

Practice-induced changes of brain function during visual attention: a parametric fMRI study at 4 Tesla

D. Tomasi,* T. Ernst, E.C. Caparelli, and L. Chang

Medical Department, Brookhaven National Laboratory, Upton, NY 11973, USA

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A parametric functional MRI (fMRI) study with three levels of task difficulty was performed to determine the effect of practice and attentional load on brain activation during visual attention tasks. Brief practice during repeat fMRI scanning (20 min) did not change performance accuracy or reaction times (RT), but decreased activation bilaterally in the inferior, middle, and superior frontal gyri, superior temporal gyrus, thalamus, and cerebellum. Increased attentional load decreased performance accuracy but not RT, and increased activation bilaterally in the inferior, posterior, and superior parietal cortices, thalamus, cerebellum, and frontal gyri. These changes suggest that practice decreases dependency on thalamus, cerebellum, and the frontal cortices for controlled task processing possibly due to increased efficiency of the attentional network. Since short-term practice-effects in the prefrontal cortex may be similar to attentional load-effects, studies of attentional load need to take practice effects into account.
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Introduction

Several studies suggest that the human brain has a limited capacity for processing new information (Kastner et al., 1998; Marois et al., 2000; McEvoy et al., 1998; Rees et al., 1997). However, practice can improve task performance by increasing accuracy, decreasing variability, as well as decreasing the effort and time required for a given task (Jansma et al., 2001).

The neural correlates of skill learning processes were studied in recent years by powerful neuroimaging techniques. For instance, the effect of practice on mirror reading (Poldrack et al., 1998) and visual attention (Weissman et al., 2002) was studied

by functional magnetic resonance imaging (fMRI), while practice effects on verbal and motor (Petersen et al., 1998) tasks was evaluated with positron emission tomography (PET). These studies found different activation patterns before and after repeated learning trials and support the theory that different subsystems are involved in novel and practiced or learned task-processing (Logan, 1988).

In contrast, practiced trials compared to the initial trial during semantic memory (Gabrieli et al., 1996), verbal working memory (Jansma et al., 2001), or visuospatial working memory (WM) (Garavan et al., 2000) all showed the same activation patterns on fMRI, except for less brain activation (i.e., BOLD signal) in the prefrontal cortex (PFC) during practiced trials. Similarly, PET studies showed decreased cerebral blood flow (CBF) in the PFC after practice for verbal (Petersen et al., 1998) and visuospatial WM (Pettersson et al., 1999). These findings suggest that practice decreases the dependence on attentional and working memory resources, possibly due to increased neural efficiency.

Compared to short-term practice, long-term practice on mirror reading tasks demonstrated further decreased activation in frontal, premotor, and occipital cortices, suggesting that skill learning (the acquisition of general task procedures with practice) and repetition priming (item-specific learning) may share common neural substrates for a particular task (Poldrack and Gabrieli, 2001). In contrast, long-term compared to short-term practice on motor tasks further increased brain activation in the primary motor cortex (Karni et al., 1998). Only one study has evaluated the effect of short-term practice on a visual attention task that involved cued attentional orienting and interference and found reduced recruitment of inferior parietal regions but increased recruitment of midline frontal regions after practice (Weissman et al., 2002). Knowledge regarding the effect of short-term practice on BOLD signals during attention-requiring tasks is particularly important since subjects often have to repeat these tasks (e.g., due to poor performance, motion, or study design) during the same scanning sessions. Furthermore, no study has evaluated the effect of practice on attentional load; it is unclear whether increasing attentional requirement would ameliorate the practice effects.

* Corresponding author. Medical Department, Building 490, Brookhaven National Laboratory, 30 Bell Avenue, Upton, NY 11973. Fax: +1 631 344 7671.

E-mail address: tomasi@bnl.gov (D. Tomasi).

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In the present fMRI study, we investigated the effect of brief practice on brain activation during a set of pure visual attention tasks with variable levels of attentional load (Pylyshyn and Storm, 1988). This visual attention paradigm has been shown to modulate brain activation with attentional load (Culham et al., 2001; Jovicich et al., 2001). To further assess the relationship between brain activation, attentional load, and practice, fMRI was performed in a larger population (25 healthy subjects) and at a higher magnetic field (4 T).

