Different slopes for different folks: Alpha and delta EEG power predict subsequent video game learning rate and improvements in cognitive control tasks

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Abstract

We hypothesized that control processes, as measured using electrophysiological (EEG) variables, influence the rate of learning of complex tasks. Specifically, we measured alpha power, event-related spectral perturbations (ERSPs), and event-related brain potentials during early training of the Space Fortress task, and correlated these measures with subsequent learning rate and performance in transfer tasks. Once initial score was partialled out, the best predictors were frontal alpha power and alpha and delta ERSPs, but not P300. By combining these predictors, we could explain about 50% of the learning rate variance and 10%–20% of the variance in transfer to other tasks using only pretraining EEG measures. Thus, control processes, as indexed by alpha and delta EEG oscillations, can predict learning and skill improvements. The results are of potential use to optimize training regimes.

Descriptors: Video game training, Space Fortress, Electroencephalogram (EEG), Event-related spectral perturbations (ERSPs), Event-related brain potentials (ERPs), Skill learning, Cognitive control, Alpha rhythm

The state of the brain can have great influence on the processing of incoming information (Boly et al., 2007; Mathewson, Gratton, Fabiani, Beck, & Ro, 2009; Romei et al, 2008a; Romei, Rihs, Brodbeck, & Thut, 2008; Thut, Nietzel, Brandt, & Pascual-Leone, 2006). Although it is clear that the current brain state can predict the short-term processing of stimulus information (e.g., Mathewson et al., 2009), the extent to which it can predict behavior further in the future remains largely untested (but see Gruber & Otten, 2010; Xue et al., 2010). It is plausible that brain states during the performance of a complex task do not merely predict immediate information processing but also individual differences in learning rate and skill transfer to other tasks. The extent to which people exhibit particular brain states when initially confronted with a particular task may reflect important individual differences in performance, cognitive styles, or attitudes towards the task. Here, we studied the relationship between electrophysiological measures of brain states—the electroencephalogram (EEG), event-related potentials (ERPs), and event-related spectral perturbations (ERSPs)—and the subsequent rate of learning in a complex video game, Space Fortress (Donchin, Fabiani, & Sanders, 1989). We tested whether the engagement of high-level attention control mechanisms at the onset of training could predict individuals’ rate of subsequent learning in a Space Fortress training regime.

We predict that successful and expedient learning in the Space Fortress game depends crucially on the ability to successfully deploy attention to meaningful task events, while simultaneously suppressing processing of distracting information. Thus, learning the Space Fortress game should depend on a subject’s ability to engage attention across the various components of the game. Further, previous Space Fortress studies indicate that this ability represents a more task general skill or “trait” (Fan, Fossella, Sommer, Wu, & Posner, 2003; Gopher & Kahnean, 1971; Hunt, Pellegrino, & Yee, 1989), with certain individuals having increased abilities in Space Fortress also having better performance across a range of high-level tasks (Boot et al., 2010; Gopher, Weil, & Bareket, 1994; Kramer, Larish, Weber, & Bardell, 1999). Thus, subjects who more effectively deploy top-down attention early in learning should be those who both learn faster and whose skills transfer most to tasks outside the game. We aim to test for evidence that ongoing brain states indexing the control and deployment of...
attention control can predict subsequent learning and behavior on a much longer time scale than previously demonstrated.

Complex video games have long been recognized as useful investigative techniques for cognitive neuroscience as well as potential cognitive training tools (e.g., Donchin et al., 1989), largely because they afford investigators the possibility of testing subjects in situations closer to the complexity of real life than standard laboratory tasks. Research using this approach has recently proliferated and broadened our understanding of the brain activity taking place during video game learning (Green & Bavelier, 2008; Koepp et al., 1998; Mishra, Zinni, Bavelier, & Hillyard, 2011; Voss et al., 2010; Wu et al., 2012).

The Space Fortress game (Figure 1) was developed as a cognitive tool for studying learning and training strategies (Donchin et al., 1989). The demanding nature of the multiple cognitive tasks embedded in this game simulates many real-world tasks such as piloting a vehicle or air traffic control. It also provides analogies to well-studied cognitive tasks from the cognitive psychology literature. Recent research has found anatomical predictors of subsequent improvement in performance. Volumetric differences in the basal ganglia can predict individuals’ change in score in the Space Fortress game with learning (Erickson et al., 2010). Pattern classification using a support vector machine algorithm of the tissue properties of basal ganglia structures can predict the level of improvement in the game (Vo et al., 2011). The basal ganglia have been shown recently to play an important regulatory role in the activity of prefrontal attention control circuits (van Schouwenburg, den Ouden, & Cools, 2010).

We used EEG to analyze the online time-resolved brain activity as it unfolds in the game environment at the beginning of a training period, in order to better understand what particular dynamic brain functions are predictive of training success as well as of improvements in other tasks outside of the game environment. Specifically, we measured EEG power in the alpha frequency range (7–12 Hz) in order to assess the level of these top-down influences on behavior and the current level of attention engagement (Babiloni et al., 2004; Macdonald, Mathan, & Yeung, 2011). Alpha oscillations have been shown from the very first EEG recordings (Berger, 1929) to be related to the current level of attention and arousal. Recent research has shown an intimate link between alpha oscillations and sensory processing, such that hemispheric-specific increases in alpha power are associated with suppression of processing in the contralateral visual hemifield (Romei et al., 2008a, 2008b; Worden, Foxe, Wang, & Simpson, 2000). This literature indicates that alpha is not merely a generic indication of “relaxation” (which would lead to undifferentiated effects across the entire visual field) as previously proposed but rather a specific mechanism for attention control. We have hypothesized this relationship to be due to pulses of inhibition associated with subsets of the alpha cycle (Mathewson, Fabiani, Gratton, Beck, & Lleras, 2010; Mathewson et al., 2009, 2011; Mazaheri & Jensen, 2010). Recent comprehensive reviews of alpha oscillations propose that alpha acts as a control and timing mechanism in all areas of the brain (Klimesch, Sauseng, & Hanslmayr, 2007; Mathewson et al., 2011; see also Jensen & Mazaheri, 2010) and predict that high-level control areas in frontal brain regions have a top-down influence on this oscillatory alpha activity (Mathewson et al., 2011). Indeed, past EEG studies of the Space Fortress game have shown a general increase in alpha power over central areas as a function of learning (Gevins, Smith, McEvoy, & Yu, 1997; Maclin et al., 2011; Smith, McEvoy, & Gevins, 1999). Therefore, we used the baseline level of scalp-recorded frontal alpha power (which we take here to reflect frontal lobe activation levels) as a measure of the effective engagement of control processes early in training. We hypothesized that the amount of frontal alpha power early in training should predict subsequent learning in the Space Fortress task. We measured alpha activity during important in-game and out-of-game events prior to training, and correlated this activity with subjects’ learning rates and with performance improvements in cognitive-control tasks outside of the game environment.

