

Training-Induced Functional Activation Changes in Dual-Task Processing: An fMRI Study

Kirk I. Erickson¹, Stanley J. Colcombe¹, Ruchika Wadhwa¹, Louis Bherer², Matthew S. Peterson³, Paige E. Scalf¹, Jennifer S. Kim¹, Maritza Alvarado¹ and Arthur F. Kramer¹

¹Beckman Institute for Advanced Science and Technology, University of Illinois at Urbana-Champaign, Urbana, IL 61810, USA, ²Department of Psychology, University of Quebec, Montreal, H3C Canada and ³Department of Psychology, George Mason University, Fairfax, VA 20152, USA

Although training-induced changes in brain activity have been previously examined, plasticity associated with executive functions remains understudied. In this study, we examined training-related changes in cortical activity during a dual task requiring executive control. Two functional magnetic resonance imaging (fMRI) sessions, one before training and one after training, were performed on both a control group and a training group. Using a region-of-interest analysis, we examined Time × Group and Time × Group × Condition interactions to isolate training-dependent changes in activation. We found that most regions involved in dual-task processing before training showed reductions in activation after training. Many of the decreases in activation were correlated with improved performance on the task. We also found an area in the dorsolateral prefrontal cortex that showed an increase in activation for the training group for the dual-task condition, which was also correlated with improved performance. These results are discussed in relation to the efficacy of training protocols for modulating attention and executive functions, dual-task processing, and fMRI correlates of plasticity.

Keywords: anterior cingulate, attentional control, basal ganglia, dual task, executive function, parietal cortex, practice, prefrontal cortex

Introduction

The bustling nature of the 21st century demands that we skillfully and jointly attend to multiple tasks so that our roles and obligations as a parent, spouse, child, employee, and boss are all met and surpassed. The sheer number of tasks and obligations that we encounter in a single day requires that at least some tasks be performed in parallel. Although intuitively multitasking is not beyond our human abilities, there also seems to be an inherent limitation in our capabilities to juggle the increasingly large number of events in our lives.

Cognitive training programs provide one promising method for reducing costs associated with multitasking (Baron and Mattila 1989; Gopher 1993; Kramer and others 1995; Kramer, Larish, and others 1999). These training programs, in which performance on a task is methodically improved through instructional strategies and often individualized adaptive performance feedback over multiple sessions, has been shown to reliably reduce costs associated with performing multiple concurrent tasks (Kramer and others 1995; Kramer, Larish, and others 1999; Schumacher and others 1999; Glass and others 2000; Bherer and others 2006). Moreover, some of these training programs have found that trained skills 1) transfer to other tasks that had not been trained and 2) are retained for at least several months after formal training is concluded (Kramer and others 1995; Kramer, Larish, and others 1999; Roenker and others 2003; Bherer and others 2006) suggesting that the cognitive training programs can improve a somewhat general

dual-task ability rather than just strengthen a stimulus-response relationship specific to the trained task.

Although behavioral improvements resulting from multitask training regimens have been well documented, the changes in the neural mechanisms that underlie the behavioral improvements are not well understood. In this study, we examine the cortical changes in activity that accompanies training-related changes in performance.

A number of neuroimaging studies have now examined the neural dynamics, or learning-induced plasticity, associated with training and practice (e.g., Poldrack and others 1998; Fletcher and others 1999; Jancke and others 2001; Iaria and others 2003; Milham and others 2003; Erickson and others 2004; Koenke and others 2004). These studies have shown several different patterns of results. For example, some studies report decreases in activation (activity present before training, but then decreases or disappears after training) (Garavan and others 2000; Jancke and others 2001; Kassubek and others 2001; Milham and others 2003; Erickson and others 2004; Landau and others 2004), whereas others report increases in activation (activity present before training, but showing increases after training) (Tracy and others 2001; Schwartz and others 2002; Nyberg and others 2003; Furmanski and others 2004; Olesen and others 2004). Finally, some studies report a shift in the brain regions active between earlier periods versus latter periods of task performance (Poldrack and others 1998; Fletcher and others 1999; Staines and others 2002). In sum, the literature suggests that learning and training-induced changes in neural activity are not accompanied by a simple monotonic increase or decrease in activity (Landau and others 2004; Kelly and Garavan 2005).

Although studies of learning-induced plasticity have become more frequent in recent years, very few of them train executive control skills per se (excluding the working memory studies) despite numerous studies showing large effects of successful behavioral training on executive control tasks such as task switching (Kramer, Hahn, and Gopher 1999) and dual tasks (Kramer and others 1995; Kramer, Larish, and others 1999; Schumacher and others 1999). Indeed, understanding the neural correlates of executive control training will allow for an articulation of the extent and degree of plasticity available to executive functions in healthy adults.

Furthermore, some prior training studies have had a variety of shortcomings. For instance, only studies of clinical rehabilitation training programs (e.g., stroke, dyslexia; however, for an exception see Jancke and others 2001) have incorporated control groups not receiving any training (Carey and others 2002; Temple and others 2003; Morgen and others 2004; Sturm and others 2004). This drawback does not allow most prior

studies to separate training-dependent changes from training independent changes. In other words, changes in activation in many studies have been interpreted as training-induced effects, but they may have been related to other nontraining-related factors such as time-dependent changes in arousal, motivation, attentiveness, or other processes. In support of this possibility, numerous studies have found both increases and decreases in the degree of activation over very short periods of practice (<10 min) without any feedback, formal training, or behavioral improvements (Weissman and others 2002; Erickson and others 2004; Landau and others 2004), suggesting that time-dependent changes can occur without any formal training. One way to overcome this shortcoming, and to elucidate and isolate the effects of training on plasticity, is to incorporate a control group that receives the same protocol without the training episodes. A Time × Group interaction in the pattern of activation would reveal brain regions that were specifically activated by the training protocol and minimize effects due to nontraining-related phenomena. Another shortcoming of previous studies is that they typically have employed 10 or fewer participants. Employing very few participants makes generalization of the results more difficult and performance-related correlations more difficult to assess.

Finally, numerous behavioral training studies have reported that training often affects 1 task condition to a greater degree than other conditions. For example, Kramer and others (1995) reported that a cognitive training protocol improved performance more for a dual-task condition than a single-task condition. In addition, Landau and others (2004) reported greater practice-related changes in activation for higher memory loads, and Erickson and others (2004) reported greater changes in activation for the incongruent condition of a Stroop task. In the current study, we were able to assess the changes in activity in 3 different conditions on a task that has shown differential improvement for a dual task relative to single tasks. Therefore, we predict that the largest effects of training will occur for the more demanding and resource-taxing condition (dual-task condition).

Furthermore, in a previous study, we have shown (Erickson and others 2005) that a comparison of randomly and unpredictably intermixed dual-task trials and single-task trials elicits activation in brain regions involved in dual-task processing. Because dual-task trials often show the largest degree of performance improvement, we expected that the training protocol would affect these areas to a greater extent than other areas unassociated with dual-task processing. Therefore, the results from a 3-way interaction of Time × Group × Condition would reveal whether the training-induced changes in the pattern of activation differs by condition, and in the present case for single and dual tasks, for each region examined.

In sum, the current study was designed to address a number of important issues with respect to the neural correlates of training-related behavioral improvements. First, training in a paradigm requiring executive control, and more specifically dual-task processing, enabled us to study a series of processes not frequently studied in neuroimaging training studies. This allowed us to articulate the degree and extent of plasticity within the executive control system. In addition, we were able to assess training-induced changes for both single and dual tasks enabling us to examine the specificity of training effects. Finally, we recruited and ran over 30 participants for this study so that our sample was far larger than previously conducted neuroimaging training studies. Because of our relatively large sample size, we were able to randomly divide participants into training and control groups. This allowed us to examine Time × Group interactions in order to isolate training-dependent effects as well as locate the brain regions that correlate with behavioral improvements.