Materials and methods

Subjects

Twenty-five healthy, non-smoking, right-handed volunteers (14 men and 9 women, age 42 ± 16 years, education: 15 ± 2 years) with normal vision participated in the study. Before the study, each subject signed a written consent, approved by the Institutional Review Board at Brookhaven National Laboratory. Subjects were screened carefully with a detailed medical history, physical, and neurological examination, blood and urine screening tests, to ensure they fulfilled all the study criteria. Inclusion criteria were (1) age 18 years or older; (2) English speaking and uses English as a first language; (3) healthy and under no medications (except for vitamins); (4) ability to provide consent and willing to participate in the study. Exclusion criteria were: (1) history of head injury with lost of consciousness >30 min; (2) current or past drug abuse or dependence (including nicotine and alcohol) or positive urine toxicology (for cocaine, amphetamines, marijuana, benzodiazepines, and opiates); (3) any past or current medical or neuropsychiatric illnesses; (4) significant abnormalities on screening blood tests, including a complete blood count, a chemistry panel, thyroid function tests, a positive HIV test or Hepatitis tests; (5) pregnancy (assessed by a urine test) or breast-feeding if female subjects; (6) any contraindications for MRI (e.g., metallic implants or claustrophobia).

Activation paradigm

Subjects performed a set of non-verbal visual-attention tasks, which involved mental tracking of two, three, or four out of 10 moving balls (Culham et al., 1998; Jovicich et al., 2001). During the “TRACK” periods, the target balls (2, 3, or 4) were briefly highlighted, and then all 10 balls started to move. Subjects were instructed to fixate on the cross while mentally tracking the target balls as they moved randomly across the display. At the end of “TRACK” periods, the balls stopped moving and a new set of balls was highlighted, and subjects were trained to press a button if these balls are the same as the target set. Hence, reaction times and accuracy in performance were recorded. After 0.5-s delay, the original target balls were then re-highlighted to re-focus the subjects’ attention on these balls, and the sequence was repeated five times. During “DO NOT TRACK” periods, all 10 balls moved in the same manner; however, no balls were highlighted. The subjects were instructed to stop tracking the balls and view them passively. The stimuli and fMRI paradigm are outlined in Fig. 1. These tasks activate a neural network that includes primarily the dorsolateral prefrontal cortex (DLPFC), inferior and superior parietal lobes (IPL and SPL, respectively),

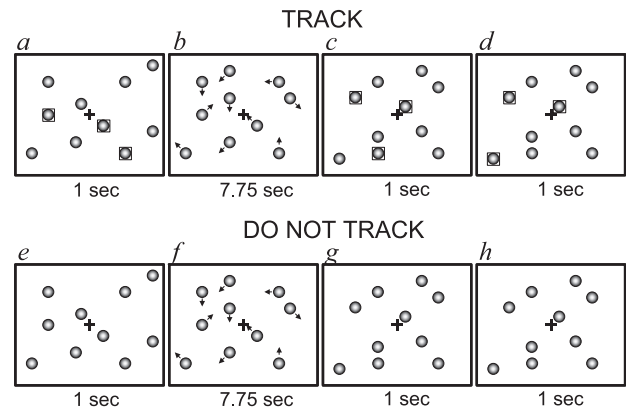


Fig. 1. Schematic representation of active tracking (top row) and passive viewing (bottom row) blocks for the “3 balls” visual stimulus. Each trial began with a text cue (for 1.25 s, not shown), indicating the type of trial. In active-tracking blocks, the text cue was followed by (a) highlighting the target set, (b) attentive tracking, (c) highlighting a 3-ball set (if this was the target set, subjects reported by pressing the response button), and (d) re-highlighting the target set to refresh the original set of balls. During passive viewing, the text cue was followed by (e) a period of static balls without highlight, (f) passive viewing of moving balls, and two periods of static balls without highlights (g and h).

cerebellum, and motion areas V5/MT+ (Culham et al., 1998; Jovicich et al., 2001).

The stimuli were created as movies in AVI (“Audio Video Interleave”) format using Matlab, and presented to the subjects on MRI-compatible LCD goggles connected to a personal computer. The display software was synchronized precisely with the MR acquisition using an MRI trigger pulse. All response button events during stimulation were recorded using the Visual Basic and Visual C languages to determine task performance.