We also tested if the evoked activity as represented by both ERPs and ERSPs elicited by these events could further predict learning rate. Evoked and/or induced oscillatory activity represents a transient and short-term response to ongoing task demands (Makeig, Debener, Onton, & Delorme, 2004), but may also be indicative of particular brain states that are predictive of subsequent performance (e.g., Gruber & Otten, 2010; Romei, Gross, & Thut, 2010). Decreases in alpha power (alpha suppression) as well as increases in delta have been associated with the subject’s attentional engagement (Babiloni et al., 2004; Klimesch, Doppelmayr, Russegger, Pachinger, & Schwaiger, 1998; Klimesch et al., 2007). We have recently reported that ERSP modulations following three important Space Fortress game events changed after training, and predicted the increased availability of attentional resources to secondary task events (Maclin et al., 2011). Specifically, alpha (7–12 Hz) and delta (0–5 Hz) ERSPs evoked by a range of game events were found to change with learning. Furthermore, concomitant with these changes, large changes in the amplitude of the P300 response to important in-game events were observed. Further, the amplitude of P300 to secondary task probes increased with mastery of the game, presumably signaling that attention resources were freed as the Space Fortress task became more automatized. We therefore tested whether the extent to which subjects showed these ERSP and ERP modulations early in training would predict the rate of subsequent learning in the Space Fortress game.

Figure 1. Typical display in the Space Fortress game. Subjects controlled the thrust and angle of a flying ship in a low-friction environment. The goal was to fire missiles at the central Space Fortress, inflicting enough damage to destroy it. The fortress fired back at the ship, and mines appeared intermittently, having to be classified and disengaged before they hit the ship. Subjects were rewarded for flying slowly, and within the hexagonal playing field, for destroying the fortress, and for handling the mines, and were penalized for getting hit by the fortress or the mines.
Recently, there has also been a growing interest in the use of video games to train basic cognitive functions. This hinges on the possibility of transferring skills learned during a game to other cognitive tasks (Basak, Boot, Voss, & Kramer, 2008; Bavelier & Green, 2004; Boot, Kramer, Simons, Fabiani, & Gratton, 2008; Boot et al., 2010; Dahlin, Neely, Larson, Bäckman, & Nyberg, 2008; Dye & Bavelier, 2004; Dye, Green, & Bavelier, 2009; Fredericksen & White, 1989; Gopher et al., 1994; Green & Bavelier, 2008). As training may be expensive in terms of both time and costs, it would be very useful to be able to identify ahead of time those individuals for whom training would not only be most expedient and beneficial, but also for whom transfer outside of the training regime scope would be optimal. We therefore also tested whether any of the electrophysiological predictors of subsequent game learning rate could also predict individuals’ improvement on other nongame cognitive and memory tasks requiring skills similar to those important in Space Fortress.

To preview our results, we indeed found that frontal alpha power before training predicts the rate of subsequent learning as well as improvement in cognitive-control task performance outside the game environment, in tasks requiring processes that closely overlap with those important for Space Fortress (see Dahlin et al., 2008). All the brain electrical measures were indeed correlated with subsequent learning. However, interestingly, whereas the ERP prediction overlapped with that provided by the initial behavior (learning score) in the task, the brain oscillatory activity (EEG alpha power and ERSPs) provided unique predictions of subsequent learning that could not be derived from initial task performance. This suggests that they tap on some form of covert brain process whose effects on behavior are visible only at a later time. Indeed, a combination of EEG and ERSP predictors evoked by game events accounted for 46% of the variance in learning rate (over and above initial game performance) when combined in a multiple regression model. Finally, the EEG and ERSP indices were also able to predict 10%–20% of the variance in some skill improvements outside of the game. Together, these results reveal that the state of the brain early in training predicts the rate of subsequent learning and the application of these skills outside of the game.

**Method**

**Participants**

Thirty-nine individuals\(^1\) (ages 18–28, 27 females) were recruited from the University of Illinois community, after indicating in an online survey that they had played fewer than 3 h of video games a week in the past 2 years. All subjects were right-handed and had normal or corrected-to-normal vision, and were paid $15 per hour for their training and recording sessions. Data from one subject were excluded due to technical problems with EEG recording.

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\(^1\) This data set is part of a larger study of Space Fortress Video game training. The data reported here is from the same experiment and data set as that reported in Boot et al. 2010, Erickson et al., 2010, Voss et al. 2011, Vo et al., 2011 & Maclin et al., 2011. It should also be noted that the present data set is collapsed across two types of training (Variable and Fixed priority), which are reported elsewhere (e.g. Boot et al., 2010). Since training group was a poor predictor of subsequent learning rate, and since in the current dataset the groups did not differ significantly in any of the electrophysiological indices, we collapsed across groups here.

**Procedures**

To familiarize themselves with the game, subjects initially watched a 20-min movie that explained the Space Fortress game, and then another 5-min movie that summarized the most important rules. After viewing these movies, participants played 24 3-min games to get acquainted with the controls and game physics.

