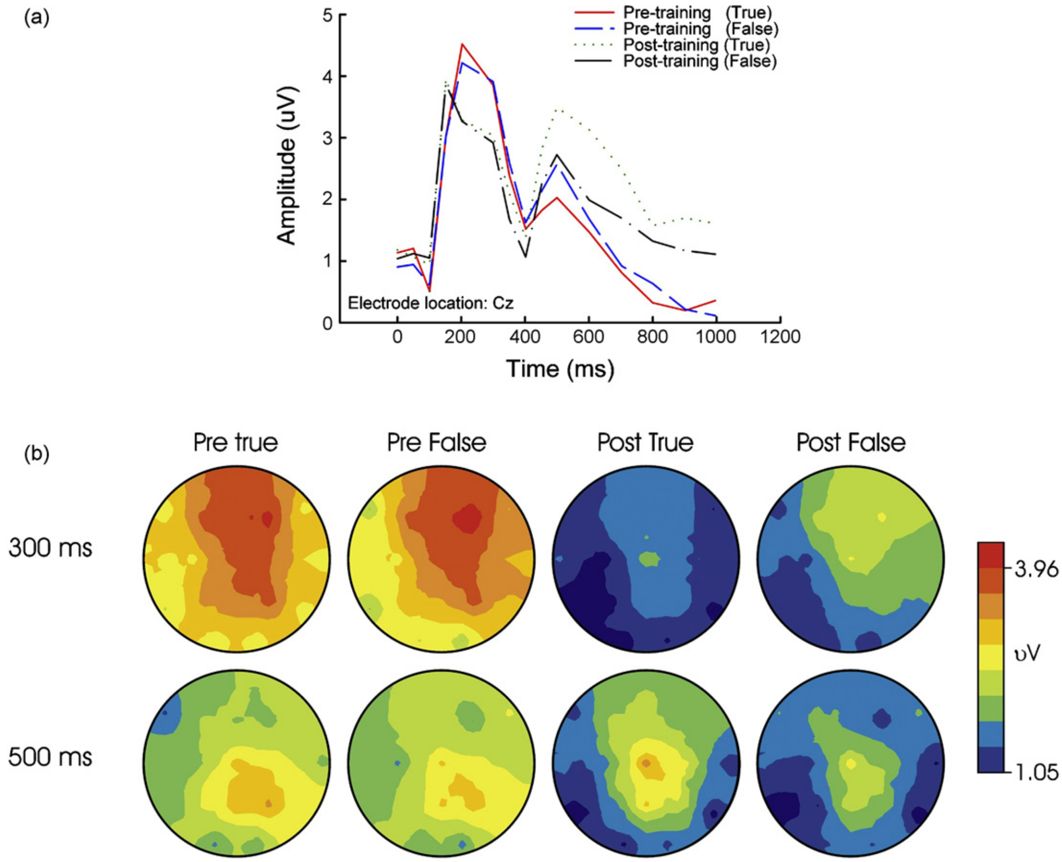

Fig. 3. (a) Example of the time-domain ERP waveform at the Cz electrode location for true and false problems, pre- and post-training. (b) Topographies of the time-domain ERP at 300 ms and 500 ms post-stimulus. Separate topographies are shown for true and false problems, pre- and post-training.

removing the time-locked component had very little effect on the overall pattern of significant effects, indicating that stimulus-induced theta oscillations were largely unlocked in nature (see Fig. 5).