Data acquisition

After a brief training session (approximately 10 min) of a shortened version of the paradigm outside the scanner to ensure that the subjects understood and could perform the tasks, subjects underwent MRI in a 4-T whole body Varian/Siemens MRI scanner, equipped with a self-shielded whole body SONATA gradient set. Before the functional study, a set of anatomical images was acquired, which included a T1-weighted 3D-MDEFT sequence (Lee et al., 1995) (TE/TR = 7/15 ms, $0.94 \times 0.94 \times 3$ mm spatial resolution, axial orientation, 256 readout and 192×48 phase-encoding steps, 8 min scan time), and a modified T2-weighted Hyperecho sequence (Hennig and Scheffler, 2001) (TE/TR = 68/8000 ms, echo train length = 16, 256×256 matrix size, 28 coronal slices, 0.86×0.86 mm in-plane resolution, 5 mm thickness, 1 mm gap, 2 min scan time). BOLD signal changes as a function of time were measured using a T2*-weighted single-shot gradient-echo EPI sequence (TE/TR = 25/3000 ms, 4 mm slice thickness, 1 mm gap, typically 33 coronal slices, 64×64 matrix size, 3.125 mm in-plane resolution, 90° -flip angle, 124 time points) covering the whole brain. The entire battery was performed twice. Thus, the first session (“Novel”) was used as training for the 2nd session (“Practiced”). Padding was used to minimize motion. Task performance and subject motion were determined immediately after each fMRI trial to assure performance accuracy better

than 80% and motion <1 mm translations and <1° rotations (Caparelli et al., 2003).

Data processing

Image reconstruction was performed using a phase correction method that produced minimal ghost artifacts (Buonocore and Gao, 1997). The statistical parametric mapping package SPM99 (Wellcome Department of Cognitive Neurology, London UK) was used for subsequent analyses. A six-parameter rigid body transformation was used for image realignment to correct for head motion. Only scans with head motion less than 1 mm translations and 1° rotations were included in the analysis. The realigned data sets were normalized to the Talairach frame with a 12-parameters affine transformation (Ashburner et al., 1997), using a voxel size of $3 \times 3 \times 3 \text{ mm}^3$, and an 8-mm full-width-half-maximum Gaussian kernel to smooth the data. A general linear model (Friston et al., 1995), and a box-car design convolved with a canonical hemodynamic response function (HRF) were used to calculate the activation maps. The time series were band pass filtered with the HRF as low pass filter and a 1/246 Hz cut-off frequency as high-pass filter.

Statistical analyses

A voxel-by-voxel statistical analysis with positive and negative contrasts was applied to the parameter estimates for each trial to identify significantly activated and deactivated brain areas. To make inferences about the population, activation maps for individual subjects were combined to create activation maps for the entire group and a mask of the attentional network using random-effects analyses (one-sample *t* tests) (Friston et al., 1999; Woods, 1996) at a voxel-level threshold $P = 0.005$. In addition, correlation analyses between BOLD signals and behavioral data (performance accuracy, and RT) during the fMRI trials were performed using simple regression random-effects analyses. Clusters with at least 15 voxels (400 mm^3) and $P < 0.05$ (cluster-level corrected for multiple comparisons) were considered significant in all group analyses (Friston et al., 1994), using a voxel-level threshold of $P = 0.005$.

Effect of attentional load

A parametric statistical model (Buchel et al., 1996; Culham et al., 2001) was used to create functional maps of regions where BOLD responses were modulated by the attentional load. Because of the three conditions (2, 3, and 4 balls), the analysis of attentional load was limited to first order. For each voxel, a linear form, $\alpha_0 L^0 + \alpha_1 L^1$, was fitted to the BOLD signal changes to identify areas associated with attentional load. The attention-regressor, L^0 , was set to one for all three tasks, while the load-regressor, L^1 , varied across tasks (L^1 : -1, 0, 1, for the 2-, 3-, and 4-ball tasks, respectively). Maps of the parameters α_0 and α_1 correspond to areas that were activated during the tasks and those that showed a linear increase with attentional load, respectively. Higher order (order 2 or higher) terms were not included in the parametric analysis because no such terms were significant in our previous study (Jovicich et al., 2001). The complete set of activation maps of individual subjects was included in random-effects analyses (multiple regression), masked with the activated neural network.