Next, participants played 10 3-min games while their EEG was recorded. This was followed in the subsequent days by 20 h of game training (see Boot et al., 2010, for a complete description of the training protocol). At the end of training, a postraining session was completed. In the present paper, only the EEG and ERP activity from the postraining session was considered as a predictor of subsequent learning during training.

**Space Fortress game.** Details of the Space Fortress game can be found in Donchin et al. (1989) and Shebilske et al. (2005). Here, we summarize the relevant aspects of the game. The final score on each game of Space Fortress is a combined measure composed of four subscores. A major component of the game is flying the ship. Players are rewarded both for keeping their ship within the hexagonal game area (see Figure 1) and for keeping their ship below a threshold velocity. Players destroy the central fortress by first hitting it 10 times with missiles, and then hitting it with a fatal double shot. Players must avoid being hit by the fortress’ missiles or onscreen mines, with four hits causing the ship to be destroyed. Finally, mines intermittently appear on the screen and must be neutralized and destroyed. Participants were comfortably seated in front of a 19-inch color LCD monitor, and made game inputs using the computer mouse and a Logitech Attack 3 Joystick.

**Additional tasks.** Participants performed a secondary “auditory oddball” task while they were playing the game. Tone bursts of 340-ms duration were presented via speakers at ~70 dB every 2,330 ms. Frequent tones (~80%) were 350 Hz and rare tones (~20%) were 500 Hz. Subjects were instructed to silently count the rare (high) tones, and report the total at the end of each 3-min game. Participants also performed the oddball task without the game (three 70-tone blocks) while EEG was recorded.

Furthermore, a battery of cognitive tasks, testing attention, cognitive control, and working memory, was completed by subjects before and after the training program. This battery was used to measure the improvement in performance in tasks requiring processes that overlap with those important for the Space Fortress game. These tasks are described in more detail in Boot et al. (2010). We selected from this battery those indices measuring skills most relevant to Space Fortress success (e.g., reaction time, task switching; Dahlin et al., 2008). The subset of tasks considered in this paper is presented in Table 1.

**EEG Recording and Analysis**

EEG data were collected in a sound and electrically attenuated chamber from 64 electrodes embedded in a flexible electrode cap (ElectroCap International, Eaton, OH). Impedance was kept below 10 KOhm. Data were filtered online using a .01–30 Hz band-pass, and sampled at 100 Hz. The electrooculogram (EOG) was collected using two bipolar electrode pairs placed above and below the left eye (vertical EOG) and on the left and right outer canthi (horizontal EOG). Scalp channels were referenced to the left mastoid during data collection and then were referenced offline to the average of the two mastoids.


**Table 1. Additional Tasks Outside the Game Environment**

<table>
<thead>
<tr>
<th>Task</th>
<th>Response</th>
<th>Dependent measure</th>
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<tbody>
<tr>
<td>Cognitive control tasks</td>
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<tr>
<td>Task switching (Pashler, 2000)</td>
<td>Odd/even vs. high/low digit</td>
<td>Switch cost (switch RT/stay RT)</td>
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<tr>
<td>Stop task (Logan, 1994)</td>
<td>X or O/stop if rare tone (staircased SOA)</td>
<td>Stop RT (averaged SOA/go RT)</td>
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<tr>
<td>Working memory tasks</td>
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<tr>
<td>Visual short term memory</td>
<td>Delayed match to 4-object sample</td>
<td>Overall accuracy</td>
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<tr>
<td>N-back</td>
<td>Delayed match to 3- to 5-letter sample</td>
<td>RT</td>
</tr>
<tr>
<td></td>
<td>1-back, 2-back letter match in stream</td>
<td>Focus switch cost (2-back RT/1-back RT)</td>
</tr>
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*Notes. SOA = stimulus-onset asynchrony; RT = response time.*

EEG data were analyzed with custom scripts using MATLAB and EEGLAB (Delorme & Makeig, 2004). EEG data were scanned for voltages at the A/D limits, and channels with excessive noise were interpolated from nearby electrodes using EEGLAB’s spherical interpolation function. The data were then epoched around the four events of interest: mine onsets, fortress hits, and rare tones in and outside the game. Epochs where any EEG channel had a range exceeding 1000 μV were discarded. Horizontal and vertical eye movements were corrected using the EMCP (eye movement correction procedure) regression algorithm (Gratton, Coles, & Donchin, 1983). After eye movement correction, the data were scanned again, and epochs with channels with a range exceeding 500 μV were discarded.2

For the frequency domain analysis, a wavelet analysis of the epoched data was performed using the “newtimef()” function of the EEGLAB toolbox. A complex group of tapered wavelets was computed with a width of 710 ms, with one cycle at the lowest frequency and increasing up to 19 cycles at the highest frequency. To increase frequency resolution, the data and wavelets were zero-padded with a ratio of 2. This allowed for the visualization of frequency information with a resolution of .75 Hz from 1.6 Hz up to 30 Hz, and from −645 ms to 1,640 ms around the event of interest. For the baseline EEG analysis, a single window of interest was created by averaging the single trial alpha power from 7 to 12 Hz and from −500 to 1,500 ms poststimulus onset around each of the four events of interest.

In order to measure the changes in oscillatory brain activity evoked by and locked to events of interest, a baseline-corrected version of the time-frequency data was computed as reported by Maclin et al. (2011). On each trial, the average prestimulus power was subtracted from activity at each time point, for each frequency. These baseline-corrected, single-trial, time-frequency transforms are then averaged over trials in each condition. The resulting ERSP data reflect changes in oscillatory brain activity elicited by or time-locked to the events of interest. We tested whether this ERSP activity predicted learning rate. Windows of interest (in time and frequency) were constructed based on the findings from Maclin et al. (2011) of modulations in ERSP as a function of training, where the largest and most consistent changes in ERSP were found in the delta and alpha ranges. We therefore included the average ERSP at both Fz and Pz in two different windows as predictors, one from 10–15 Hz (alpha) from 300–700 ms after the three game events, and the other from 0–5 Hz (delta) from 250–600 ms after events.