Methods

Participants

Thirty-one volunteers from the University of Illinois student community between the ages of 19 and 32 years participated. All participants were right-handed native English speakers and were screened for claustrophobia, metallic implants, and previous head trauma. The University of Illinois Institutional Review Board approved the study, and all volunteers signed an informed consent and were paid \$15 per hour for participating in the magnetic resonance imaging (MRI) session. The training and behavioral sessions paid \$10 per hour for participation. The 31 volunteers were randomly placed into either training or control group. Demographics of the 2 groups are presented in Table 1. All participants were also part of a slightly larger sample (34 volunteers) that focused on the results from the 1st MRI session before training on the task began (Erickson and others 2005).

Task

Both behavioral training and MRI trials were conducted in the following manner: a fixation point (*) was presented in the middle of the screen for 500 ms at the beginning of each trial. Participants were instructed to attend to the fixation point at all times. The stimuli were then presented on the screen and the participant was asked to respond to the stimuli by using their index and middle fingers of the right or left hand for each task. Response hand mapping was counterbalanced across subjects and was maintained throughout the training and MRI protocol. In the behavioral training sessions, the next trial was begun by the depression of the space bar. In the functional magnetic resonance imaging (fMRI) sessions, the next trial began after a fixed interval (2.5 s).

One of the single tasks presented the letter "X" in either the color yellow or the color green against a black background directly above a fixation cross in the middle of the screen. Participants were asked to respond as quickly and accurately as possible, via a button press, to the color of the "X", one button if yellow and another button if green. A star

Table 1

Demographic information for both the training and control groups

Variable	Training group	Control group	t-test	DM	SM
Sex	10 females, 6 males	9 females, 6 males	—	—	—
Age	25.75	21.73	3.01 (<i>P</i> < 0.005)	0.09 (<i>P</i> < 0.92)	0.41 (<i>P</i> < 0.68)
Years of education	17.62	14.18	3.53 (<i>P</i> < 0.001)	0.23 (<i>P</i> < 0.82)	0.02 (<i>P</i> < 0.98)
Health rating (1 = low, 5 = high)	4.56	4.73	0.71 (<i>P</i> < 0.48)	0.30 (<i>P</i> < 0.76)	-1.27 (<i>P</i> < 0.21)
Kaufman Brief Intelligence Test score (intelligence quotient)	107.15	112.92	1.87 (<i>P</i> < 0.07)	1.12 (<i>P</i> < 0.27)	0.65 (<i>P</i> < 0.52)

Note: The t-test column represents the results from a t-test for each variable between the 2 groups. Because of the significant differences in age and education we ran an additional linear regression analysis to examine whether any of the demographic variables reliably predicted training-related improvements in performance. These data are represented in the Dual-Mixed (DM) and Single-Mixed (SM) columns in the table (T-scores and probability values are represented).

(*) was simultaneously presented below the fixation cross at the same position as the 2nd single task. The 2nd single task presented the letter "B" or the letter "C" on the screen in white against a black background and directly beneath a fixation cross. Similar to the 1st single task, a star (*) was presented simultaneously above the fixation cross in the same position as the 1st single task. The stars (*) served to equate the total number of visual stimuli on the screen for both single- and dual-task conditions. Participants were asked to respond as quickly and accurately as possible, via a button press, to the letter, one button if "B" and another button if "C." Different buttons and different hands were used to respond to each of the single tasks. In the single-pure (SP) trial blocks, subjects were presented with the 2 different tasks in different blocks of trials. The presentation sequence of the 2 single-task trials was counterbalanced across subjects. This paradigm has been employed previously for studying the effects of randomly presenting single tasks with dual tasks in a mixed block (Erickson and others 2005).

The mixed block condition was a pseudorandom presentation of both types of single-task single-mixed (SM) trials presented individually as well as dual-task dual-mixed (DM) trials in which both single-task trials were presented simultaneously (0 ms stimulus onset asynchrony). The stimuli from the color discrimination condition were always presented above fixation, and the stimuli from the letter discrimination condition were always presented below fixation. Parameters from each of the stimuli remained the same from each of the single tasks. Participants were instructed to respond as quickly and accurately as possible and not to withhold any responses. Participants were not instructed to respond to the stimuli in a particular sequence, but most participants responded to the color discrimination task first followed by the letter discrimination task. The sequence of the trial order was unpredictable. This mixed block of trials has shown to reliably reduce potential confounds such as differential levels of task preparation between single- and dual-task trials (Erickson and others 2005).

Training Procedure

Participants were randomly assigned to either the training group or the control group. Before training began, both groups participated in an initial fMRI session with the single- and mixed-task blocks as described above. This session served as a baseline comparison to assess for changes in activation in the 2nd (posttraining) fMRI session. The resulting activation for the initial fMRI session has been described in a separate report (Erickson and others 2005).

After the 1st fMRI session, participants in the control group had approximately 2-3 weeks (mean of 17.20 days) of a break before being called back to the laboratory for the 2nd fMRI session. The training group, however, over a 2- to 3-week interval (mean of 16.94 days), received five 1-h sessions of formal training on the single and dual tasks with continuous and adaptive performance feedback. The feedback (response times only) was reported to participants by a histogram located in the top left corner of the screen. The bars indicated performance for the previous 5 dual-task trials. The bars appeared in red and changed to yellow and then green to indicate progressively better (faster) performance. This was done to motivate participants to continuously improve performance. A line at the top of the histogram showed the threshold criterion for good performance, which was continuously updated based on the participants response times to the SM trials. The criterion was continuously updated as the session evolved, and the response distribution of the SM tasks changed. Good performance was based on the 63rd percentile of the response time (RT) distributions of each task when last performed (Bherer and others 2006). Response times (instead of accuracy rates) were chosen as the measure to report to participants because previous dual-task training studies have shown that response times show the greatest improvement with training and effectively motivate participants to improve their performance (Glass and others 2000; Bherer and others 2006). However, accuracy was also monitored, and if participants responded to 2 sequential trials incorrectly the words "Be Careful!" appeared on the screen to indicate to them their error. Importantly, these feedback histograms were individualized and adaptive because they depended on the individual subjects performance. Individualized and adaptive feedback takes into account the starting points of each participant and does not rely on an absolute value as criterion. After 5 training sessions,

participants had completed 400 SP trials, 1600 SM trials, and 1600 DM trials. Similar trial counts have been employed in previous training studies (Bherer and others 2005). Because the procedure was self-paced during the training sessions, the amount of time it took to complete each block of trials not only varied between participants but also varied between sessions (as the participants became faster).

Once the training (or break for the control group) was over, both groups participated in a posttraining/interval fMRI session in which they were run in the same single- and dual-task protocol as the pretraining session.

fMRI Procedure

All stimuli were presented via a magnetic resonance compatible fiber optic goggle system (Magnetic Resonance Technologies), and responses were collected via a 4-button response pad. Visual acuity was corrected to at least 20/30. The stimulus onsets were fixed at an interval of 4.5 s, and each stimulus remained on the screen for 2 s, which left an interstimulus baseline of 2.5 s. In addition, an 18-s fixation period was introduced after every 8th stimulus trial. Each SP block had a total of 40 trials, whereas each mixed block had 60 SM trials and 60 DM trials for a total of 120 trials per mixed block. Although the trial order within a block of trials was pseudorandom and changed across participants, the order in which the blocks were presented was fixed for all subjects. Specifically, a block of color discrimination trials was presented first, followed by a block of letter discrimination trials, and then by a mixed block of dual and single trials. These 3 blocks were then repeated in the opposite order (mixed block, letter discrimination, color discrimination). This type of presentation controls for habituation and practice effects, while allowing the single tasks to be performed before the dual tasks so that participants have experience performing each task in isolation before being required to perform them simultaneously in the dual-task condition. These blocks were performed in the same sequence for both the fMRI sessions as well as the behavioral training sessions. In between each block of trials was a short break (~30 s) in which the participant was able to rest. The response button mappings for each stimulus condition were counterbalanced across participants. Pretraining and posttraining fMRI sessions had identical protocols. Similar types of hybrid paradigms have been used previously to investigate the effects of task switching (Braver and others 2003) and Stroop tasks (Milham and others 2001) on brain function.

