

Interactive report

Effects of practice on executive control investigated with fMRI

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8 September 2002

Abstract

Various models of executive control predict that practice should modulate the recruitment of executive brain mechanisms. To investigate this issue, we asked 15 participants to perform a cued global/local attention task while brain activity was recorded with event-related functional magnetic resonance imaging (fMRI). Practice significantly reduced the recruitment of left inferior parietal regions that were engaged when participants oriented attention in response to global and local cue stimuli. In contrast, practice increased the recruitment of midline frontal regions that were engaged by interference between global and local forms during target processing. These findings support models of executive control in which practice increases the tendency for stimuli to automatically evoke task-relevant processes and responses.

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Theme: Neural basis of behavior

Topic: Cognition

Keywords: Anterior cingulate; Selective attention; Response interference; Global/local processing; Practice; fMRI

1. Introduction

Many theories of attention posit an executive control system that recruits and oversees task-specific processes in order to facilitate appropriate behavior [1,10,16,36,46]. This supervisory system is engaged by complex and novel situations including those that require planning, implementation of strategies, switching between stimulus dimensions and performing multiple tasks at the same time. It is also recruited when new associations (schemas) are formed between task stimuli and task-relevant processes and responses, especially when new schemas must guide behavior in the face of older, stronger schemas [36].

In some models of executive control, practice strengthens new schemas such that stimuli become capable of automatically engaging associated processes and responses [10,36]. The effect of strengthening schemas on the recruitment of executive control processes should vary, however, depending on the specific task situation. When practice increases the degree to which task-relevant stimuli

activate appropriate processes and responses (i.e. strengthens task-relevant schemas), then correct behavior should be possible with less intervention by the supervisory system. For example, practice reduces the time (and, by inference, the involvement of executive processes) necessary to switch between different tasks in cued selective attention paradigms [23,31,45], perhaps by strengthening associations between cues and task-appropriate attentional processes and responses [31]. Thus, practice appears to decrease the recruitment of executive processes that are engaged during cued attentional orienting.

On the other hand, when practice strengthens associations between task-irrelevant stimuli and inappropriate processes and responses, then correct behavior may require additional recruitment of executive control mechanisms to resolve processing conflicts. For example, when participants are asked to identify the ink color in which a word is printed, they are slower to respond when the irrelevant word names an ink color that is mapped to a competing motor response (incongruent trials) than when it names an ink color that is mapped to the same response (congruent trials) (see Ref. [27] for a review). This effect appears to be due to our extensive experience with reading, which leads

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to the word automatically activating task-relevant responses that interfere with color naming [10,11]. Consistent with this view, training participants to associate random polygons with task-relevant color names allows those polygons to produce Stroop-like behavioral interference effects when they serve as distractors in Stroop-like tasks [29]. In sum, the behavioral findings discussed above support the view that practice strengthens new schemas. Further, they demonstrate that strengthening schemas can either decrease or increase the recruitment of executive control processes depending on the specific task situation.

Studies of brain–behavior relationships can also provide a powerful tool for testing the effects of practice on the recruitment of executive control processes. Functional neuroimaging, lesion, and single-unit recording studies have revealed that distinct brain areas contribute differentially to specific executive processes [48]. For example, previous studies have indicated that prefrontal regions help to maintain and manipulate information held in working memory [40], midline frontal regions help to detect response conflict [27] and superior/inferior parietal regions contribute to attentional orienting [42]. Given that such relationships exist, it should be possible to determine whether practice modulates the recruitment of distinct brain areas that implement specific executive control processes.

In the present study, we used event-related fMRI to investigate whether practice affects the recruitment of executive brain mechanisms engaged by (a) cued attentional orienting [27,41] and (b) Stroop-like interference between global and local aspects of an object's form [35]. As discussed earlier, the view that practice strengthens schemas predicts that practice should reduce neural activity associated with cued attentional orienting while increasing neural activity associated with Stroop-like interference. Recent advances in event-related fMRI methods have allowed separate estimates of cue and target activity in cued attention paradigms [12,19]. To our knowledge, however, the effects of practice on neural activity associated with cued attentional orienting have not yet been investigated. The present study therefore provides the first test of the hypothesis that practice should reduce the recruitment of executive brain mechanisms that are recruited by cued attentional orienting.