Given that participants were controlling the ship with a joystick in their right hand, it could be argued that the alpha modulations and correlations that we observe are related to 8–12 Hz mu rhythms from the motor cortex associated with flying the ship. In this case, 8–12 Hz activity over the motor cortex in the left hemisphere should be lower than that in the right. To test this, we computed the lateralized power of mu rhythms by subtracting on each trial the raw power over time at electrodes ipsilateral to the joystick hand from the analogous contralateral electrodes. The more negative the values in the alpha range, the greater the suppression of the mu rhythm in the motor cortex controlling the joystick.

To complement the frequency-domain EEG and ERSP measures, we also computed time-domain ERP averages of the brain activity elicited by the three important in-game events. An extensive comparison of time-domain and frequency-domain measures of brain activity in the Space Fortress game can be found in Maclin et al. (2011). Due to the complex game environment, the low frame refresh period (40 ms) of the video game to which the EEG activity was locked, and the large variability in the timing of cognitive activities in such a situation, many of the early ERP components were not identifiable in the subjects’ average or grand average ERPs. We therefore focused our analysis on the largest and most consistent ERP component, the P300 elicited by the critical game events. We averaged single trials time-locked to mine onsets, fortress hits, and the onset of in-game oddball tones, baseline-corrected with the average voltage in the 200 ms preceding each game event. The P300 amplitude was measured at Pz, where it is normally maximal, in time windows determined from the grand average waveform (mine onset: 300–500 ms; fortress hits and oddball tones: 400–600 ms).

**Correlations Between Measures and Stepwise Regression Analysis**

To evaluate the relationship between the time-domain and frequency-domain measures, as well as to test how they related to the initial game score, we computed a variable-wise correlation matrix. As the interest of this study is to assess the degree to which electrophysiological variables predict subsequent learning, we also computed simple correlations between each of these variables and learning rate. However, because learning rate was correlated to the initial game score, and the different electrophysiological variables were correlated to each other, interpretation of these simple correlations can be difficult. For this reason, we set up a stepwise multiple regression analysis to determine which variables did provide unique contributions to the prediction of learning rate. Although this stepwise multiple regression analysis was based on entering the variables according to a predetermined order (explained in the Results section), by and large it corresponded to

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2. Relatively lenient artifact rejection measures were required in order to retain sufficient number of trials for reliable analysis, given the more demanding and dynamic video game environment.
a “forward” procedure (i.e., in which at each step the next largest partial predictor is entered in the regression equation, this variance is partialled out from all remaining predictors, and all partial correlations are computed again, repeating this procedure until no further significant residual predictor is found). First, we evaluated the extent to which learning rate could be predicted by the subject’s initial performance. This initial game score was partialled out of all other predictor variables. We then entered the variable with the highest partial correlation with subsequent learning (raw EEG alpha power during the mine period). This variable was partialled out from all the other predictors. We then entered the subsequent larger predictors (delta ERSP elicited by fortress hits and alpha ERSP elicited by fortress hits).

For all regression steps, we further tested the significance and visualized the error by computing 10,000 bootstrapped samples of size 38 (the number of participants) with replacement from the original sample and computed the regression coefficients on these new samples. To provide a visual impression of the variability of the bootstrapped regression coefficients, we plotted the first 1,000 of these regression lines and reported the number of slopes greater than or less than zero as tests of the relationship’s significance.

Results

Behavioral Results

Subjects were trained for 10 2-h sessions. Figure 2A shows the overall behavioral improvement of individuals over the 20 h of training (i.e., 10 training sessions). For each participant, we modeled the learning curve based on the total game score \( \hat{p}' \) over the 20 h of training using a logarithmic function:

\[
\hat{p}' = a + r \times \ln(\text{training hour})
\]

where \( a \) (the intercept) represents an estimate of the initial level of game play, and \( r \) is the slope estimated for each subject as a measure of the rate of learning to be predicted from electrophysiology. Median split of the initial 2 h of composite total score indicated that participants with higher initial proficiency had a significantly lower learning rate (1,086.91 game points per hour) than those with lower proficiency (1,518.35), \( t(37) = 2.60, p < .05 \). Figure 2B shows the relationship between learning rate and initial score in the raw data (black solid line) and for 1,000 bootstrapped samples (thin gray lines). The higher the initial score in the game, the lower the learning rate \( r = -.41; R^2 = .17; \) bootstrapped \( p < .005 \). Therefore, to avoid this potential confound, in the hierarchical stepwise regression procedure we first partialled out the variance accounted for by the initial score.

Figure 3 presents the correlation matrix between all considered variables. The simple correlations between learning rate and each of the predictor variables are presented on the first row. Evident is the large negative correlation between learning rate and the initial game score, as well as a number of positive and negative correlations with EEG, ERSP, and ERP variables that will be discussed further below in turn. As variables are entered into the hierarchical regression model, the remaining variance in learning rate (regression residuals) is considered as the new outcome variable on each of the four subsequent rows of the correlation matrix. The correlations are again presented across the row between each of the predictor variables and these learning rate residuals, having now been controlled for the predictor variables already in the model. Lower parts of the matrix represent the intercorrelations between predictor variables. We will refer back to the rows of this figure as we discuss each of the results in turn.