The single and dual tasks that were used in the behavioral training sessions and MRI sessions were identical and conformed to the description above, except for the following differences: 1) the MRI sessions did not provide participants with any feedback, whereas the behavioral training sessions provided adaptive, individualized, and continuous performance feedback (see Training Procedure), 2) due to the necessity of time-locking events to the hemodynamic response in the fMRI sessions, the presentation of the trials in the fMRI sessions were force paced, whereas they were self-paced in the behavioral training sessions, 3) fewer trials were presented during a fMRI session than during a behavioral training session. This was due to a limited amount of time that participants could spend within the MRI environment, 4) a 4-button response pad was used for the MRI sessions, whereas a standard computer keyboard was used in the behavioral training sessions, and 5) a standard computer monitor was used for the behavioral training sessions, whereas an MRI compatible goggle system was used for presentation purposes in the MRI environment.

MRI Parameters and Preprocessing

A 3-T head-only Siemens Allegra MRI scanner was used for structural and functional MRI measures. For the fMRI protocol, we employed a fast echo-planar imaging (EPI) sequence with blood oxygenation level-dependent contrast and collected a total of 1760 T_2^* -weighted images per participant (time repetition = 1.5, echo time = 26, flip angle = 60) for pretraining and posttraining sessions. Sixteen slices (5 mm thickness, 3.75 mm in plane resolution, 0 gap) were collected in an ascending interleaved fashion parallel to the anterior and posterior commissures.

Two sets of anatomical images were also collected during both pretraining and posttraining MRI sessions: a high-resolution T_1 -weighted magnetization prepared rapid echo (0.96 × 0.96 × 1.3 mm) and a lower resolution T_1 -weighted image collected in the same plane as the EPI data.

Both sets of anatomical images were skull stripped using a brain extraction technique (Smith 2002) and subsequently used for registration purposes.

After reconstruction, the first 6 images were removed in order to allow the magnet to reach steady state. The data from the pretraining and posttraining sessions for every participant were preprocessed separately using FSL (FMRIB's Software Library) version 3.1 (<http://www.fmrib.ox.ac.uk/fsl/>). Images were slice-time corrected, motion corrected, temporally filtered with a Gaussian high-pass cutoff of 50 s and a low-pass cutoff of 1.5 s, and spatially smoothed with a 7-mm full-width half-maximum 3-dimensional Gaussian kernel.

Behavioral Data Analysis

We analyzed both the behavioral data collected in the MRI machine (response time and accuracy) and the behavioral data collected outside the MRI machine (pretraining and posttraining) with 2 separate repeated measures analyses of variance (ANOVAs) with Time (pretraining, posttraining) and Condition (SP, SM, DM) as within-subject factors and Group (control, training) as a between-subjects factor. To simplify the analyses, we only assessed the reaction time and accuracy from the pretraining and posttraining sessions. In addition, we conducted post hoc analyses to assess the effects of Time, Group, and Time \times Group for each of the conditions in order to determine the conditions that were most affected by the training manipulation. We also assessed differences between the control group and the training group for each condition at posttraining by a series of 1-way ANOVAs with the factor of Group (control, training) at 3 levels (SP, SM, and DM). This was done to assess whether the 2 groups reliably differed by the end of training and for which conditions they differed. All behavioral data were corrected for multiple comparisons using a Bonferroni correction at $P < 0.05$. All behavioral data were analyzed using SPSS 11.02 for Mac.

Neuroimaging Data Analysis

The neuroimaging data were analyzed separately for the pretraining and posttraining sessions and then compared at a higher level analysis (see below). For each session (pretraining, posttraining), we used a conventional linear convolution model where stimulus functions encoded the occurrence of each specific trial. These functions were convolved with a canonical hemodynamic response function (double gamma function) to form regressors in a general linear model (Beckmann and others 2003). Trial type-specific parameter estimates were computed using ordinary least squares for each subject in a 1st-level analysis. Temporal derivatives for each variable, motion correction vectors, and error trials were also modeled as covariates in the model (Calhoun and others 2004; Colcombe and others 2004; Erickson and others 2005). Errors were recorded in the dual-task condition when participants incorrectly responded to one or both of the stimuli. The direct comparisons (DM $>$ SM and SM $>$ SP) were performed on each subject separately at the 1st-level analysis. These subject-specific summaries of activation were then taken to a 2nd level for inference using between-subject error where we could assess the effects of each condition at each session (time 1 and time 2) and directly compare the activation across time. This 2-stage procedure (Holmes and Friston 1998) emulates a random-effects model and allows us to generalize our inferences to the population from which our subjects were drawn.

Although we analyzed both pretraining and posttraining sessions via a whole-brain approach, we used the peak results from the pretraining session (Erickson and others 2005) as regions-of-interest (ROI) in a hypothesis-driven approach to assess training-induced changes in activity via Time \times Group interactions and correlations with behavioral performance. Importantly, using a priori ROIs from the activation during the pretraining session allowed us to specifically examine the effect that training had on initial activation levels without having to control for effects due to differences in deactivation (Kelly and Garavan 2005) and provides us with a criterion for inclusion of regions into the longitudinal analysis. This hypothesis-driven approach of particular voxels of interest has been successfully used in prior studies (e.g., Wheeler and Buckner 2004; Greenberg and others 2005; Koenigsberg and others 2005). Therefore, the changes in the regions that we examined were in areas that were already known to be involved in task-relevant processing before training. Finally, choosing a series of ROIs and assessing the

effects of training in SPSS produce statistically identical results as that of FSL.

An ROI analysis on particular voxels that have been reported to be active in previous sessions of a longitudinal analysis has both benefits and drawbacks. First, as discussed earlier, prior cognitive training neuroimaging studies have not employed a control group. Because of this, the robustness of the effects from Time \times Group and Time \times Group \times Condition interactions across the entire brain was unknown. Therefore, a hypothesis-driven voxelwise ROI analysis provides predictions of training-induced activity change and minimizes the level of exploratory analyses in a whole-head analysis. In addition, examining ROIs in this way reduces the number of multiple comparisons and reduces overly conservative statistical thresholds in a priori ROIs. A drawback, however, of performing ROI analyses in this way is that we are limiting our analyses to specific voxels, despite the possibility of other training-induced changes occurring throughout other regions of the cortex. In relation to this, analyzing a voxel instead of a larger manually defined ROI may not provide an accurate representation of what is occurring throughout the rest of that region. For example, locating and assessing the activity in a voxel of the superior parietal lobule may not be representative of what is actually occurring throughout the rest of the superior parietal lobule. However, because of our interest in assessing how the cortical processors adapt to performing a dual task, we felt that a hypothesis-driven approach on peak voxels resulting from the pretraining session would be the most appropriate.

The results from the pretraining session have previously been described (Erickson and others 2005). Although the previous study (34 participants) shares participants with the current study, the training results from the current study are orthogonal to the results from the previous study and therefore are not biased based on the results from the pretraining session. The results from Erickson and others (2005) revealed that before training on this task, participants showed the following patterns of activation: 1) the comparison between the DM and SM conditions elicited activation in regions that were involved in dual-task processing including the left and right inferior frontal gyrus, dorsal anterior cingulate cortex, superior parietal lobules, and basal ganglia and 2) the comparison between the SM and SP conditions revealed areas of activation unrelated to dual-task processing. These regions overlapped with areas commonly associated with preparatory processes including a dorsal region of the right inferior frontal gyrus and superior parietal lobule. The peak voxels from each of the regions reported as active at pretraining (left and right inferior frontal gyrus, left and right superior parietal lobules, dorsal anterior cingulate cortex, and basal ganglia) were used as the voxels for the ROI analysis in the current study and interrogated for training effects using SPSS. The Montreal Neurological Institute coordinates for each ROI employed in the current study are described in Table 2.