Effect of practice

Maps reflecting BOLD signal differences between “Novel” and “Practiced” trials were calculated for each task and subject from individual BOLD contrasts, and included in a combined statistical analysis of variance (ANOVA). For this random-effects analysis, a voxel-by-voxel repeated measures ANOVA was performed with three conditions (2, 3, and 4 balls) using the mask of the activated neural network. The repeated measures ANOVA model was also used to determine practice-related changes in attentional load. Differential “Novel vs. Practiced” load-related increases in brain activation were calculated for the group using the 2- and 4-ball tasks.

Region-of-interest (ROI) analysis

Functional ROIs with volume of 729 mm^3 (cubic, 27 voxels) were defined at specific locations in the Talairach frame to extract the average BOLD signal from regions that showed practice-related changes of brain activation in random-effects analyses. For ROI analyses (paired *t* test), statistical significance was defined as $P = 0.05$.

Results

Behavioral

The average values of task performance and RT during fMRI are presented in Fig. 2 for “Novel” and “Practiced” tasks. The subjects were able to perform the tracking tasks with high accuracy (>85%) for all tasks and both trials. Performance accuracy was significantly lower for tracking 4 balls compared to tracking 2 or 3 balls (P value < 0.0001), but no difference was observed between the 2-ball and 3-ball tasks. In addition, no differences in performance accuracy were observed between “Novel” and “Practiced” sessions for any of the tasks. Similarly, no significant differences were observed in the RT.

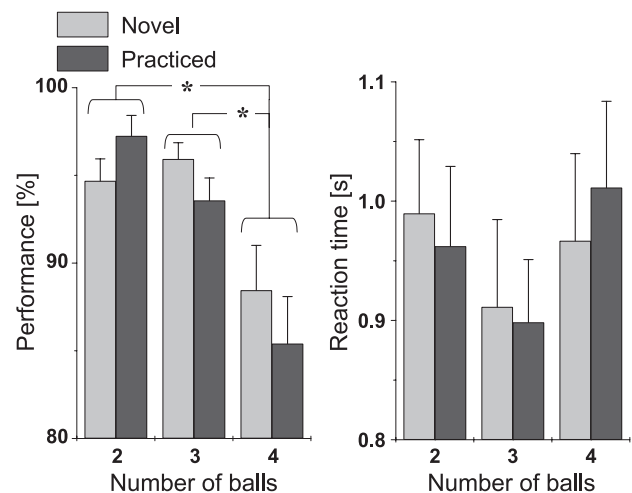


Fig. 2. Task performance and RT as a function of the attentional load (number of balls tracked). *Two-sample *t* test, $P < 0.05$.

Activation on fMRI

All three tasks produced significant activation in a visual attention network (Table 1) that includes the prefrontal (PFC) cortex [inferior (IFG; BA: 9), middle (MFG; BA: 6, 10), and superior (SFG; BA: 8, 10) frontal gyri], parietal lobes [inferior (IPL; BA: 40); and superior (SPL; BA: 7)], posterior intraparietal sulcus (PostIPS; BA: 19), superior temporal gyrus (STG; BA: 38), insula (BA: 13), and subcortical regions (cerebellum, thalamus, and globus pallidus); these activated regions are consistent with our prior observations at 1.5 T (Jovicich et al., 2001). The statistical significance (corrected for multiple comparisons at the cluster level) was $P < 0.0001$ for all these regions. The surface-rendered maps in Fig. 2 show the extent of the bilateral activation produced by all three visual attention tasks. In these random-effects analyses, the highest statistical significance was observed in the left cerebellum (Lobule VI; $T > 22$; Table 1, “Attention”).

Effect of practice

Several regions of the PFC (IFG, MFG, and SFG; bilateral but predominantly right) as well as the cerebellum and the pulvinar thalami were activated more during the “novel” trials compared to the “practiced” trials (Table 1 and Fig. 3). Specifically, significant practice-related decreases of brain activation were observed in the rostral PFC [right SFG, cluster-level corrected $P = 0.03$], and bilaterally in the cerebellum (Lobule VI, predominantly right, cluster-level corrected $P < 0.001$). In contrast, practice did not lead to increased brain activation in any brain region on any task, and

did not alter the BOLD signals in the parietal cortex. The ROI analyses for regions that showed practice-related changes in brain activation are summarized in Fig. 4. On these analyses, task difficulty did not modulate the effect of practice on brain activation. Accordingly, Fig. 5 shows practice-related decreases of BOLD signal in the ROIs across all three tasks.