The effects of practice on activity associated with Stroop-like interference have been investigated somewhat more with fMRI. The results of such studies, however, do not provide clear evidence that practice increases interference-related activity. For instance, using block designs multiple researchers have reported that practice actually reduces neural activity that is associated with interference in the Stroop task, contrary to the present hypothesis [7,33]. Given the nature of block designs, however, participants can predict whether an upcoming trial will contain conflicting distractor information. It has been suggested that such predictability often leads to the use of top-down strategies during epochs of mostly incongruent

trials, which reduce interference effects [28]. Practice-related reductions of interference-related activity in block designs might thus indicate that top-down strategies become easier to implement during blocks with incongruent trials. Also, neither of the two block-design studies discussed above specifically manipulated the amount of practice that participants were given at associating distractor stimuli with task-relevant responses, which is usually necessary for conflict from distractors to increase in behavioral studies [29]. Therefore, it is unclear whether practice should have been expected to increase the tendency of incongruent distractors to activate the incorrect response. Finally, it is possible that participants simply became less aroused by the more difficult incongruent trials over the course of the experiment, thereby reducing the difference in brain activation between incongruent and either neutral or congruent blocks of trials.

Data from a recent fMRI study are also relevant to our hypothesis that practice should increase interference-related activity. In this study [32], participants were trained to associate polygons with either a pattern or a color patch, although associations between polygons and specific button presses were specifically avoided. Following training, these polygons were used as distractors in a variant of the Stroop task. In this task, participants identified a color patch on each trial that was accompanied by a distractor polygon. During training, the distractor polygon had been associated with (1) a pattern, (2) a different (i.e. incongruent) color patch, or (3) had not been presented at all. Across multiple training and fMRI scanning sessions, the presence of polygons associated with incongruent color patches, compared to those associated with patterns, produced increasing amounts of neural activity, especially in the dorsolateral prefrontal cortex.

While the finding above is highly consistent with the present hypothesis, the effects of practice on interference were not measured, since congruent trials were not included in the block design (i.e. trials in which the distractor polygon and target color patch were positively associated during training). It could be argued that polygons associated with patterns provided a neutral baseline against which to measure brain activity for polygons associated with incongruent color patches. From this perspective, practice increased brain activity related to inhibition of incongruent color patches [28]. It is also possible, however, that practice simply increased all neural activity associated with task-relevant distractors (i.e. color patches) relative to task-irrelevant distractors (i.e. patterns). An effect of task-relevance could be independent of conflict between two task-relevant representations (i.e. incongruent versus congruent). Therefore, this experiment also does not provide conclusive evidence that practice increases interference-related activity.

With these issues in mind, we investigated the effects of practice on neural activity associated with cued attentional orienting and interference using a relatively novel event-related fMRI approach [53,54]. In the present adaptation of

this approach, participants were cued on a trial-by-trial basis to attend for and identify either the global or the local form of an upcoming hierarchical stimulus [35], which could be either congruent (e.g. a large, global H made up of small local Hs) or incongruent (e.g. a large, global S made up of small local Hs). Since each stimulus dimension (i.e. global and local) was task-relevant on approximately one-half of the trials, participants became more practised at identifying and responding to both global and local forms as the experiment progressed. Therefore, we could determine not only whether practice reduced cue-related activity, but also whether practice at identifying and responding to target stimuli increased interference-related activity from those same stimuli when they served as incongruent distractors.

We investigated the present hypotheses using a region of interest approach that was informed by current knowledge of the functional neuroanatomy of executive control. Much evidence indicates that parietal regions play a crucial role in orienting both spatial and non-spatial attention [20], and it has been specifically demonstrated that the left inferior parietal lobe is critical for orienting attention in the global/local paradigm [43]. Consequently, we predicted that practice would decrease neural activity in the left inferior parietal cortex that was associated with orienting attention to global and local stimulus dimensions. Other evidence indicates that midline frontal regions (i.e. the anterior cingulate and medial frontal gyri) play a role in detecting response conflict between target and distractor stimuli in selective attention paradigms [2,9,27]. We therefore predicted that practice would increase interference-related activity in midline frontal regions. Other data from the present study, which do not include analyses of the practice effects reported here, are published elsewhere [50].

2. Materials and methods

2.1. Participants

Fifteen participants (nine male, age range 20–36) were recruited from the Duke University community in accordance with the rules of the local human subjects committee. Each participant was told that the study investigated the neural bases of selective attention and each gave his or her written consent to participate. All were right-handed, with normal or corrected-to-normal vision, with no history of serious neurological traumas or disorders. Prior to the experiment, informed consent was obtained from each participant. Each participant practised one or two blocks of the experimental task before the MR session. The study lasted ~2 h and participants were paid \$10 per hour for participating.