Higher frequency spectra (25–49 Hz) were analyzed next, in four 6 Hz wide bins. Again we focused only on effects of session, EEG frequency, level-of-difficulty, and problem type. The interactions between session × frequency × problem type $F(3,27) = 3.22$,

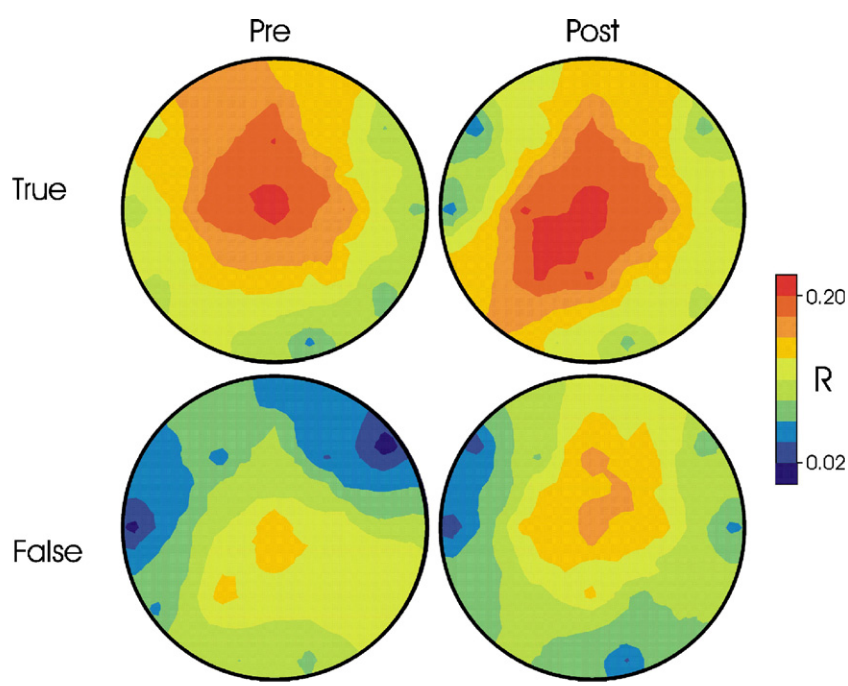

Fig. 4. Correlation topographies of Pearson's r (baseline vs. stimulus periods) for the 3 Hz (theta) bin. Separate topographies are presented for true and false problems pre- and post-training.

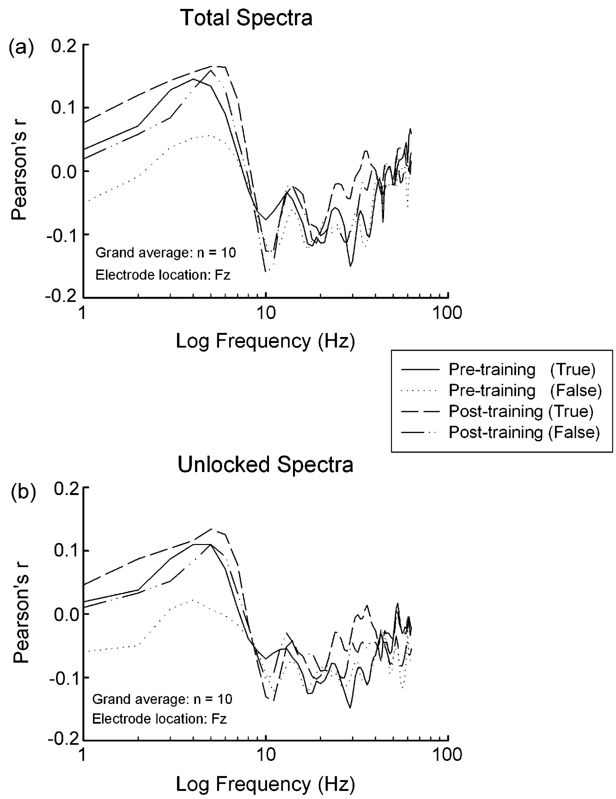

Fig. 5. (a) Spectra of Pearson's *r* (baseline vs. stimulus periods) at Fz for true and false problems pre- and post-training. (b) Spectra of Pearson's *r* (baseline vs. stimulus periods), corrected for the contribution of time-locked activity, at Fz for true and false problems pre- and post-training.