In order to assess training-induced increases and/or decreases in activation in ROIs that were already active before training, we extracted the parameter estimates from both the pretraining and posttraining sessions for each of the 3 conditions from the ROIs described above and

Table 2

The voxel locations, coordinates, and Brodmann's areas (BA) used from Erickson and others (2005) as ROI in the current paper

Region	x	y	z	BA
Dual-task related (DM-SM)				
Anterior cingulate	7	21	28	32
Left ventral inferior frontal gyrus/insula	-37	19	-5	13
Right ventral inferior frontal gyrus	35	23	-11	47
Left superior parietal lobule	-31	-55	54	7
Right superior parietal lobule	25	-53	48	7
Left caudate	-10	14	-6	
Right caudate	9	10	-6	
Preparatory related (SM-SP)				
Right dorsal inferior frontal gyrus	34	10	24	9

Note: These areas were chosen because they were the peak coordinates that were reported from the pretraining session and therefore acted as a priori regions in the analysis described in this manuscript.

in Table 2. The parameter estimates at these voxels can be conceptualized as the effect size (compared against baseline) for that comparison at that point in space. In registered space (MNI space), these voxels have a resolution of $2 \times 2 \times 2$ mm. These values were then interrogated in SPSS in a similar fashion to the behavioral results using a series of repeated measure ANOVAs with Group (control, training) as a between-subjects factor and Time (pretraining, posttraining) and Condition (SP, SM, DM) as within-subject factors. These repeated measures ANOVAs were performed for each ROI, corrected for multiple comparisons (Bonferroni), and thresholded at $P < 0.05$. In addition, similar to the 1-way ANOVAs described in Behavioral in the Results section, the parameter estimates from the posttraining session were examined separately to investigate group differences in levels of activation for each condition after training. Finally, to examine the relationship between the behavioral improvements with training and the changes in neural activation associated with performance on the task, we conducted a number of correlations between change in performance and change in the degree of activation. The absolute change in reaction time for each condition was calculated, and the absolute change in activation for that same condition was used to perform the linear correlations. Results from all analyses were thresholded at $P < 0.05$. Similar to the behavioral analyses, the results from the Time \times Group interaction and Time \times Group \times Condition interaction were important to assess the regions of activation that do not just change with time, but that disproportionately change for the training group relative to the control group and for one condition more than the others.

Numerous neuroimaging studies of training and practice have reported new areas of activation in regions not active before training (e.g., Poldrack and others 1998). We investigated this possibility in our data by examining the voxel-based statistical parametric map for areas that did not reach the statistical threshold at pretraining but were above the threshold by posttraining. In order to ensure that the results from this analysis were not due to differences in deactivation across time and were instead activations in new areas, we extracted the parameter estimates from these areas from both pretraining and posttraining sessions and assessed whether the results from pretraining reliably differed from zero.

Analyses were carried out using FMRI Expert Analysis Tool version 5.1, part of FSL (<http://www.fmrib.ox.ac.uk/fsl>). Higher level analyses were carried out using FMRIB's Local Analysis of Mixed Events stage 1 only (i.e., without the final Markov chain Monte Carlo-based stage) (Behrens and others 2003). All results from the final whole-head analysis resulted in Z-statistic images that were thresholded using clusters determined by $Z > 3.1$ and a (corrected) cluster significance threshold of $P = 0.01$ (Friston and others 1994).

Results

For the sake of brevity, only the comparisons and interactions of interest for the questions posed in this study will be discussed.

Behavioral

Response Times

The mean RTs, accuracies, and standard deviations for the pre- and posttraining sessions are presented in Table 3 and Figure 1. First, results from the repeated measures ANOVA revealed a significant main effect of Time ($F_{1,29} = 49.67$, $P < 0.001$). Post hoc comparisons revealed significant reductions in mean RTs from pretraining to posttraining for the SP condition ($F_{1,29} = 18.48$, $P < 0.001$), the SM condition ($F_{1,29} = 37.30$, $P < 0.001$), and the DM condition ($F_{1,29} = 38.08$, $P < 0.001$).

Importantly, we found a significant Time \times Group interaction ($F_{1,29} = 15.57$, $P < 0.001$) such that there was a greater change in RTs between pretraining and posttraining for the training group relative to the control group. Finally, as predicted, we found a significant 3-way interaction between Time \times Group \times Condition ($F_{2,28} = 4.93$, $P < 0.01$). To isolate the effects from the 3-way

Table 3

Mean response times and percent accuracy scores with the standard deviations (in parentheses) for each task performed during the pretraining and posttraining sessions inside the MRI

Condition	Training		Control	
	Pretraining	Posttraining	Pretraining	Posttraining
Response time:				
SP	744.63 (132.53)	661.31 (133.05)	716.99 (157.31)	683.23 (154.41)
Single-mix	1074.61 (168.79)	877.59 (187.25)	1080.47 (158.52)	1032.18 (93.53)
Dual-mix	1364.80 (209.28)	1059.66 (222.96)	1320.32 (151.24)	1237.23 (184.95)
% Accuracy:				
SP	96.1 (3.0)	96.8 (3.0)	97.1 (2.0)	96.4 (2.0)
Single-mix	93.7 (4.0)	98.9 (2.0)	93.1 (2.0)	95.5 (2.0)
Dual-mix	8.1 (5.0)	98.4 (3.0)	90.2 (5.0)	91.8 (4.0)

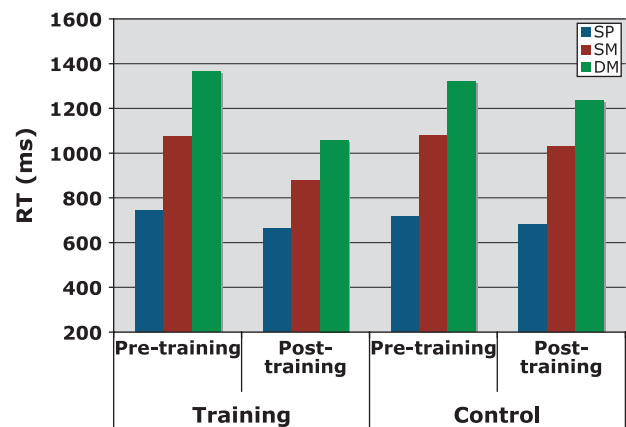


Figure 1. Reaction times for both the training and control groups for pretraining and posttraining sessions and for SP, SM, and DM conditions conducted inside the MRI (also see Table 4, for accuracy scores and standard deviations). The 1-way ANOVA, for the posttraining results, revealed no difference between the control and training groups for the SP condition ($F_{1,30} = 0.18$, $P < 0.68$) but a significant difference between control and training groups for the SM condition ($F_{1,30} = 7.81$, $P < 0.009$) and the DM condition ($F_{1,30} = 5.54$, $P < 0.02$), suggesting that the training group was reliably faster than the control group for both the SM and DM conditions after training.

interaction, we performed post hoc tests which revealed a trend for the SP condition ($F_{1,28} = 3.31$, $P < 0.08$) and a significant effect for the SM condition ($F_{1,28} = 13.71$, $P < 0.001$) as well as the DM condition ($F_{1,28} = 12.46$, $P < 0.001$). Therefore, we can conclude that the Time \times Group \times Condition interaction results from an improvement in performance for the training group relative to control only for the DM and SM conditions.

Accuracy

First, we found a significant main effect of Time ($F_{1,29} = 26.89$, $P < 0.001$). Post hoc tests revealed significant increases in accuracy from pretraining to posttraining for the SM condition ($F_{1,29} = 18.48$, $P < 0.001$) and DM condition ($F_{1,29} = 25.03$, $P < 0.001$), but no effect for the SP condition ($F_{1,29} = 0.003$, $P < 0.958$).

Importantly, we found a significant Time \times Group interaction ($F_{1,29} = 11.81$, $P < 0.002$) such that there was a greater improvement in accuracy between pretraining and posttraining for the training group relative to the control group. We also found a significant 3-way interaction of Time \times Group \times Condition ($F_{2,28} = 4.01$, $P < 0.03$). Post hoc tests revealed that this interaction was due to a significant effect for the DM condition ($F_{1,29} = 13.34$, $P < 0.001$), but not for the SP condition ($F_{1,29} = 1.26$, $P < 0.27$) or the SM condition ($F_{1,29} = 2.57$, $P < 0.12$). The 1-way ANOVA, for the posttraining results,

revealed no difference between the control and training groups for the SP condition ($F_{1,30} = 0.22$, $P < 0.64$) but a significant difference between control and training groups for the SM condition ($F_{1,30} = 8.45$, $P < 0.007$) and the DM condition ($F_{1,30} = 22.20$, $P < 0.001$), suggesting that the training group performed more accurately than the control group for both the SM and DM conditions after training.