2.2. Apparatus

Stimulus presentation and the recording of response data

were controlled by customized software running on a PC. Stimuli were projected onto a screen at the back of the magnet's bore. Participants viewed the stimuli through a mirror and responses were recorded with an MR-compatible response box.

2.3. Paradigm and procedure

We used a novel fast-rate event-related fMRI paradigm recently developed by Woldorff and co-workers [53,54] (c.f. Shulman and co-workers [37,38,47]). In this paradigm (Fig. 1), compound-event trials containing a cue and a target stimulus are randomly interspersed with trials containing only a cue stimulus. On each 3-s trial, participants viewed a cue ('G', 'L', 'P', or 'O'; $1.6^\circ \times 1.0^\circ$ of visual angle; duration=200 ms), which instructed them to attend for and identify either the global ('G') or local ('L') aspect of an upcoming hierarchical stimulus, or to passively wait until the next trial (either a 'P' cue or an 'O' cue). On cue-only trials (all passive cue trials and one third of both global task and local task trials), a cue was not followed by a target stimulus. We contrasted neural activity for attention-directing global and local cues with that for passive cues. This contrast isolated neural activity associated with executive aspects of cued attentional orienting while controlling for basic sensory and semantic processing of attention-directing cue stimuli.

On cue-plus-target trials (66% of global-task and local-task trials), either a congruent (e.g. a large S made of small Ss) or an incongruent (e.g. a large S made of small Hs) hierarchical stimulus appeared for 200 ms, 1500 ms after cue onset (Fig. 1). The global and local forms of each stimulus subtended $3.3^\circ \times 2.1^\circ$ and $0.6^\circ \times 0.4^\circ$ of visual angle, respectively. For both the global and the local task, 50% of the targets were congruent while the other 50% were incongruent. Participants were instructed to respond to targets with their right hand, using their index finger to press one button if an H appeared at the cued dimension and their middle finger to press a different button if an S appeared. We contrasted incongruent with congruent targets to isolate neural activity that was associated with interference between global and local aspects of target stimuli.

In all trials, the fixation dot changed color, from white to red, 1500 ms after cue presentation (i.e. coincident with target presentation in cue-plus-target trials). Participants were told that if a target did not appear at this point, then they should cease attending and simply wait for the next trial. This manipulation was performed to ensure that demands on pre-target attention-biasing processes would be equated for cue-plus-target and cue-only trials [12].

All seven trial types were included within each run. They were presented equally often and in a counterbalanced order such that, within every run, each trial type was preceded equally often by every trial type in the design. Such counterbalancing allows subtraction of response