Effect of attentional load

The parametric analysis demonstrated a positive correlation between task difficulty (number of tracked balls) and BOLD responses in the PFC (insula, IFG, MFG, and both caudal and rostral SFG), all parietal regions (IPL, PostIPS, and SPL), the cerebellum (Lobule VI and vermis, P (corr) < 0.001) as well as the thalamus (bilateral dorsal, P (corr) = 0.015). Higher attentional load increased brain activation bilaterally (right greater than left), but did not decrease the BOLD signals in any brain region. Novel compared to practiced trials showed larger attentional load modulation in the PFC (SFG bilateral, P (corr) = 0.04). These findings were confirmed by the ROI analyses at the cluster maxima of the activation maps (coordinates in Table 1 and Fig 4).

BOLD signals vs. performance and reaction time

Negative correlations were observed between the subject’s performance accuracy and the BOLD signals in the cerebellum (Lobule VI, P (corr) = 0.001) and the SPL (P (corr) = 0.035). Similarly, negative correlations were observed between the subject’s reaction time and the BOLD signals in the SPL (bilateral,

Table 1
Location of major areas of brain activation in the Talairach frame of reference and statistical significance of BOLD responses in these regions

Region	Side	[mm]			Maximum <i>T</i> -scores		
		<i>x</i>	<i>y</i>	<i>z</i>	Attention	Load	Practice
IPL	R	42	−33	42	20.22	4.75	NS
	L	−39	−33	42	17.48	4.47	NS
PostIPS	R	33	−72	33	15.58	3.26	NS
SPL	R	24	−63	57	16.52	3.67	NS
	L	−18	−54	60	18.04	3.00	NS
Cerebellum	R	27	−51	−30	20.02	4.21	3.98
	C	3	−75	−21	18.00	3.62	3.61
	L	−27	−51	−27	22.87	3.22	3.42
Thalamus	R	12	−15	6	13.65	2.43	NS
	C	3	−33	9	6.20	NS	4.83
Globus pallidus	L	−9	−15	6	8.23	2.47	NS
	R	21	−3	0	8.19	NS	NS
STG	L	−15	−3	3	9.71	NS	NS
	R	45	15	−15	6.14	NS	3.81
Insula	L	−42	15	−15	7.24	NS	NS
	R	33	21	0	15.86	2.83	NS
IFG	L	−33	18	0	14.75	2.20	NS
	R	48	12	27	18.28	4.25	2.41
MFG	L	−45	9	30	12.74	3.56	NS
	R	27	15	54	12.40	2.77	3.48
SFG	R	36	36	24	13.82	4.00	NS
	L	−33	42	30	11.36	3.17	NS
	R	27	3	51	21.65	2.96	NS
	L	−21	0	51	18.06	2.21	NS
	C	6	15	48	17.17	3.18	2.20
	R	33	51	18	8.32	2.00	2.72
	L	−36	54	12	9.55	2.20	4.62

Sample size: 25 healthy subjects. Random-effects analyses.