Neuroimaging Results

We defined our hypothesis-driven functional ROIs based on the results from our previous single-session study (Erickson and others 2005). The comparison between the DM and SM conditions revealed regions that were involved in dual-task processing while minimizing effects related to task preparation and working memory between dual tasks and single tasks. As noted above, these regions included the left and right inferior frontal gyrus, anterior cingulate, left and right superior parietal lobules, and basal ganglia (see Table 2, for a list of the coordinates for each voxel used as an ROI in this study). We expected these regions to show the largest training-induced changes in activity. In addition, the dorsal inferior frontal gyrus, which was found in the comparison between the SM and SP conditions and thought to play a role in task-preparatory processes, was also examined for training-related effects.

Regions of Interest

First, from the repeated measure ANOVAs performed on each of the ROIs, we found main effects of Time in the following regions: right ventral inferior frontal gyrus ($F_{1,29} = 16.65$, $P < 0.001$), right superior parietal lobule ($F_{1,29} = 4.21$, $P < 0.05$), left superior parietal lobule ($F_{1,29} = 5.19$, $P < 0.03$), and right dorsal inferior frontal gyrus ($F_{1,29} = 562.07$, $P < 0.001$). Each of these regions showed a reliable reduction in activity from the pretraining session to the posttraining session (see Figs 2, 3, and 4). Moreover, as predicted, most of these regions showed a greater change from pretraining to posttraining for the DM condition than either the SM or the SP conditions. Other ROIs did not show main effects of Time.

One of our main interactions of interest was the Time \times Group interaction. This interaction reports regions that change differentially between the 2 groups. We found a significant Time \times Group interaction in the right ventral inferior frontal gyrus ($F_{1,29} = 12.40$, $P < 0.001$), right superior parietal lobule ($F_{1,29} = 4.71$, $P < 0.03$), right dorsal inferior frontal gyrus ($F_{1,29} = 75.23$, $P < 0.001$), and a trend for the left superior parietal lobule ($F_{1,29} = 3.44$, $P < 0.07$) (see Figs 3 and 4). These interactions all resulted from a larger reduction in activity for the training group relative to the control group. The other regions did not show Time \times Group interactions.

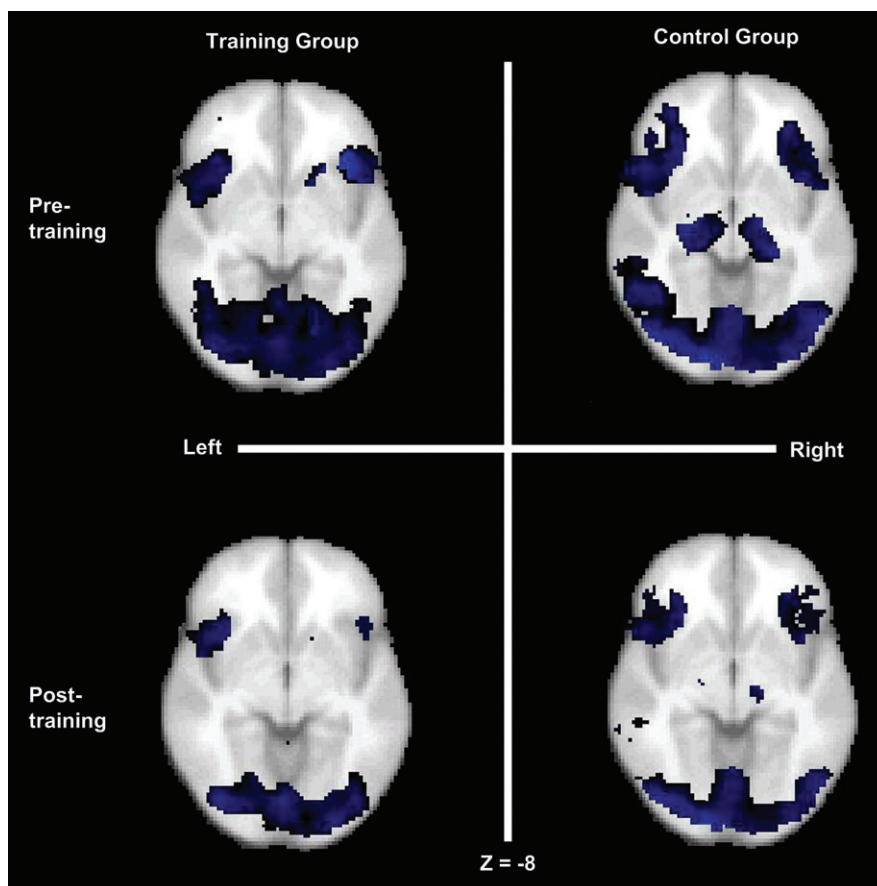


Figure 2. Neuroimaging results for the DM condition for the training group and control group at pretraining and posttraining sessions. As described in Methods, both pretraining and posttraining sessions were analyzed via a whole-brain approach, but the interactions (e.g., Time \times Group) and correlations with performance were conducted on a hypothetically driven voxelwise approach. The images shown here are the results from the whole-brain approach for both groups at both pretraining and posttraining time points. The images are represented in neurological convention and thresholded at a voxelwise $Z > 2.33$ and a cluster threshold of $P < 0.01$. The training group showed a reliable reduction in the right ventral prefrontal region.

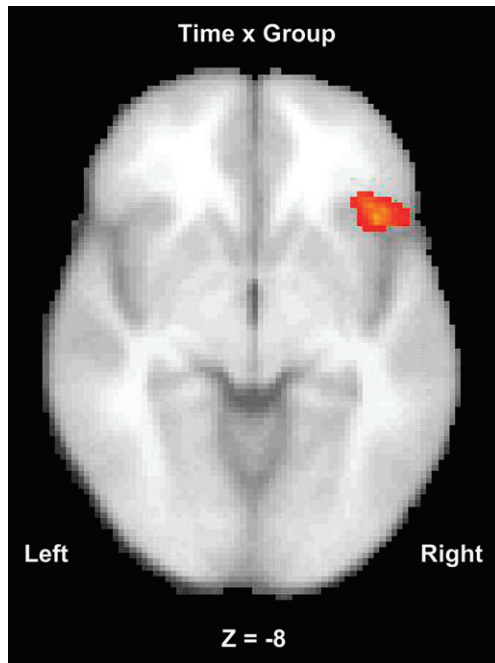


Figure 3. The image here shows the results from the Time \times Group interaction resulting from a significant decrease in activation from pretraining to posttraining for the training group relative to the control. As discussed in Methods, the Time \times Group interactions were conducted on voxel ROI, however, in this figure we show results from a whole-head analysis of the Time \times Group interaction and the resulting decrease in activation in the right ventral inferior frontal gyrus.

It should be noted, however, that the Time \times Group interaction was moderated by Condition in 1 region. There was a significant Time \times Group \times Condition interaction located in the right dorsal inferior frontal gyrus ($F_{2,29} = 8.32, P < 0.001$) ROI. However, we also found a trend for a 3-way interaction in the anterior cingulate ($F_{2,28} = 2.67, P < 0.08$) and right superior parietal lobule ($F_{2,28} = 3.09, P < 0.06$). In order to determine which conditions were driving these interactions, we conducted a series of post hoc comparisons to assess each individual condition. These results revealed that although all 3 conditions reliably changed with training, the effect was much greater for both the DM and SM conditions relative to the SP condition.