$p < 0.03$, $\eta^2 = 0.263$ and session × level-of-difficulty × frequency × channel × problem type, $F(96,864) = 1.72$, $p < 0.01$, $\eta^2 = 0.127$, were significant. The five-way interaction was evaluated by assessing the four-way interaction at each 6 Hz frequency bin. This session × level-of-difficulty × channel × problem type interaction was only significant at two bins: 28.5 Hz, $F(32,288) = 2.18$, $p < 0.01$ and 34.5 Hz, $F(32,288) = 1.76$, $p < 0.01$, but not at 40.5 Hz or 46.5 Hz. These effects are illustrated by the correlation topographies shown in Fig. 6 for the 28.5 Hz (beta band) response. As shown in Fig. 6, there is a beta band ERD over left central areas that increased with task difficulty in the pre-training data. Following 6 days of practice, this effect was clearly diminished.

4. Discussion

The behavioral results presented herein constitute direct replications of earlier studies with the alphabet-addition task (Logan, 1988; Rickard, 1997). These findings demonstrate that participants became more skilled at the alphabet-addition task by responding faster and more accurately after practice. Furthermore, the data on strategy probing (Fig. 1c) and the non-linearity in the power function fits support earlier findings, indicating that gains in performance were due to a shift in strategy from counting-up in the alphabet to retrieval of the correct answer from memory. Also consistent with previous findings with the alphabet-addition task (i.e., Logan and Klapp, 1991) and the findings of Pauli et al. (1994) was the two-way interaction between level-of-difficulty and session (Fig. 2a). Whereas RTs increased monotonically with task difficulty before practice, this trend was not observed after practice. For example, when using the counting strategy the problem A + 3 was less difficult than the problem A + 9 because it takes longer to count up nine places in the alphabet than to count up 3 places. In contrast, when participants were able to retrieve the answer from memory, there was no difference between these two problems. The other two-way interaction between problem type and session has not been reported before, but can be reconciled in a similar fashion. Participants responded faster in the pre-practice session to false problems than to true problems. Although this seems paradoxical, it is probably due to the fact that half of the false answers were 5 letters away (either alphabetically before or after) from the correct answer in the alphabet. Thus, when participants were using a counting-up strategy (at the beginning of

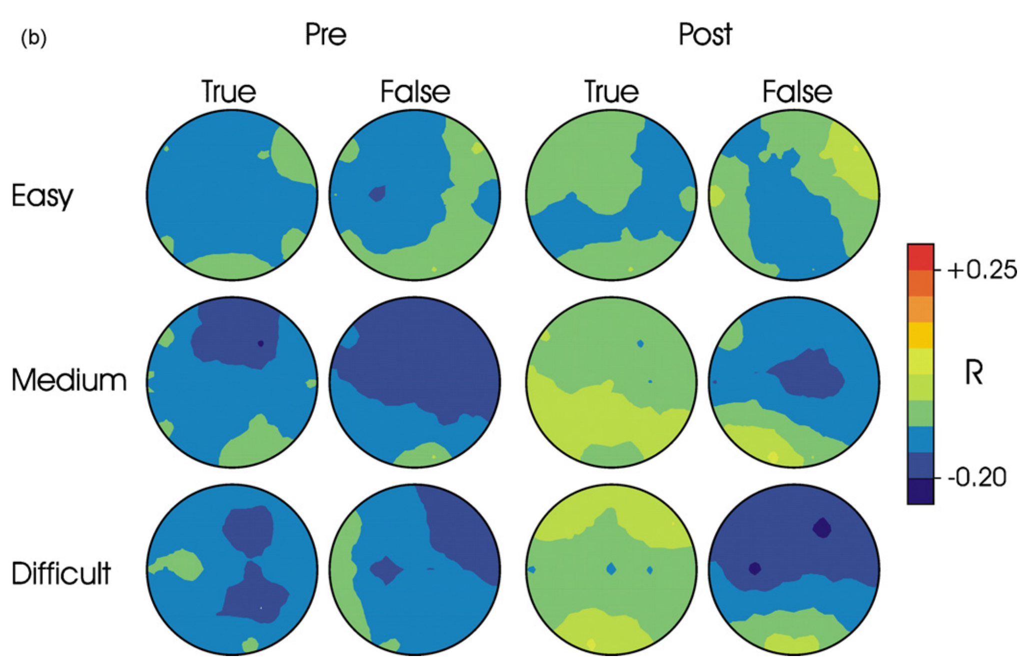

Fig. 6. Correlation topographies of Pearson's *r* (baseline vs. stimulus period) for the 28 Hz bin. Separate topographies are presented for easy, medium, and difficult problems pre- and post-training.