Alpha Power Predicts Learning Rate

We hypothesized that the amount of top-down control, as indexed by EEG alpha power early in training (raw levels averaged across single trials), would predict the slope of the subsequent learning curves. The amount of alpha power was highly correlated across all in-game events (all \( r > .98, p < .05 \)). In all cases, there was a strong
correlation between baseline levels of alpha power and uncorrected rate of learning (Figure 3, row 1; mines $r = .46$, $p < .05$; fortress $r = .44$, $p < .05$; oddball in game $r = .44$ $p < .05$). The higher an individual’s alpha power before they started their training, the steeper was his/her improvement in score during the training program. Figure 4 shows the correlations between the learning rate for each subject and their average power at each frequency and time point, aligned to two important game events (mine onset, fortress hits) as well as the oddball tones both in and outside of the game, all from the left frontal electrode F3 where this correlation was maximal. To assess whether this effect was specific to game play in the Space Fortress environment, we also measured EEG from an additional oddball task outside of the game. Figure 4 (lower right panel) shows this effect’s specificity in the alpha band, albeit slightly weaker than for the in-game events ($r = .35$, $p < .05$). There was also a significant correlation between alpha activity during oddball tones in and out of the Space Fortress game ($r = .83$, $p < .05$).

Figure 4 also shows topographic plots of the correlation between alpha power and learning rate across subjects. For all events, a consistent frontal distribution was found in the strength of the correlation of alpha power with subsequent improvement. Due to the intercorrelations between predictors. Each cell shows the signed Pearson correlation between the pair of variables in that row and column, and is colored based on its value according to the scale presented on the right. The top row shows the correlations between learning rate and each of the EEG, ERSP, and ERP predictors. The square box in row 1 shows the negative relationship from Figure 2B that is partialled out to control for initial game score. Each of the subsequent four rows represents the correlations between the residual variance in learning rate after accounting for the variable in the square on all of the superior rows. Predictors included in the final model are in bold. Note the strong correlations among the measures of raw alpha power. Also note that although P300 to the fortress is a strong predictor of Time 1 score, it does not predict learning rate strongly after this relationship has been accounted for.

Figure 3. Correlation matrix. Shown are the correlations between learning rate (LR) and each of the considered predictor variables, as well as the intercorrelations between predictors. Each cell shows the signed Pearson correlation between the pair of variables in that row and column, and is colored based on its value according to the scale presented on the right. The top row shows the correlations between learning rate and each of the EEG, ERSP, and ERP predictors. The square box in row 1 shows the negative relationship from Figure 2B that is partialled out to control for initial game score. Each of the subsequent four rows represents the correlations between the residual variance in learning rate after accounting for the variable in the square on all of the superior rows. Predictors included in the final model are in bold. Note the strong correlations among the measures of raw alpha power. Also note that although P300 to the fortress is a strong predictor of Time 1 score, it does not predict learning rate strongly after this relationship has been accounted for.
to these high correlations across conditions, in the hierarchical stepwise regression we include only the average baseline alpha power around mine appearance.

To test if this relationship could be explained by the lateralized mu rhythm associated with controlling the ship with the right hand, we also tried predicting the initial-score-corrected learning rate with the amount of 8–12 Hz raw lateralized alpha locked to oddball tones in the game. Counting oddball tones requires no specific hand movement, so any effect is largely due to motor activity associated with flying the ship with the joystick control. Figure 5A and B show the amount of lateralized oscillatory activity associated with three in-game events. A peak in lateralized activity is found in the alpha range and is maximal over motor areas. This activity was very consistent and highly correlated across conditions (all \( r > .9; \ p < .05 \)). Therefore, we selected only the lateralized mu activity around the in-game oddball for further analyses. Since no overt response is required, this activity was thought to be associated mostly with joystick control. Figure 5C shows that lateralized mu activity was not strongly predictive of learning rate (Figure 3; \( r = .06; \ n.s.; \) bootstrapped \( p > .1 \)). In fact, mu activity did not strongly predict the remaining variance in learning rate at any stage in the regression (Figure 3, column 6).

ERSP Predictors

We also wanted to assess whether the oscillatory activity evoked or modulated by each of the important game events was predictive of the subsequent rate of learning as measured by the ERSP, since both alpha and delta oscillations have been shown to change with proficiency at the Space Fortress game (Maclin et al., 2011). Figure 6 shows the ERSPs from electrode Fz evoked by the same four events displayed in Figure 4. We submitted to the stepwise regression the average ERSP in each of the time-frequency windows of interest at two electrodes (Fz and Pz) where maximal training effects were found in Maclin et al. (2011), to see if they explained additional variance in the learning rate over and above that explained by baseline alpha power and initial game score alone. Specifically, we tested whether reduced alpha activity (alpha suppression) and increased delta oscillations in the periods following events of interest were associated with subsequent rates of learning, as both of these phenomena changed with learning in Maclin et al. (2011).

ERP Predictors

We predicted that time-domain ERPs would also serve as valuable predictors of subsequent improvements in the game given their change with learning and tight coupling with ERSP delta activity reported by Maclin et al. (2011). The rightmost three columns of Figure 3 show the correlations between each subject’s average P300 amplitude and their rate of learning. Like the ERSP delta activity, the P300 evoked by fortress hits trends towards a significantly positive correlation with subsequent learning (\( r = .27 \)). However, controlling for initial performance (row 2) greatly attenuates this relationship (\( r = .10 \)), while it does not do so for the ERSP delta activity. Note that despite the positive correlation (\( r = .37 \)) between ERSP delta and P300 amplitude evoked by fortress hits, only the P300 amplitude is negatively correlated (\( r = -.44 \)) with Time 1 score (row 5), whereas delta ERSP is not (\( r = -.01 \)). In other words, the P300 elicited by fortress hits does provide a moderate prediction of learning rate, but in a way that is redundant with that provided by Time 1 score, presumably reflecting online trial-by-trial processing. In contrast, the ERSP delta elicited by the same stimuli provides unique prediction of learning rate, which is not
Figure 5. Lateralized mu rhythm does not predict learning rate. A: Lateralized frequency spectrograms showing the difference in EEG power between electrode C3 and C4. The peak frequency in the alpha range confirms this is the mu rhythm, with decreased 8–12 Hz activity over the hemisphere controlling the joystick during the game. This is shown for three in-game events. B: Topographic plots showing only for the left hemisphere the differences in 8–12 Hz mu activity between each left hemisphere electrode and their corresponding right hemisphere counterpart. All right hemisphere and midline electrodes are set to zero. These plots indicate that the mu rhythm is maximal over motor cortex. C: Scatter plot showing the lack of relationship between mu rhythm (abscissa) and learning rate (ordinate).