Time \times Group interactions and Time \times Group \times Condition interactions do not test whether the 2 groups reliably differed in their performance levels at the end of training. Therefore, we also conducted a series of post hoc t -tests to determine whether the 3 conditions differed from each other at the posttraining session. There are 2 potential outcomes from this analysis for the training group: 1) the differences between the conditions are reduced but still remain at posttraining or 2) the differences between the conditions are not present at the posttraining session. We found that this outcome differed by region. First, we found that the difference between the DM and SM conditions was not present after training in the anterior cingulate ($t_{1,15} = 0.04, P < 0.97$) or the right ventral inferior frontal gyrus ($t_{1,15} = 0.51, P < 0.62$). However, we did find a difference between the DM and SM conditions at posttraining in the left inferior frontal gyrus ($t_{1,15} = 3.08, P < 0.008$), left caudate ($t_{1,15} = 3.97, P < 0.001$), right caudate ($t_{1,15} = 3.09, P < 0.008$), left superior parietal lobule ($t_{1,15} = 2.36, P < 0.03$), and right

superior parietal lobule ($t_{1,15} = 2.31, P < 0.03$). Furthermore, we found that the right dorsal inferior frontal gyrus, although showing a reliable reduction in activity from pretraining to posttraining, continued to show reliably more activation for the SM than for the SP condition at posttraining ($t_{1,15} = 3.13, P < 0.007$). These results suggest that a few regions show an absence of a difference between the DM and SM conditions at the posttraining session, but most of the regions continue to show greater activity for the DM condition than the SM condition even after training. Furthermore, the difference between the SM and SP condition is greatly reduced by the posttraining session in the dorsal inferior frontal gyrus, but the difference between the two conditions still remains.

Whole-Head Analysis

We also conducted a whole-head voxelwise analysis to determine whether any regions outside of our functionally defined ROIs were changing as a function of training. We found that 2 new regions were active for the Time \times Group interaction for the DM condition (see Figs 5 and 6). Both of these regions were located in the inferior and middle frontal gyrus of the dorsolateral prefrontal cortex (DLPFC) in homologous regions in both hemispheres. To ensure the direction of this effect and to reveal whether this change was an actual increase in activity or a reduction in a deactivation from pretraining (Kelly and Garavan 2005), we extracted the parameter estimates from the peak voxel from both hemispheres from both the pretraining and posttraining sessions (see Fig. 6). The parameter estimates revealed that although this region was not statistically different from zero at the pretraining session, it became active by the posttraining session, but only for the training group. From a repeated measures ANOVA, we found a significant Time \times Group \times Condition interaction for both the left ($F_{2,28} = 24.48, P < 0.001$) and right ($F_{2,28} = 12.68, P < 0.001$) DLPFC. Post hoc analyses found that this 3-way interaction resulted from a significant increase in activity for the training group relative to the control group for both the SM condition ($F_{1,29} = 11.93, P < 0.002$) and the DM condition ($F_{1,29} = 111.17, P < 0.001$) for the left DLPFC and for the DM condition ($F_{1,29} = 122.61, P < 0.001$) for the right DLPFC (see Table 4 and Fig. 6).

In addition, similar to the ROI analyses described above, we conducted a post hoc 1-way ANOVA at the posttraining session to determine if the 2 groups reliably differed at the end of training. We found that the 2 groups did not differ for the SP condition in either the left ($F_{1,30} = 0.007, P < 0.93$) or the right ($F_{1,30} = 0.49, P < 0.49$) DLPFC, but did reliably differ for both the SM condition ($F_{1,30} = 6.50, P < 0.016$) and the DM condition ($F_{1,30} = 115.86, P < 0.001$) in the left DLPFC and for the DM condition ($F_{1,30} = 128.32, P < 0.001$) in the right DLPFC. These results argue that although these 2 groups did not differ in the magnitude of activity in this region before training, they reliably differed after training.

Correlations

We also conducted correlations between the changes in activity (parameter estimates) from the pretraining session to the posttraining session for the training group with the change in performance (reaction time). These analyses were only conducted with the training group because they, and not the control group, showed reliable changes in activity and performance between pretraining and posttraining. Therefore, our

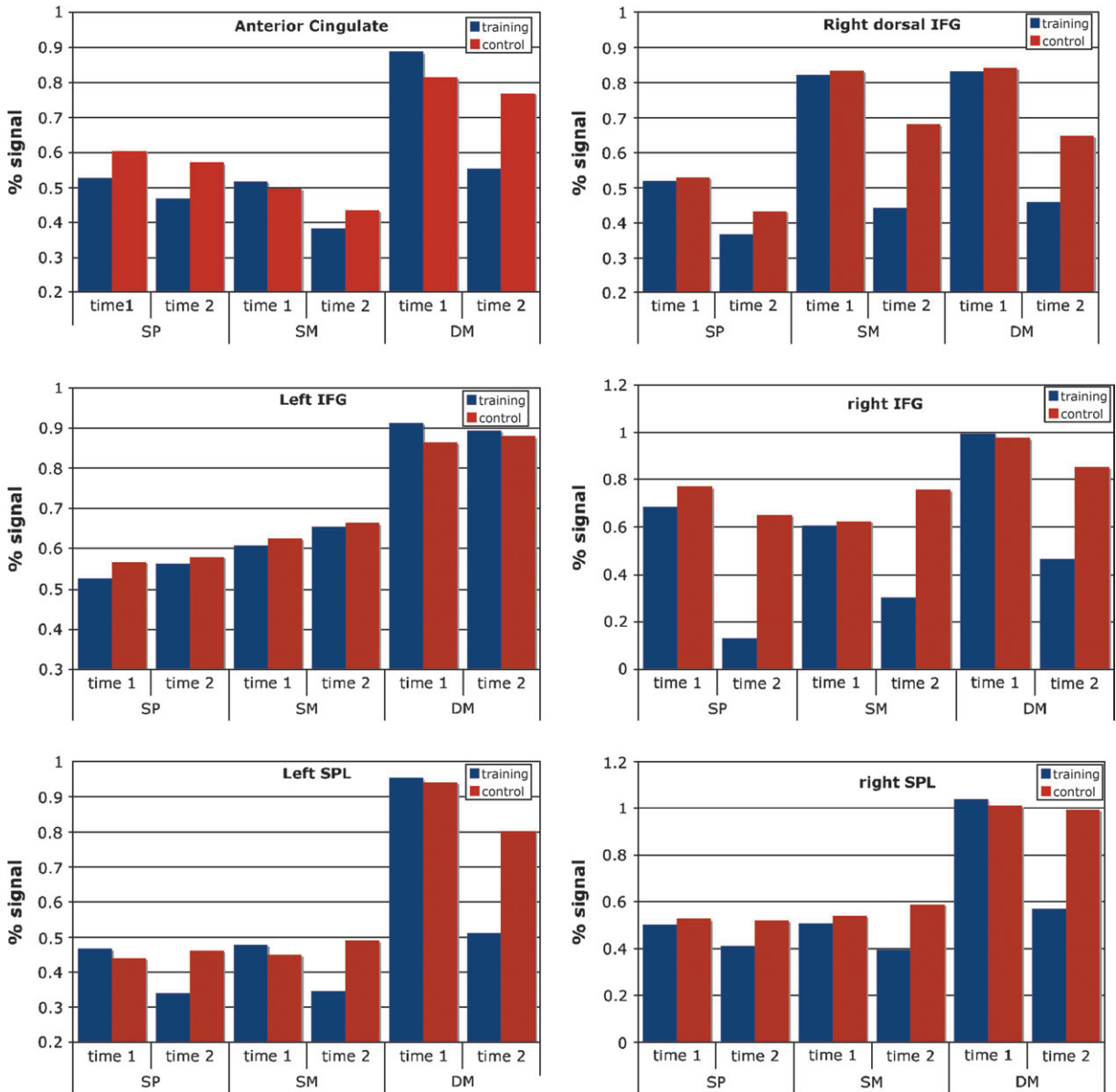


Figure 4. The percent signal change for each condition (SP, SM, DM) for pretraining (time 1) and posttraining (time 2) sessions for the anterior cingulate, right dorsal inferior frontal gyrus (right dorsal IFG), left inferior frontal gyrus (left IFG), right inferior frontal gyrus (right IFG), left superior parietal lobule (left SPL), and right superior parietal lobule (right SPL). All regions show a decrease in activation for the training group.

questions regarding the correlations are specific to the effects of the training group and the relationship between the training-induced changes in activity and behavior.