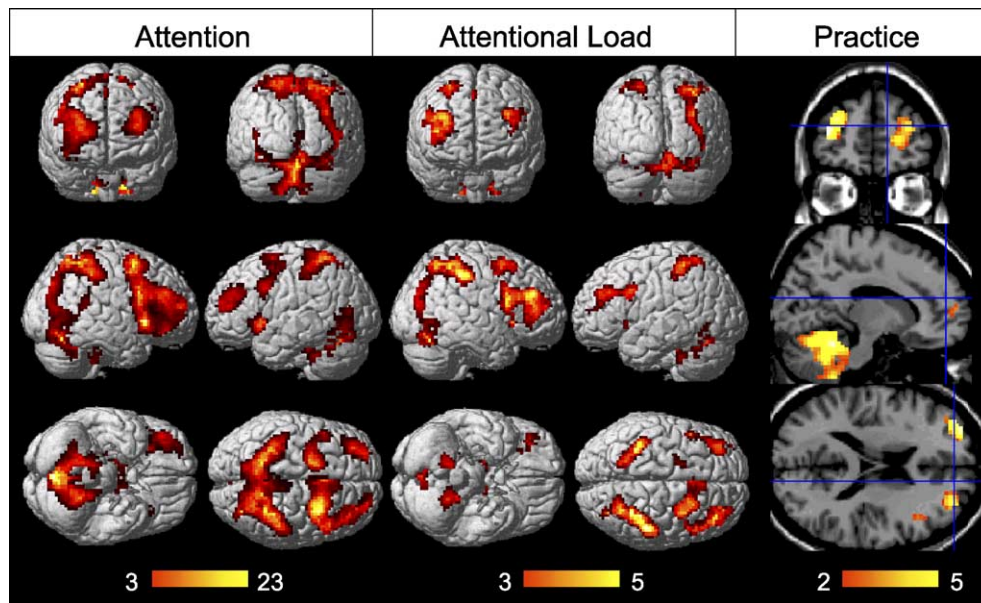


Fig. 3. Statistical maps of BOLD signals during visual attention tasks. The surface rendering maps show brain areas that activated during all three tasks (Attention), and those that showed a linear increase with the number of tracked balls (Attentional load). The three orthogonal views show the difference between “Novel” and “Practiced” trials for all conditions (Practice). Sample size: 25 healthy subjects; random-effects analyses. Color bars are the T score windows.

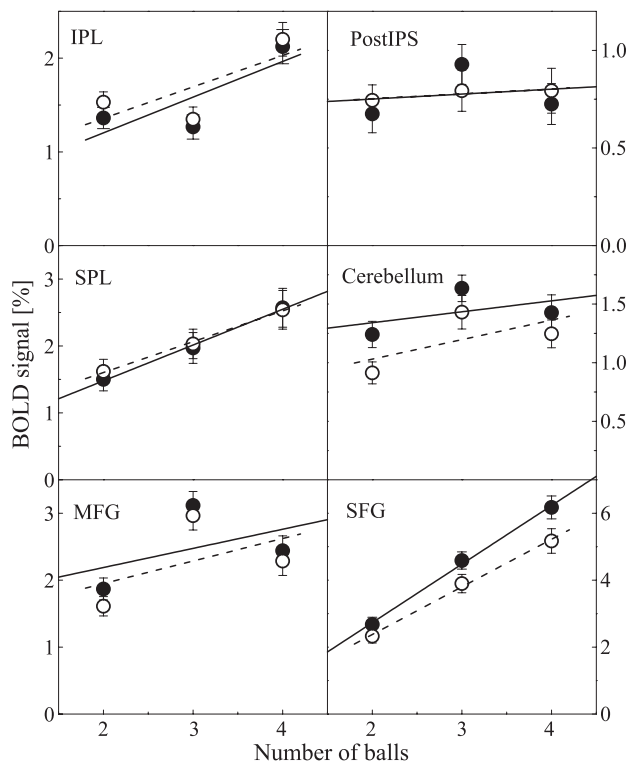


Fig. 4. BOLD signals at specific ROIs for “Novel” (solid circles) and “Practiced” (open circles) trials for the 2-, 3- and 4-ball tasks. Sample size: Twenty-five healthy subjects. IFG: inferior frontal gyrus; MFG: middle frontal gyrus; SFG: superior frontal gyrus. ROI-volume = 0.729 cc. * Paired t test, $P < 0.05$. Solid and dashed lines correspond to linear fits for “Novel” and “Practiced” trials, respectively. Error bars are the standard deviation of the mean BOLD signals in the ROI.

P (corr) < 0.001), SFG (midline and right: P (corr) < 0.001), thalamus (P (corr) < 0.001) and left insula (P (corr) = 0.03). BOLD signals did not show positive correlations with performance accuracy or RT during the fMRI trials.

Discussion

The major findings of this study are that brief practice leads to (a) decreased activation primarily in the right prefrontal cortices, bilateral cerebellum, and thalamus in subjects who performed visual attention tasks, and (b) decreased attentional-load modulation in the PFC. These results are in general agreement with findings in previous fMRI studies of working memory (Gabrieli et al., 1996; Garavan et al., 2000; Jansma et al., 2001) and mirror reading (Poldrack and Gabrieli, 2001), which reported decreased activation in the PFC after practice. Therefore, the larger bilateral activation in the PFC, thalamus, and cerebellum for “Novel” compared to “Practiced” trials suggests greater usage of attentional resources during “Novel” trials. More importantly, attentional load modulation of brain activation was larger for novel trials compared to practiced trials, particularly in the PFC (see Figs. 4 and 6). Furthermore, activation patterns for regions that showed attentional load and practice effects overlapped in a large extent, especially in the cerebellum and the PFC. Compared to “Novel” trials, increased task difficulty during “Practiced” trials was associated with lower recruitment of brain resources in those regions. These findings suggest that practice leads to lower usage of regions that are typically reserved for more difficult tasks, which are regions that illustrated load effects with increasing difficulties.