Figure 6. A: Pretraining ERSP evoked by three in-game events and by the out-of-game oddball task at electrode Fz. These data were reported by Maclin et al. (2011). We used the eight ERSP windows from the Maclin et al. (2011) study as additional predictors of learning rate in a multiple regression at Fz and Pz. Only the 0–5 Hz delta activity and the 10–15 Hz alpha activity further predicted learning rate over and above the baseline alpha level. B: Topographic maps of the correlation between ERSP alpha (top) and delta (bottom) activity elicited by fortress hits.
redundant with Time 1 score, presumably reflecting control processes whose effects on behavior are only evident at a later time.

The P300s to the mines were not predictive of learning rate at any stage in the regression, although they were correlated with ERSP alpha and delta activities elicited by the same stimuli. Some unique variance in learning rate did seem to be accounted for by the P300 to the oddball tones, but this was never the strongest of the remaining predictors.

### Learning Rate Prediction Summary

Table 2 and the upper rows of Figure 3 summarize the hierarchical stepwise regression procedure. First, in order to control for the influence of initial game score on the predictive value of the EEG (Figure 2B), we added initial game score in the EEG session to the model. Next, to test the hypothesis that cognitive control engagement early in training (as measured by alpha oscillations over frontal cortex) predicts subsequent learning, we added the EEG alpha activity around mine onset to the model. This predictor remained significant after controlling for initial score. Figure 7A shows a strong relationship between raw alpha power and learning rate over and above the variance accounted for by initial score ($\Delta R^2 = .15$, bootstrapped $p < .005$). Note that including mu activity in the stepwise regression first did not eliminate the significant relationship between raw alpha activity and learning rate, $\Delta R^2 = .15; F(1,35) = 3.88; p < .05$, indicating that this relationship is not due to motor control, but rather to other types of control processes indexed by frontal alpha. Furthermore, none of the P300 predictors explained significant variance in learning rate at any stage in the stepwise regression, all $F(1,35) < 3.6; n.s.$, once initial scores were partialled out.

Finally, we entered the ERSP predictors from our two windows of interest into the model. Only the ERSP activity evoked by fortress hits predicted subsequent learning rate, over and above the initial game score and the raw alpha relationship. Specifically, ERSP activity in two time-frequency windows appeared important. First, the 0–5 Hz delta activity from 250–600 ms after fortress hits was positively associated with learning rate. Second, the higher the 8–12 Hz alpha power from 300–700 ms following fortress hits, the greater was the subsequent learning rate. Figure 7B shows the predicted scores from a linear combination of the three significant EEG predictors revealing that almost half of the variance in learning rate not predicted by the initial game score could be accounted for by these predictors (baseline frontal alpha power, frontal delta and posterior alpha ERSP to fortress hits; $R^2 = .46$, bootstrapped $p < .0005$). In other words, we can explain 53% of the variance in the rate of learning Space Fortress using EEG variables together with the initial game score.

### Prediction of Improvement in Tasks Outside of the Game Environment

The aim of these analyses was to assess whether any of the electrophysiological variables from the initial game performance also

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**Table 2. Hierarchical Stepwise Regression**

<table>
<thead>
<tr>
<th>Step</th>
<th>Predictor</th>
<th>$\beta$</th>
<th>$R^2$</th>
<th>$R^2_{adj}$</th>
<th>$F$ to enter (df)</th>
<th>$p$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Planned Step 1</td>
<td>Initial score</td>
<td>-0.41</td>
<td>.17</td>
<td>.15</td>
<td>7.21 (1,36)</td>
<td>&lt; .05</td>
</tr>
<tr>
<td>Planned Step 2</td>
<td>Initial score</td>
<td>-0.45</td>
<td>.20</td>
<td>.15</td>
<td>1.05 (1,35)</td>
<td>n.s.</td>
</tr>
<tr>
<td>Planned Step 3</td>
<td>Initial score</td>
<td>-0.32</td>
<td>.30</td>
<td>.26</td>
<td>6.51 (1,35)</td>
<td>&lt; .05</td>
</tr>
<tr>
<td>Stepwise 1</td>
<td>Initial score</td>
<td>-0.30</td>
<td>.38</td>
<td>.45</td>
<td>8.73 (1,34)</td>
<td>&lt; .01</td>
</tr>
<tr>
<td>Stepwise 2</td>
<td>Initial score</td>
<td>-0.23</td>
<td>.41</td>
<td>.54</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Mine EEG $\alpha$</td>
<td>0.48</td>
<td>.48</td>
<td>.53</td>
<td>10.27 (1,33)</td>
<td>&lt; .01</td>
</tr>
<tr>
<td></td>
<td>Fortress ERSP $\delta$</td>
<td>0.40</td>
<td>.58</td>
<td>.53</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

---

**Figure 7.** Predicting learning rate from EEG. A: Regression plot showing the prediction of learning rate from the EEG alpha activity before training, after controlling for the participants’ score during first-game play. Approximately 15% of the variance in learning rate was accounted for by pretraining alpha activity over frontal cortex. Gray lines indicate 1,000 bootstrapped samples, of which only three did not have a positive slope. B: When the two ERSP predictors were added to the multiple regression model, an additional 30% of variance in learning rate was accounted for. All 1,000 bootstrapped samples had a positive slope.
predicted the level of skill improvement in the subset of tasks whose processes overlapped with those important for Space Fortress (Dahlin et al., 2008). The means and standard deviations of the cognitive tasks before and after training, as well as the number of participants retained for each cognitive task, are presented in Table 3. There were missing data for one participant for the task-switching task, one participant for the Sternberg task from the before-training session, and one participant for the 1-back task from the after-training session, resulting in reduced numbers of participants (for these tasks, see Table 3). Greater fortress-locked delta ERSP power was predictive of reductions in response times in the Sternberg memory search task, \( r(37) = -0.33, p < 0.05 \), and in the stop task, \( r(38) = -0.35, p < 0.05 \). Reduced alpha suppression following hits predicted decreases in both Sternberg response time, \( r(37) = 0.53, p < 0.05 \), and focus switch costs in the N-back task (i.e., in the capacity of efficiently switching between items in working memory), \( r(37) = 0.425, p < 0.05 \).