We found a significant correlation between an improvement in reaction times for the SP condition and change in activity for the right ventral inferior frontal gyrus ($r = 0.85, P < 0.001$) and right dorsal inferior frontal gyrus ($r = 0.86, P < 0.001$). We also found a significant correlation between an improvement in reaction times for the SM condition and change in activity for the right ventral inferior frontal gyrus ($r = 0.59, P < 0.015$), right dorsal inferior frontal gyrus ($r = 0.85, P < 0.001$), and a trend for the right superior parietal lobule ($r = 0.47, P < 0.06$). Finally, we found a significant correlation between an improvement in reaction times for the DM condition and change in activity for the anterior cingulate ($r = 0.62, P < 0.01$), right ventral inferior frontal gyrus ($r = 0.58, P < 0.01$), right superior parietal lobule

($r = 0.86, P < 0.001$), left superior parietal lobule ($r = 0.86, P < 0.001$), and right dorsal inferior frontal gyrus ($r = 0.88, P < 0.001$). These correlations suggest that the training-related improvements in behavior are related to the degree of reduced activation in these areas.

In addition, we found that the 2 areas that showed an increase in activity with training also correlated with improved performance. Specifically, the improvement in reaction times for the SM condition and change in activity for the left DLPFC was significantly correlated ($r = -0.51, P < 0.05$). Furthermore, we found a significant correlation between an improvement in reaction times for the DM condition and change in activity for the left DLPFC ($r = -0.73, P < 0.001$) and right DLPFC ($r = -0.72, P < 0.001$). These correlations suggest that the training-related improvements in behavior for the DM condition were also related to the degree of increased activity in both these areas.

It is important to note that these correlations are unlikely to simply reflect the duration of neuronal activity before a response was made because we find both positive and negative correlations between performance and neuronal activity, and second, the response times in this paradigm and analysis are a behavioral-dependent measure and not an explanatory variable.

Discussion

There are several general conclusions that can be drawn from the results of this study. First, executive control processes and their underlying brain regions are plastic and adaptive and can be modified by training. We found that learning, or training of a task requiring executive control, clearly results in specific changes in task-related brain activity, even after accounting for nontraining-related changes in the control group. Whether these training-induced effects can be applied to populations

with executive dysfunctions, or people who have deficits in performing executive tasks—such as older adults, is an important question and deserves future research (Ball and others 2002; Kramer and others 1994).

Second, cognitive training regimens did not influence the performance exhibited in each condition equally. Similarly, we find that the magnitude of the change in brain activity was not equivalent for all conditions. Instead, the magnitude of the change was sometimes related to the condition that showed the largest behavioral improvements (dual-task condition)—but this was also dependent on the brain region examined. Previous studies have examined training effects and shown a variety of patterns, but some of this variance between studies may be accounted for by the condition being studied, how amenable the process is to being trained, and the degree to which the training successfully reduces cognitive costs or workload associated with that condition. In our study, the dual-task condition was not only the most demanding but also the most amenable to training.

Importantly, the cortical changes that occurred in the dual-task condition shed light on how the brain responds to challenging tasks. The results of our study suggest that training reduces the differences between conditions (e.g., between dual-task conditions and single-task conditions) and that brain activity associated with performing these tasks converges over time and practice. Although our analyses indicated that many regions still showed a reliable difference between dual-task and single-task activation after training, there was a decrease in the magnitude of the difference after training—such that the dual-task condition began to converge toward the single-task conditions. This indicates that the cortical processors involved in dual-task performance became more adept at a process more specific to the dual-task condition, such as managing and coordinating multiple tasks.

Third, the training program resulted in two general changes in brain function: 1) many of the regions that were active before training showed “decreased” activity by the end of training and 2) one area in the dorsal prefrontal cortex that was below statistical threshold before training became active after training, thus showing a training-related “shift” in the location of dual-task-related activity. This shift in the location of activity may represent a training-induced reorganization of the cortical areas involved in dual-task processing (Poldrack and others 1998; Fletcher and others 1999; Staines and others 2002) resulting in more efficient task performance. These results support previous

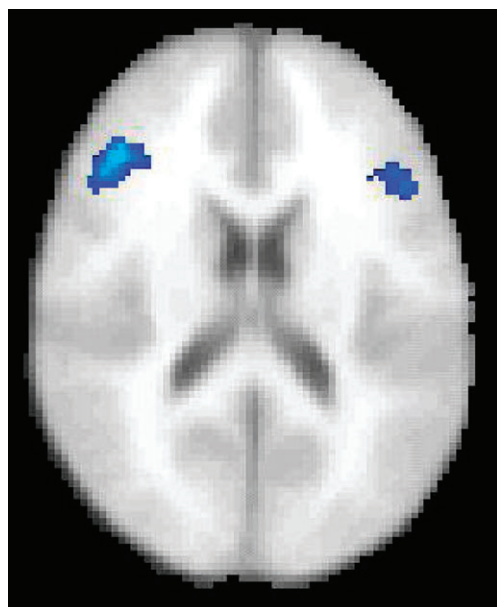


Figure 5. The DLPFC regions (inferior and middle frontal gyrus [Brodmann area 45]) that show increases in activity from pretraining to posttraining sessions for the training group. Shown here is the increase in activity for the DM condition in neurological convention (left is on the left). The statistical map is thresholded at a $Z > 3.1$ and a (corrected) cluster significance threshold of $P = 0.01$.

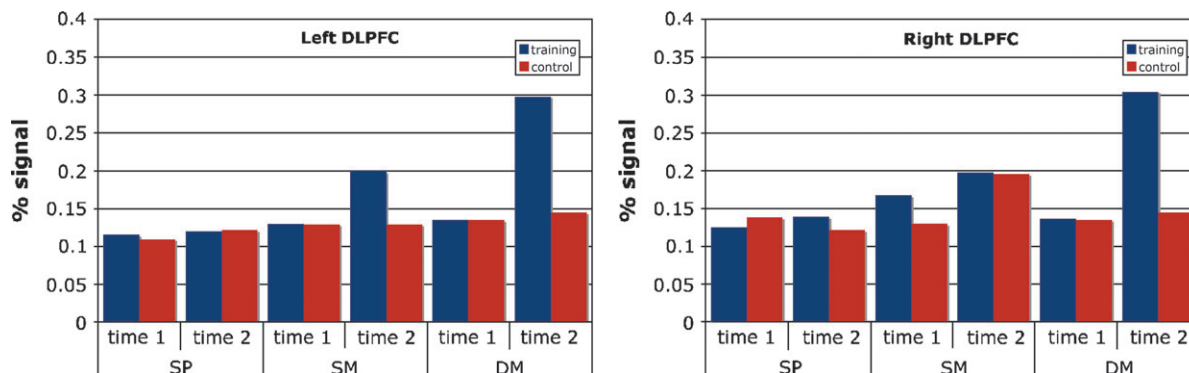


Figure 6. The percent signal change for each condition (SP, SM, DM) for pretraining (time 1) and posttraining (time 2) sessions. Both regions showed a training-induced increase in activation from pretraining to posttraining for the DM condition.

Table 4

The regions, coordinates, Brodmann's areas (BA), and Z-scores for the results from the Time \times Group increases in activation for the DM condition

Region	x	y	z	BA	Z-score
Left inferior/middle frontal gyrus	-50	24	20	45	3.73
Right inferior/middle frontal gyrus	-46	22	8	45	3.45

claims that training does not result in a monotonic increase or decrease in activity (Landau and others 2004; Kelly and Garavan 2005).

Training-Induced Changes

In this section, we focus mainly on the results from the Time \times Group interactions in different brain regions, as well as the role that the different conditions play within the interaction (Time \times Group \times Condition).

First, similar to previous dual-task training studies, we found a reliable improvement in performance with training (Kramer and others 1995; Kramer, Larish, and others 1999; Schumacher and others 1999; Bherer and others 2006). We found that the training group showed the largest improvement in the DM condition, but also showed a reliable improvement in the SM condition. These results indicate that the trained participants reliably learned to reduce both reaction time and accuracy costs associated with multitasking.