practice), they were able to dismiss answers that were far away from the correct answer more quickly (i.e., before they have actually finished counting-up in the alphabet). After practice, however (i.e., when participants are relying on memory retrieval), this attribute of the problem set had no effect on memory processing. Similar findings have been reported in multiplication verification tasks (e.g., Romero et al., 2006). In both cases, these interactions suggest that factors that affect the execution of the counting strategy do not affect performance once participants rely on memory retrieval. Although the bulk of the behavioral findings are not new, they were noteworthy because they served to constrain the interpretation of the connections between the electrophysiological results and the cognitive processing.

4.1. Event-related potential analysis

The results of the time-domain ERP analyses were consistent with and also extended previous findings of Pauli et al. (1994). First, similar to Pauli et al. (1994), the ERPs from the present study showed a positive peak at ~300 ms that was reduced with practice. Also similar to the previous study: the spatial distribution of this activity was focused over right fronto-central scalp locations. Pauli and colleagues interpreted the reduction in frontal positivity with practice as an indication of reduced working memory resources associated with automatization of the task. Similarly, in the present data there were no effects of stimulus manipulations (problem type or level-of-difficulty) on this peak, suggesting that it is probably associated with a more generalized process necessary for solving all problems. The interpretation that the 300 ms positive peak was due to increased attention or working memory processing in the pre-practice recording session was consistent with reports that participants used counting-up as the predominant strategy. The counting strategy involves more working memory or attentional resources than simple memory retrieval because participants would have to keep in mind the specific attributes of the problem as well as their place in the alphabet during counting. The practice-induced switch from counting to a memory retrieval strategy would lead to a reduction of the use of these task general processes. Nevertheless, if this peak was due to the demands of holding intermediate results of the counting strategy in working memory, it might be expected to persist or occur later than 300 ms. Since this was not the case, this peak was probably due to the control of information processing necessary for the execution of a cognitive strategy. Before practice, this control signal would be larger due to the greater number of processes necessary for the counting operation to occur (i.e., alphabet and counting representations). After practice, this control signal would be reduced because there were fewer processes necessary to retrieve the correct answer.

Pauli et al. (1994) reported that the topography of the 300 ms peak changed such that the frontal and central positivity decreased but the parietal positivity was unaffected after practice. While there was no change in topography of the early peak in the present study, there was a second prominent positive peak at ~500 ms that was centered over more posterior scalp regions. Interestingly, this second peak varied with problem type, such that it was greatest for true problems after practice. These findings suggest that the increased positivity with practice was due to the use of a memory retrieval strategy. This interpretation is roughly consistent with earlier ERP studies of recognition memory that showed a (left) parietal peak at about 500 ms after stimulus presentation (Rugg, 1995; Allan et al., 1998).

The differences in the ERP findings between the present study and the Pauli et al. (1994) study may have important theoretical implications. Pauli et al. (1994) used the multiplication production task (e.g., $4 \times 7 = ?$) whereas the present study utilized the alphabet-addition task. It is generally accepted that adult performance with multiplication production is primarily a result of memory retrieval (Campbell, 1987). In contrast, it is also well established that skill acquisition with alphabet addition is due to a switch in strategy from counting to memory retrieval. Multiplication production is a task in which participants have prior experience with, but alphabet addition is by all accounts a new cognitive task. Thus, the ERP findings of Pauli et al. (1994) were associated with neuroplasticity due to increased facility with a single strategy based on a previously known task. The findings of the present study, however, demonstrated skill-related neuroplastic changes in a previously unused skill due to a change in strategy. This means that when participants already have experience with a given task in which the underlying performance is due to a single strategy, it can be expected that all of the brain areas associated with the strategy are active and that any changes in brain activation are due to the increased facility with one type of processing (i.e., a decreased need for attentional/control processes and decreased frontal activation). When improvement is due to a strategic switch, it can be expected that new processing areas will become activated to facilitate a change in processing strategy (formation and activation of newly formed representations to facilitate memory retrieval and increased activity in posterior regions).