Importantly, baseline levels of EEG alpha power significantly predicted only changes in task switching. That is, reductions in task-switching cost were positively correlated with all four EEG alpha power measures (i.e., with mine onset, fortress hits, and oddball tones inside and outside the game; \( r_s(37) > 0.33 \), all \( ps < 0.05 \)). However, reductions in task-switching costs were not significantly related to any of the ERSP measures.

Note that in several cases the electrophysiological measures were correlated with individual differences in skill improvement, even when all participants did not show this improvement. This suggests that (a) improvement may occur only in some subjects but not others, and (b) electrophysiological indices may be useful to identify which subjects will produce optimal improvement of similar skills outside of the game.

Table 3. Mean (and Standard Deviation) of the Subset of Cognitive Tasks Considered for the Pre- and Posttesting Sessions

<table>
<thead>
<tr>
<th>Task</th>
<th>Pretest mean (SD)</th>
<th>Posttest mean (SD)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Task switching ((n = 38))</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nonswitch RT</td>
<td>921 (135)</td>
<td>852 (116)</td>
</tr>
<tr>
<td>Switch RT</td>
<td>1142 (187)</td>
<td>1023 (1603)</td>
</tr>
<tr>
<td>Switch cost</td>
<td>221 (115)</td>
<td>172 (113)</td>
</tr>
<tr>
<td>Stopping task ((n = 39))</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stop RT</td>
<td>211 (64)</td>
<td>192 (62)</td>
</tr>
<tr>
<td>Go RT</td>
<td>615 (187)</td>
<td>617 (180)</td>
</tr>
<tr>
<td>Stop probability</td>
<td>0.52 (.06)</td>
<td>0.51 (.04)</td>
</tr>
<tr>
<td>Visual spatial short-term memory ((n = 39))</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Accuracy</td>
<td>0.68 (.09)</td>
<td>0.69 (.09)</td>
</tr>
<tr>
<td>Sternberg memory test ((n = 38))</td>
<td>816 (229)</td>
<td>769 (234)</td>
</tr>
<tr>
<td>N-back task ((n = 38))</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1-back RT</td>
<td>610 (111)</td>
<td>600 (129)</td>
</tr>
<tr>
<td>2-back RT</td>
<td>831 (225)</td>
<td>731 (165)</td>
</tr>
<tr>
<td>Focus switch cost</td>
<td>221 (191)</td>
<td>131 (126)</td>
</tr>
</tbody>
</table>

Discussion

We predicted that the engagement of brain cognitive control systems, as reflected by baseline EEG alpha power, could predict the subsequent rate of learning in a complex game. We indeed found that EEG alpha power measured before training in Space Fortress predicts the rate of subsequent learning. Previously, we showed that 20 h of Space Fortress training lead to significant improvement in game performance (Boot et al., 2010). However, it was evident that learning rate varied across individuals, and thus we set to determine what controlled this variability. We hypothesized that cognitive control exerted early in the task (as indexed by electrophysiological variables) would be a core predictor of learning rate. Therefore, we used a number of EEG, ERSP, and ERP variables (pretraining baseline alpha power, alpha and delta ERSPs, and P300 to important in-game events) measured during early phases of training to predict subsequent learning rate for each participant.

The electrophysiological measures provided robust prediction of subsequent behavior. Using a linear combination of these predictors, we accounted for almost 50% of the total variance in learning rate, in excess of what was accounted for by the initial game score. The baseline alpha and ERSP indices showed to be the best predictors, and also predicted the amount of skill improvement in tasks measuring cognitive control and reaction time outside of the game.

We first confirmed our hypothesis that brain activity associated with cognitive control, as indexed by the level of frontal EEG alpha power, can predict learning rate. Subjects with greater levels of alpha power benefited most from the training program. This correlation with overall frontal EEG alpha power is intriguing. It was present almost identically in all epochs during the game and was also evident during the oddball task outside the game environment. These data, and the high correlation between measures of alpha between different events in the game, indicate that the relationship between frontal alpha power and subsequent learning is consistent across a number of different conditions, and perhaps represents a general mode of responding of individuals to the experimental situation. Those subjects who most engaged in this mode of responding ended up being the better learners.

Historically, researchers proposed that alpha oscillations serve as a general indicator of boredom or task disengagement, or a general measure of the inactivity of the brain (e.g., Berger, 1929). Using this framework, we would need to assume that subjects with increased frontal alpha power early in training did not engage in the task early on but did so at a later time—thus generating both a low initial score and a greater amount of learning. However, our data indicate that the increased learning rate in subjects with high frontal alpha is independent of the initial score (i.e., it can be observed even when the initial score was partialled out). This suggests that the relationship between alpha and subsequent learning is not a spurious correlation due to both these variables being related to low initial performance. Rather, frontal alpha is related to some other phenomenon that supports better learning. Following our initial prediction, we propose that this phenomenon is cognitive control.

Note that this prediction is derived from recent reports (Jensen & Mazaheri, 2010; Klimesch et al., 2007; Mathewson et al., 2011; Thut et al., 2006) linking frontal alpha to control processes and attentional engagement, perhaps related to the suppression of irrelevant information (such as might occur while switching between different subcomponents of the game) or to the control of motor activities (such as ship flying). Although the current study was not designed to test predictions from these different models of alpha oscillations, the fact that the raw EEG alpha’s predictive power is constrained to a limited area over the frontal cortex provides further support for the proposal that this alpha activity does not represent a general state of inactivity or disengagement, as that would predict a more widespread or posterior alpha power relationship. The
frontal distribution of the effect indicates some degree of specialization of this activity, which is more consistent with the control process account.