Attentional load clearly modulated the amplitude of fMRI signals in the attentional network. An overall linear correlation

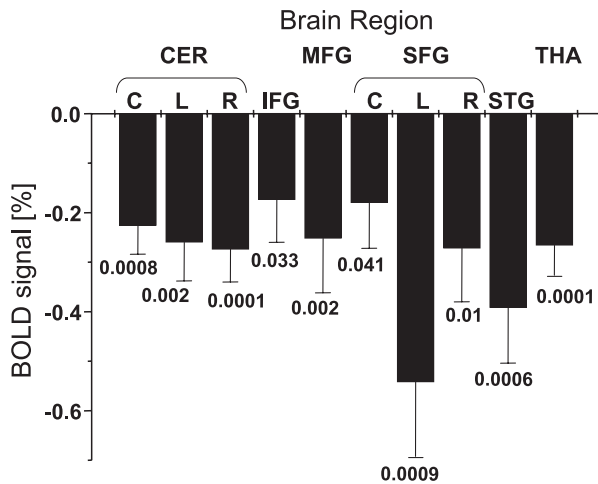


Fig. 5. Practice-related decreases in BOLD signal at specific ROIs across all three conditions. Sample size: 25 healthy subjects. CER: cerebellum; IFG: inferior frontal gyrus; MFG: middle frontal gyrus; SFG: superior frontal gyrus; STA: superior temporal gyrus; THA: thalamus. ROI-volume = 0.729 cc. Numbering labels indicate the P value for paired t test (“Novel” vs. “Practiced” trials).

between BOLD responses and the number of balls being tracked was observed in several activated regions, particularly in the PFC, parietal cortices, and cerebellum (Figs. 3, 4, and 6; Table 1). These findings are in general agreement with previous reports using the same activation paradigm (Culham et al., 2001; Jovicich et al., 2001), except for a prior study that did not observe the attentional load effect in the cerebellum, possibly due to incomplete coverage of the cerebellum (Culham et al., 2001). Other studies that evaluated the working memory tasks also reported increased activation in the cerebellum with increased task difficulty (Smith and Jonides, 1997). More detailed analyses showed that a U-shape rather than a simple linear model would better model the load-dependent BOLD responses in the cerebellum, PostIPS, and MFG. These U-shaped patterns suggest interactions between an attentional load effect and a practice effect with increasing task difficulty in these brain regions. For example, in the cerebellum, BOLD signals increased from tracking 2 balls to tracking 3 balls due to the increased difficulty; however, when the subjects proceed to tracking 4 balls, the practice effect dominates and hence decreases the BOLD signals.

Several studies of motor tasks indeed have observed reduction in cerebellar activation following practice, which suggests that the cerebellum is more important during the early stages of learning and may be involved in skill acquisition (Doyon et al., 1996; Jenkins et al., 1994). For instance, PET and fMRI studies found decreased cerebellar activation in the left lateral hemisphere after practice of motor tasks (Van Mier and Petersen, 2002). For mirror reading tasks, however, practice resulted in decreased activation in the left, but increased activation in the right cerebellum. Practice-related decreases of brain activation in the PFC, thalamus, and cerebellum have not been reported for visual attention tasks; the only study that evaluated a cued-attention orienting and interference task found decreased BOLD signals only in the inferior parietal regions but increased activation in medial frontal regions after practice (Weissman et al., 2002). Such relocation of neural processing also has been reported in prior PET studies of practice effect. With practiced trials of motor tasks, activation shifts from