Our neuroimaging results revealed a number of regions showing greater changes in activity for the training relative to the control group. Both the right and left superior parietal lobules were active before training began and were more active for the DM condition than the SM condition (Erickson and others 2005) suggesting a specific role for this region in the management of multiple tasks. Our training results revealed that both regions showed reliable training-induced reductions in activity correlated with behavioral improvement. Erickson and others (2005) argued that the parietal regions active in this task were involved in mediating stimulus-response associations and attending to relevant stimuli. It is possible that the training results represent a change in the ability to respond to the appropriate stimulus-response association (Corbetta and Shulman 2002; Brass and Von Cramon 2004; Erickson and others 2005), or a change in the allocation of attentional resources needed to efficiently deal with task demands (Corbetta and Shulman 2002). An additional possibility is that because our paradigm presented stimuli in 2 different spatial locations, the change in activation in the parietal regions may represent an increased ability to allocate attention over a larger field of view.

Interestingly, both the right and left ventral inferior frontal gyri were more active for the DM condition than the SM condition at the beginning of training. By the end of training the activity in these 2 regions differed. First, the activity in the left ventral inferior frontal gyrus continued to show more activity for the DM condition than either the SM or the SP condition, and importantly, there was no change in the magnitude of the activity for either group from pretraining to posttraining. In short, the activity in this region did not change with training. Interestingly, this area was located near language production centers (Broca's area). Therefore, it may be that subvocalization of stimuli is present before and after training and is minimally affected by the training protocol. In support of this argument, recent research suggests that inner speech production provides

an important contribution to the flexible reconfiguration of task sets in task-switching paradigms (Kray and Lindenburger 2000; Gruber and Goschke 2004; Kray and others 2004). These studies have shown that preparation for a task switch consists of the retrieval of verbal representations or goals into working memory (Goschke 2003). In addition, people who have left hemisphere damage show larger switch costs than those participants without speech deficits (Mecklinger and others 1999). In the current study, subvocalization processes are likely to be greater for the dual-task condition in which 4 different stimuli and their responses are likely being rehearsed and recalled than single-task conditions in which only 2 stimuli and their associated responses are being rehearsed. It is likely that verbal recall of the task goals, stimuli, and responses remain important in successful completion of task demands, even after training, resulting in no training-related changes in activity in regions such as the left inferior frontal gyrus.

The right ventral inferior frontal gyrus, however, showed a different pattern between pretraining and posttraining. In this region, we found a significant Time \times Group interaction such that the training group showed a reliably larger reduction in activity than the control group. Although this region showed greater activation for the DM condition relative to the SM condition at pretraining, the magnitude of activity in the DM condition was reduced to the same level of the SM condition by posttraining. We also found that this region showed a reduction in activity for all 3 conditions and was not just specific to the DM task. Finally, significant correlations between improved performance and reduction of activity in this region were found for all conditions, suggesting that the effect of training on this region is affecting a process common to all 3 conditions. Importantly, similar right inferior frontal gyrus regions have been shown to be involved in other dual task and psychological refractory period tasks (e.g., Herath and others 2001) and have been the focus of some of them (Jiang and others 2004). One possible explanation for this training-related change in activity is a reduction in the cognitive and neural resources needed to select the appropriate responses after training as similar areas have been implicated in response selection processes (Milham and others 2001; van Veen and others 2001).

Interestingly, although the caudate and basal ganglia structures have been related to some types of learning and memory (Packard and Knowlton 2002), we found that in our study the caudate did not show any changes from pretraining to posttraining sessions for either group. The caudate and basal ganglia have been associated with sequence learning, response-based learning, and procedural learning as well as dual-task processing (Brown and Marsden 1991). In addition, previous studies have reported increases in caudate activation after training on mirror-reading tasks (Poldrack and Gabrieli 2001). We find, however, that this region is involved in dual-task performance both before and after training and does not change in the degree of activity for any condition for either group. The difference between the results from the current study and Poldrack and Gabrieli (2001) may be due to differences in the tasks employed or differences in the strategies used to perform each task or may be related to the type or length of training conducted.

Interestingly, we also found that an area of the DLPFC in both hemispheres showed an increase in activity from pretraining to posttraining, and this increase was largest for the DM condition and present only for the training group. Furthermore, this increase in activity was correlated with improved performance

on the task. A recent working memory training study also reported increases in activation in the DLPFC regions (Olesen and others 2004). It is interesting that this region shows opposite effects of training from that of every other region that we examined in this study. The meaning of this “re-organization of function” (e.g., Kelly and Garavan 2005) has been argued as representing a fundamental change in the strategy and cognitive operations employed to perform the task. Furthermore, this region was not significantly greater than zero before training and was not characteristic of the definition of Kelly and Garavan (2005) of redistribution of function in which the levels of activity change, but the regions do not change. At this point, we can only speculate about what cognitive operations have changed from pretraining to post-training, but one possibility is that the training group learned to rely on central executive operations in order to maintain heightened and efficient task performance.

It should be noted that we found and reported a number of training-related changes in activity that were correlated with improved performance on the dual task. There are a few important considerations regarding these correlations. First, although there were not a large number of participants in our study, the size of the correlation proved quite large, indicating that there was a relatively close coupling between brain and behavior. Despite this robustness, the smaller sample size is one limiting factor of our study. Future studies should address whether these correlations remain after including more participants. Second, both training-related increases and decreases in activity were correlated with performance, indicating that these correlations cannot be explained according to an argument that the training group had a shorter duty-cycle after training. If this were the case, and the correlations driven by a duty-cycle effect, then a correlation with increased activity in DLPFC regions would not have been found. Finally, the correlations with performance were found for multiple brain regions, indicating that training and behavioral improvements result in a change across the entire network involved in task demands and not just in an isolated region. It may be interesting for future research to assess the training-induced changes in the cortical network by connectivity analyses to assess how these regions interact to produce behavioral improvements.

One potential caveat of this study and any other neuro-imaging study that assesses training-related improvements in behavior is the possibility that the inclusion of more (correct) trials after training provides a better statistical estimate of the effect than control groups that have more errors and fewer included trials (Poldrack 2000). Although it is difficult to determine what effect the error trials had in this particular study, we did remove errors from the statistical model both before and after training. To elaborate on the potential size of this effect, the greatest change in performance occurred for the DM condition (nearly a 10% improvement), which in terms of the total number of trials would have added an average of 12 trials out of 120 total trials to the estimation of the effect at the posttraining session. This can be compared with the control group that showed a 1.5% improvement in accuracy from pretraining to posttraining, which would have added a total of 2 trials out of 120 total trials. This difference of 10 trials between the groups may have some influence on the outcome of the results, but it is difficult to tell exactly how much. Additionally, adding the error trials back into the analysis would not be able to remedy this potential confound. However, the reason for

conducting this study with this paradigm was to examine the neural correlates of training on a task that shows large improvements in behavior. Despite this fact, the change in the number of errors remains a potential caveat that other training studies should also take into consideration.

In sum, we find that many of the areas that were involved in dual-task processing and task-preparation decrease in activity as a result of an individualized and adaptive cognitive training regimen. It is likely that this change in activity represents an increase in neural efficiency such that fewer brain regions are needed to perform dual tasks (Garavan and others 2000; Kassubek and others 2001; Poldrack and Gabrieli 2001; Callan and others 2003; Landau and others 2004). The correlations with improvement in behavior support this claim. However, bilateral DLPFC regions show a training-related increase in activity for the DM condition indicating a potential switch in the strategy employed to perform the tasks. Therefore, we can conclude that 1) cognitive training regimens result in both decreases and increases in brain activity, 2) the largest changes occur for the DM condition, and 3) the changes in activity are highly correlated with improvement in performance. Further research on the applicability and transfer of these effects to other tasks and populations is warranted.

Notes

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Address correspondence to Kirk I. Erickson, Beckman Institute for Advanced Science and Technology, 405 North Mathews Avenue, Urbana, IL 61810, USA. kiericks@uiuc.edu.

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