4.2. EEG oscillations

One prominent new result from the present data was the observation that theta synchronizations increased across frontal and midline scalp locations, which was especially striking for true problems after practice. These results suggest that theta-related practice effects were due to semantic memory retrieval. Direct support for this interpretation comes from strategy probing data (Fig. 1c), which implies that increased frontal midline theta activity coincided with the switch to a memory retrieval strategy with practice. This interpretation fits with other experiments using language tasks that associated theta activity with semantic retrieval (Bastiaansen et al., 2005) and is consistent with neuroimaging studies that implicated both hippocampal and frontal lobe involvement in memory encoding and retrieval (Schacter et al., 1996; Nyberg et al., 1998). Moreover, these findings extend previous observations that have linked theta oscillations to hippocampo-cortical feedback loops and cell assembly formation associated with memory encoding (see Klimesch, 1999; Kahana et al., 2001 for reviews). Together with previous studies, the present results support the conclusion that theta oscillations are involved in both episodic encoding and also in semantic retrieval.

Beta band ERDs were also observed over central scalp locations and these effects were larger for the more difficult problems in the pre-practice recordings; an effect that was not found in the post-practice recordings. Generally, beta band ERDs has been associated with active processing. Thus, the ERDs observed over central scalp locations suggest that neural activation associated with increased problem difficulty is most likely a result of task related increases in cognitive load or attention.

Before moving on to the larger implications of the present study, it is important to point out that the literature linking EEG oscillations and specific cognitive processes is relatively new and many of the previous studies have not focused on skill-related changes. Much of this work has been interested in cognitive processing measured during a single recording session and with tasks traditionally used to study memory and language. Thus, the differences between the present results and those reported before could be related to variations associated with different tasks. Caution is also necessary when comparing brain–behavior relationships between the human and animal literature regarding specific EEG oscillations, like theta. These relationships are inherently complex, difficult to study, and cross-species comparisons are not always straightforward. Clearly, further research will be necessary to clarify many of these relationships.

4.3. General implications

The findings of the present study support two important general conclusions. First, these data underscore the utility of combining two different approaches to the analysis of scalp-recorded EEG activity when used in conjunction with a well-understood cognitive task. Given that alphabet addition has been widely used in previous behavioral studies of skill acquisition and is well defined from a cognitive point-of-view, it was possible to make strong conclusions about the relationship between the electrophysiological results and specific cognitive processes. This has not been the case in previous studies of skill-related changes in electrophysiological data, where the complex tasks used have not been extensively studied with behavioral methods. Thus, the earlier conclusions were not as well constrained by previous understanding of the links between behavioral findings and the underlying task-specific cognitive processes.

4.3.1. Combination of EEG and ERP analyses

Analysis of both ERPs and EEG oscillations leads to a more comprehensive account of the electrophysiological correlates of skill acquisition, than data obtained from either paradigm alone. This conclusion is supported by the fact that removing the stimulus locked ERP component from the analysis of the EEG oscillations did not lead to any substantive change in the oscillation results. This novel finding provides evidence that there are changes in the EEG that are not phase-locked to the stimulus and therefore were independent of the standard time-domain ERP data. Thus, this study demonstrates how the combination of the two types of analysis of electrical scalp recordings with a well delineated cognitive task provides a more comprehensive account of the underlying cognitive and neuronal changes and establishes this combination as a new standard for future electrophysiological studies in cognitive neuroscience.