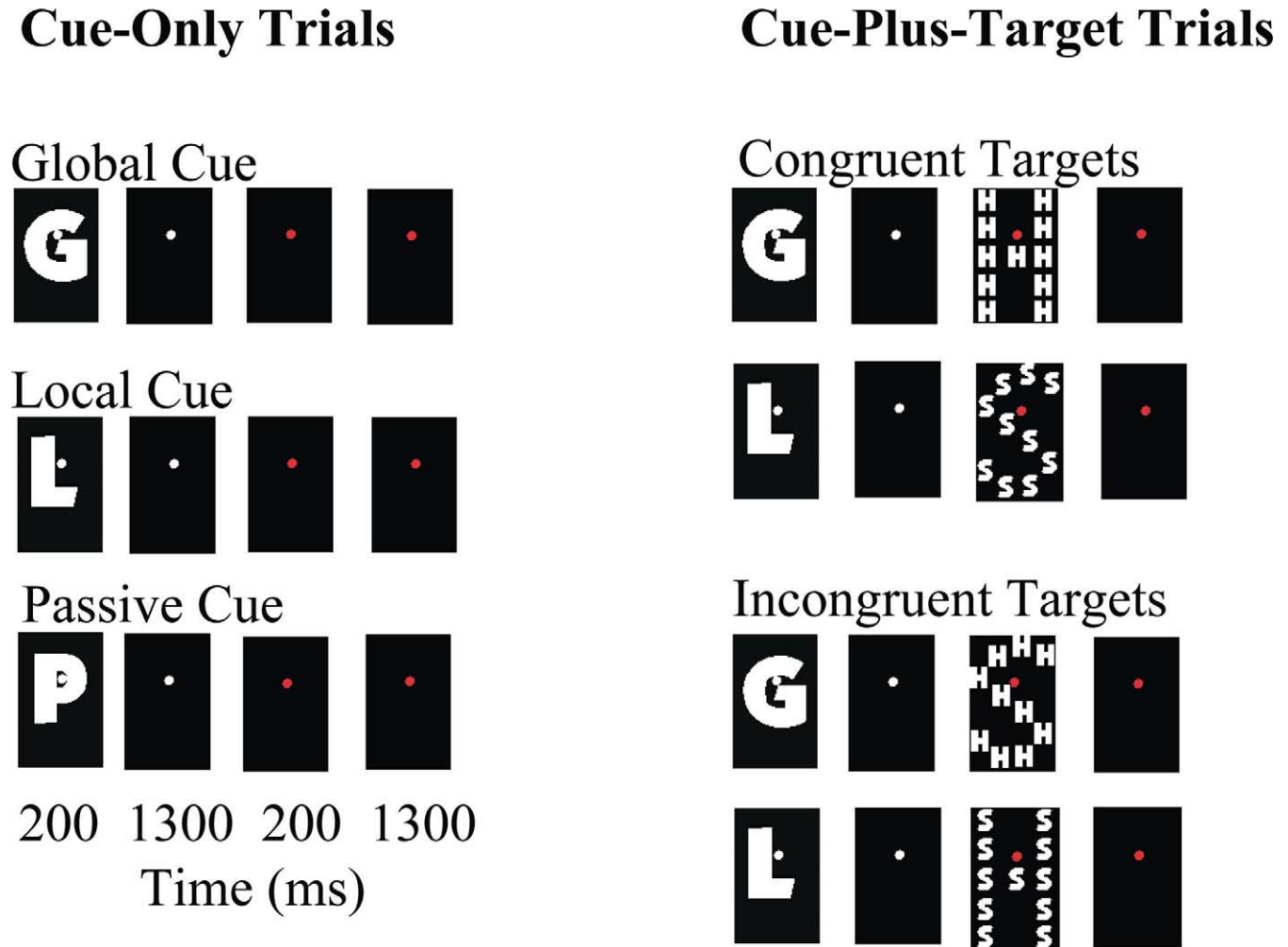


Fig. 1. Examples of the stimuli and timing of stimulus presentation for the seven trial types used (see text for more details).

overlap from adjacent trials when comparing the average time-locked responses to different trial types [6,14,52]. Most relevant for the present method of data analysis, the presence of cue-only trials allows calculation of independent parameter estimates for the response amplitudes to different types of cues (i.e. global, local and passive) and targets (i.e. global congruent, global incongruent, local congruent and local incongruent) within a multiple regression framework [37,38].

2.4. fMRI data acquisition

The blood oxygenation dependent response (BOLD) signal was measured with an echo-planar imaging sequence (TR=1.5 s, TE=40 ms, flip angle=90°, 18 contiguous 7-mm-thick slices—in plane resolution=3.75 mm×3.75 mm) during the collection of functional images. Each participant completed 10 runs of ~5 min duration each (although one completed only nine). During each run, 206 brain volumes were collected. The first six functional images of each run contained no trials and were discarded

prior to analysis of the functional data. Structural images for each participant were also collected using a T1-weighted spin echo sequence (TR=500 ms, TE=14 ms, flip angle=90°, 18 contiguous 7-mm-thick slices—in plane resolution=0.94 mm×0.94 mm).

2.5. Data analysis

The software analysis package SPM'99 [18] was used to correct functional images for temporally asynchronous slice acquisition and head motion, to warp the functional images to MNI (Montreal Neurological Institute) standard space, and to spatially smooth the functional images with a Gaussian filter (FWHM=8 mm in the x , y , and z dimensions). Next, responses to cue and target stimuli were modeled by convolving a vector containing the onset times of the different types of cues and targets with a canonical hemodynamic response function. This function was composed of the sum of two gamma functions. In total, there were seven regressors: one for each type of cue and target. Included were regressors for passive cues, global cues,

local cues, global congruent targets, global incongruent targets, local congruent targets, and local incongruent targets. Multiple linear regression (SPM'99) was implemented on the data from each participant to determine the parameter estimate for each regressor within each run.