In any case, engagement of cognitive control mechanisms appear closely related to task learning in and out of the game. The finding that frontal EEG alpha oscillations were also predictive of increases in task switching ability provides further support for the interpretation that this form of brain activity is related to individual differences in cognitive control. Interestingly, this raises the possibility that transfer of learning between the Space Fortress game and other tasks (such as task switching) may vary between subjects and depend on the extent to which the video game engages cognitive control operations, and that EEG measures, such as frontal alpha, may be used to monitor this engagement.

We were also interested in the oscillatory activity evoked by particular task events measured with the ERSPs and ERPs. This activity also reflects mobilization of attentional and processing resources. Predictive of subsequent learning was the amount of alpha activity evoked 300–700 ms after a fortress hit. This predictive ERSP alpha activity was largest over parietal brain areas and was clearly distinguishable from the frontal raw EEG alpha power reported above. Alpha activity in a frontoparietal network of brain regions has been tied to the engagement of attention systems (e.g., Klimesch et al., 1998; Romei et al., 2008a, 2008b, 2010; Mathewson et al., 2011). Within the context of this study, alpha activity may indicate the exertion of top-down control following successful fortress hits, which in turn may lead to faster learning. Since the phasic reduction of alpha after stimulation likely reflects a shift of attentional resources, this finding further corroborates the idea that the extent to which cognitive control operations are engaged during the Space Fortress task is a good predictor of subsequent learning.

It should be noted that the brain seems to have a number of different functions that produce 8–12 Hz activity. Indeed, in the current paper we discussed three: baseline level of EEG alpha, ERSP changes in alpha compared to baseline following important events, and lateralized oscillations over the motor cortex. These distinct oscillations may only share the frequency at which they operate, and further research is needed to disentangle the sources and functional relevance of these different alpha generators. It was interesting to observe that only the ERSPs following fortress hits were predictive of subsequent learning. Hitting the fortress is the main point of the game and a likely focus for participants early in training before they can juggle the multiple subtasks associated with the game, and thus may have particular salience and importance. We also found that the amount of ERSP delta activity evoked after fortress hits could predict subsequent learning, over and above the variance accounted for by initial game score and raw alpha EEG. Conversely, once initial score was partialled out, we did not find any relationship between ERPP300 amplitude early in training and subsequent improvements, even given a strong positive correlation between ERSP delta and P300 amplitude reported both here and by Maclin et al. (2011). This indicates a dissociation between these two measures. P300 appears closely related to online performance, whereas the ERSP measures may be better predictors of long-term behavioral outcomes. It should be noted, however, that ERSP measures may be less influenced than the ERP ones by temporal variations in the onset of cognitive processes, and by experimental error in the stimulus timing due to the video game environment (see Maclin et al., 2011, for a discussion). The P300 may also be more influenced by such things as the number of trials and both cognitive and technical jitter. Indeed, the P300 to fortress hits was more strongly correlated to initial game performance than the ERSP delta activity. Here, we were restricted to measurement of the P300, but we would predict that earlier sensory components should be even less associated with long-term behavioral outcomes. Future research should consider other high-level attention and control components such as the event-related negativity or the N2pc shift with attention, as the more removed a brain process is from the incoming sensory processing the more it should influence a task general manner.

In order to test the relationship between the various predictors, we submitted them to a stepwise multiple regression. The resultant model, including baseline alpha power, ERSP alpha power, and delta increases following fortress hits, accounted for almost 50% of the variance in learning rate, once the effect of initial game score was partialled out. Thus, our model based on the EEG activity recorded from individuals playing their first game of Space Fortress predicted relatively accurately the rate of their subsequent improvement. This provides an inexpensive and easy method of determining which subjects or trainees will most benefit from training. This predictive information is especially useful given the high test-retest reliability of EEG and ERSP measures (e.g., Fabiani, Gratton, Karis, & Donchin, 1987; Neuper, Grabner, Fink, & Neubauer, 2005; Towers & Allen, 2009).

Importantly, frontal alpha power predicted learning over and above the variance accounted for by the initial score in the game. This indicates that brain states manifested by frontal alpha have explanatory power over and above merely reflecting the current skill level. The predictive brain activity we observed here may represent a state of the brain favoring learning. In previous work, we have found a positive relationship between the size of frontal and parietal brain regions and learning of a complex, strategic video game (Basak et al., 2011), as are changes in long-range connectivity and functional relevance of these different alpha generators. It was interesting to observe that only the ERSPs following fortress hits were predictive of subsequent learning. Hitting the fortress is the main point of the game and a likely focus for participants early in training before they can juggle the multiple subtasks associated with the game, and thus may have particular salience and importance. We also found that the amount of ERSP delta activity evoked after fortress hits could predict subsequent learning, over and above the variance accounted for by initial game score and raw alpha EEG. Conversely, once initial score was partialled out, we did not find any relationship between ERPP300 amplitude early in training and subsequent improvements, even given a strong positive correlation between ERSP delta and P300 amplitude reported both here and by Maclin et al. (2011). This indicates a dissociation between these two measures. P300 appears closely related to online performance, whereas the ERSP measures may be better predictors of long-term behavioral outcomes. It should be noted, however, that ERSP measures may be less influenced than the ERP ones by temporal variations in the onset of cognitive processes, and by experimental error in the stimulus timing due to the video game environment (see Maclin et al., 2011, for a discussion). The P300 may also be more influenced by such things as the number of trials and both cognitive and technical jitter. Indeed, the P300 to fortress hits was more strongly correlated to initial game performance than
Electrophysiological predictors of learning rate


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