The conclusion that ERPs and EEG oscillations are independent allows for a specific window to additional processing associated with learning. Not only can semantic memory retrieval after practice be associated with the ~500 ms time-locked peak, it is also independently associated with increased synchronization in the theta band after practice. Similarly, cognitive control and/or attention can be associated with both the changes in a peak at ~300 ms prior to practice, and can also be independently associated with greater desynchronization in the beta band prior to practice. Because the EEG oscillations at different frequencies are by definition not phase locked to the presentation of the stimuli and therefore are relatively independent of the ERPs, these findings may indicate different aspects of neuronal plasticity associated with a given cognitive process. For example the ERP changes maybe associated with one type of plasticity and the changes in the EEG oscillations maybe associated with another type altogether. Clearly more research is needed to support such specific conclusions.

4.3.2. Implications for future studies of neuroplasticity

Finally, it may also be useful to apply the methods used in the present study to the study of neuroplasticity associated with recovery of function. As mentioned above, Pauli et al. (1994) demonstrate neuroplasticity associated with the improvements in an established skill associated with improved processing due to a single strategy, whereas the present study demonstrates neuroplasticity associated with the improvement in a skill due to a strategic switch in a previously unknown task. Accordingly, these two studies offer differing predictions depending on if the neuroplasticity associated with recovery of function is due to changes with single strategy or as a function of a switch in strategy, or if any changes are associated with a previously learned task or a completely new task. For example, in one case, if the recovery of function was expected to be due to increased facility with an existing strategy for a previously known task, it could be predicted that all of the brain areas associated with the task would be activated early in the recovery and any changes in the ERP/EEG signal would be due to improved processing with that strategy. Alternatively, if the recovery of function is expected due to the learning of a new strategy, then it would be predicted that the EEG/ERP data would reflect a new process coming online.

Combined with Pauli et al. (1994), the results from the present study strongly support the use of scalp recordings to study neuroplasticity associated with the acquisition of a skill. This result has important implications for the study of neuroplasticity in patient groups. As mentioned above, the interpretation of the results pertaining to the changes in the ERP peak at ~300 ms that were not specific to the type of problem and found over frontal electrodes were probably due to processing in the frontal areas of the brain that are associated with cognitive control (i.e., top down processing). Independent but similar to this finding the oscillations in the beta band also seem to reflect cognitive or attentional load. As one might expect from ERP studies of attention focused on the P300 (see Linden, 2005 for a review), this change in control occurs early in the cognitive time-course, and could reflect the resources necessary for the execution of a particular strategy. The second peak from the ERP analyses at ~500 ms provides evidence that semantic memory retrieval occurs later in the cognitive time-course and also changes as a function of strategy. Thus, these peaks could serve as potential diagnostics of cognitive control deficits and memory retrieval in patient populations. For example it maybe useful to assess any difference in these peak in different learning deficits or the inability of brain injured patients to learn new tasks or recover specific functions.

Each method has its own advantages and disadvantages. For example, EEG has very good temporal resolution while fMRI has better spatial resolution (Gevins, 1998). Both of these methods establish correlations with behavior. In contrast, stimulation techniques are useful for inferring causal effects but they have problems related to spread of activation and whether certain parameters result in facilitation or disruption of function. Ultimately theories of neuroplasticity should use all three techniques to acquire data that can be explained by a comprehensive model in a coherent manner.

5. Summary

The present study combined scalp recordings of electrophysiological activity with a well-understood cognitive/behavioral paradigm to study neuroplasticity involved in the acquisition of a previously unlearned skill. The results provide evidence that: (1) EEG and ERP analyses can be used in a complementary fashion to study skill-related neuroplasticity due to a change in cognitive strategy in previously unlearned tasks; (2) the ~300 ms ERP peak may be associated with control processing; (3) the ~500 ms ERP peak may indicate memory recognition; (4) theta band ERS may indicate semantic memory retrieval; and (5) beta band ERD may be associated with cognitive load.

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