To identify effects of practice on neural activity associated with cued attentional orienting, a voxelwise analysis was used to create regions of interest (ROIs). The voxelwise analysis contrasted the mean parameter estimate for global and local attention-directing cues with the parameter estimate for passive sensory/semantic control cues (termed the cue difference) in each voxel separately. This contrast revealed voxels that were involved in cued attentional orienting [53,54]. The t -map was thresholded at a level ($t=2.625$, $P<0.01$ and 10 contiguous voxels) that revealed several clusters of activation, major foci of which are revealed in Table 1. These clusters were then divided into different regions of interest (ROIs) using the atlas of Talarach and Tournoux (1988).

To identify effects of practice on neural activity associated with interference, a second voxelwise analysis was performed. This analysis contrasted the mean parameter estimate for incongruent targets with that for congruent targets (termed the target difference) in each voxel separately. The target difference was calculated by averaging across global and local targets to increase statistical power. The resulting t -map was thresholded in the same way that

the t -map for cued attentional orienting was thresholded ($t=2.625$, $P<0.01$ and 10 contiguous voxels). This contrast revealed voxels that were engaged by interference, major foci of which are indicated in Table 3. The resulting t -map was then decomposed into ROIs using the atlas of Talarach and Tournoux (1988) [49].

2.6. Region of interest (ROI) analyses

We first performed an ROI analysis to determine whether practice significantly reduced neural activity in the left inferior parietal lobe that was associated with cued attentional orienting. In this analysis, the average cue difference across all voxels in the left parietal ROI was calculated separately for runs 1–3, runs 4–6, and runs 6–9 in each participant. To determine whether practice affected neural activity that was associated with cued attentional orienting, we performed paired t -tests to contrast the average cue difference for runs 1–3 versus runs 4–6 and runs 4–6 versus runs 7–9. Since we hypothesized that activity associated with cued attentional orienting would decrease with practice, each t -test was one-tailed. Since two t -tests were performed for each ROI, however, only P -values less than $0.05/2=0.025$ were considered significant ($t>2.15$). For completeness, we also calculated separate t -values for the average cue differences in runs 1–3, runs 4–6, and runs 7–9 (Table 2). Exploratory analyses in other ROIs activated by cued attentional orienting were performed in the same way. We make no strong conclusions, however, regarding the significance of effects in these other ROIs (Table 2) since they were not predicted a priori.

We also performed two ROI analyses to determine whether practice significantly increased neural activity associated with interference in midline frontal regions (i.e. the anterior cingulate and medial frontal gyri). In these analyses, the average target differences across all voxels in (1) the medial frontal gyrus and (2) the anterior cingulate cortex were calculated separately for runs 1–3, runs 4–6, and runs 6–9 in each participant. To determine whether practice affected neural activity associated with interference in each of these two ROIs, we performed paired t -tests to contrast the average target differences for runs 1–3 with runs 4–6 and runs 4–6 with runs 7–9. As for our analyses of cue activity, each of these two t -tests was one-tailed and therefore only P -values less than $0.05/2=0.025$ were considered significant ($t>2.15$). For completeness, we also calculated separate t -values for the average target differences in runs 1–3, runs 4–6, and runs 7–9 (Table 4). Exploratory analyses in other ROIs were performed in exactly the same way. We make no strong conclusions, though, regarding the significance of effects in these other ROIs (Table 4) since they were not predicted a priori.

To further illustrate the findings from the ROI analyses above, we performed selective averaging to determine the

Table 1
Major foci activated by cued attentional orienting

Region	BA	x	y	z	T	P
Frontal						
L. SFG	6	−8	10	51	3.41	0.0021
L. MFG	6	−26	−12	46	3.32	0.0025
R. MFG	6	26	−8	52	3.32	0.0025
L. MeFG	6	−11	10	51	3.87	0.0008
L. ACC	24	−11	6	45	2.75	0.0078
L. PrCG	4	−38	−19	59	5.88	<0.0001
R. PrCG	6	30	−8	52	3.41	0.0021
Parietal						
L. PostCG	3	−41	−16	52	4.04	0.0006
L. SPL	7	−26	−66	55	4.63	0.0002
L. IPL	40	−45	−41	47	4.71	0.0002
L. Prec	7	−23	−67	48	4.62	0.0002
L. SMG	40	−41	−38	34	2.75	0.0078
L. AG	39	−27	−57	37	4.69	0.0002
Occipital						
L. MOG	18	−26	−91	5	3.28	0.0027
R. MOG	18	23	−95	5	3.56	0.0016
L. Cun	17	−26	−91	1	2.69	0.0088
R. Cun	18	15	−98	5	3.38	0.0022
R. LG	18	23	−87	2	3.02	0.0046