the right premotor and parietal cortex and left cerebellum to the supplementary motor area (Petersen et al., 1998), which was thought to represent a transition from controlled to automatic processing. Similarly, PET studies of visuo-motor coordination tasks found decreased rCBF in prefrontal, and posterior parietal cortices, and increased rCBF in medial temporal regions after practice (Pettersson et al., 1999). Analogous practice-related shifts in neural processing, from superior parietal and posterior occipital to inferior temporal cortices, occurred during visual skill learning (Poldrack et al., 1998). However, relocation of neural processing after brief practice is not observed in the present study, since practice did not increase brain activation in any of the initially activated regions or in any other region. In contrast, decreased activation in the PFC and cerebellum suggests that practiced and novel processing may have a similar functional anatomical representation but differs in the efficiency of information processing. Furthermore, decreased activation was not related to changes in task performance or RT, which were similar for “Novel” and “Practiced” trials.

Another possible mechanism for the decreased activation in PFC and cerebellum after practice might be habituation to the environment and experimental conditions. A recent PET study using verbal tasks observed larger deactivation in the medial PFC during “Novel” compared to “Practiced” trials (Simpson et al.,

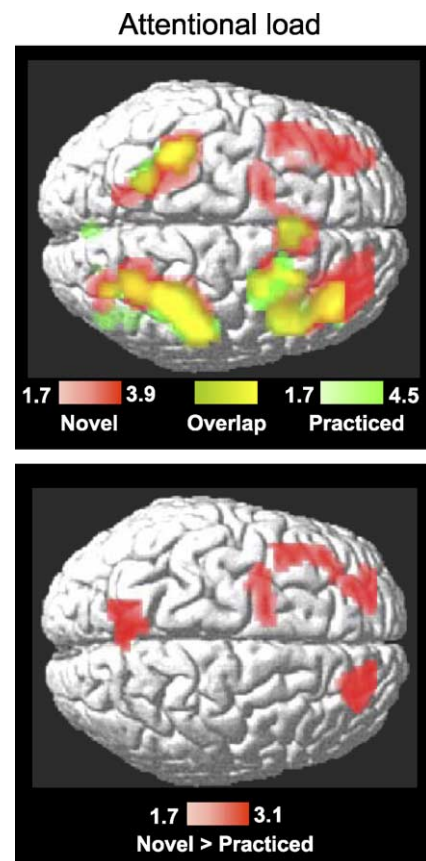


Fig. 6. Statistical maps of attentional-load modulation of BOLD signals during visual attention tasks. [Top] Attentional load effect for “Novel” and “Practiced” trials. [Bottom] Differential effect of attentional load between trials. Random effect analyses, minimum cluster size = 0.4 cc. Color bars are the T score windows.

2000a,b). The authors suggested an interplay between emotion and cognitive task performance, since anxiety (initially high) decreases after practice (Simpson et al., 2000a,b), while CBF in the medial PFC increases with practice (Simpson et al., 2000a,b). However, we did not specifically evaluate the effect of anxiety in relation to decreased deactivation in the MPFC after practice. Future studies measuring anxiety ratings in relation to brain activation changes are needed to assess this possible relationship.

The negative correlation of BOLD responses with performance accuracy in regions that modulate with attentional load, such as the SPL and the cerebellum, indicates that increased attentional resources (i.e., increased BOLD signals) in these regions is required for increased task difficulty (i.e., lower performance accuracy). Our findings of negative correlations between BOLD responses and subjects' RT further demonstrate that increased attention led to quicker responses (shorter RT) in the PFC. This inverse correlation between BOLD signal and RT is in agreement with previous fMRI studies showing that shorter RT are associated with higher BOLD responses in the anterior cingulate cortex during visual stimulation (flickering checkerboard) (Winterer et al., 2002).

In summary, a set of visual attention tasks consistently activated the visual attentional network (IFG, MFG, SFG, IPL, SPL, PostIPS, STG, insula, cerebellum, thalamus, and globus pallidus), and attentional load-dependent increases in BOLD signals were observed in most of these regions. Brief practice decreased activation in the PFC, cerebellum, and thalamus, and reduced attentional-load modulation in the PFC; this probably reflects the transition from a state that required more neural resources to perform the novel task to more automated information processing during the practiced trial. Overall, our results demonstrate that some brain subsystems, particularly the PFC and the cerebellum, develop increased efficiency and hence decreased attentional requirement after a brief period of practice. The effect of short-term practice in the prefrontal cortex may be similar to attentional load-effects; therefore, studies of attentional load need to take practice effects into account.

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