BA, Brodmann area; x , y , z , coordinates of peak activation from Talarach and Tournoux's (1988) atlas [49]. T , peak voxel T -score within a region; P , probability that a voxel T -score occurred by chance. L, left; R, right; SFG, superior frontal gyrus; MFG, middle frontal gyrus; MeFG, medial frontal gyrus; ACC, anterior cingulate cortex; PrCG, precentral gyrus; PostCG, postcentral gyrus; SPL, superior parietal lobule; IPL, inferior parietal lobule; Prec, precuneus; SMG, supramarginal gyrus; AG, angular gyrus; MOG, middle occipital gyrus; Cun, cuneus; LG, lingual gyrus.

Table 2
ROIs for which practice significantly reduced activity related to cued attentional orienting

Region	<i>N</i>	BA	<i>x</i>	<i>y</i>	<i>z</i>	<i>T</i> -1	<i>T</i> -2	<i>T</i> -3	<i>T</i> -1 vs. 2	<i>T</i> -2 vs. 3
Frontal										
L. SFG	9	6	-8	10	51	4.26	1.44	2.65	2.95	0.91
L. MFG	9	6	-26	-12	46	4.91	1.99	1.58	3.35	0.11
R. MFG	7	6	26	-8	52	4.34	1.04	1.83	2.98	0.80
L. MeFG	27	6	-11	10	51	4.67	1.44	3.00	3.28	1.43
L. ACC	1	24	-11	6	45	2.94	-0.04	2.15	2.84	1.93
L. PrCG	72	4	-38	-19	59	5.99	2.83	2.40	3.03	0.77
R. PrCG	5	6	30	-8	52	5.37	1.03	1.67	3.77	0.89
Parietal										
L. IPL	57	40	-45	-41	47	6.14	1.39	2.39	2.97	1.13
L. AG	3	39	-27	-57	37	5.08	0.63	1.37	3.32	0.79
Occipital										
L. MOG	10	18	-26	-91	5	4.00	1.44	1.98	2.88	0.52
R. MOG	5	18	23	-95	5	5.67	1.02	1.75	3.28	0.51
L. Cun	1	17	-26	-91	1	4.53	0.48	2.45	3.69	1.53
R. Cun	5	18	15	-98	5	5.75	1.30	1.96	3.37	0.85
R. LG	4	18	23	-87	2	4.91	0.85	2.69	3.08	1.46

T-1, 2, 3 = *T*-score indicating reliability of activation for runs 1–3, runs 4–6, and runs 7–9. *T*-1 vs. 2 = *T*-score testing whether activity was greater for runs 1–3 versus 4–6 ($t > 2.15$, $P < 0.025$). *T*-2 vs. 3 = *T*-score testing whether activity was greater for runs 4–6 than runs 7–9 ($t > 2.15$, $P < 0.025$). ROI, region of interest; *N* = number of voxels; BA, Brodmann area; *x*, *y*, *z*, geographic center of mass coordinates from Talarach and Tournoux's (1988) atlas [49]. L, left; R, right; SFG, superior frontal gyrus; MFG, middle frontal gyrus; MeFG, medial frontal gyrus; ACC, anterior cingulate cortex; PrCG, precentral gyrus; SPL, superior parietal lobule; IPL, inferior parietal lobule; AG, angular gyrus; MOG, middle occipital gyrus; Cun, cuneus; LG, lingual gyrus.

average time-locked response to each of the seven trial types across all voxels within each ROI. We then plotted the difference in peak amplitude (in units of percent change) between (a) attention-directing and passive cues (Fig. 2) and (b) incongruent and congruent targets (Fig. 3) for ROIs with a *P*-value less than 0.025.

2.7. Conversion from MNI to Talarach coordinates

Following statistical analyses in MNI space, we converted sites of activation to Talarach coordinates to allow better comparison with activations from prior studies. Conversion from MNI to Talarach coordinates was implemented with a non-linear combination of two linear transformations that has been used in other published studies [8,17] (<http://www.mrc-cbu.cam.ac.uk/Imaging/mnispace.html>). Coordinates above the anterior commissure (AC) were transformed as follows: $X' = 0.99X$; $Y' = 0.9688Y + 0.0460Z$; $Z' = -0.0485Y + 0.9189Z$. Coordinates below the AC were transformed with these equations: $X' = 0.99X$; $Y' = 0.9688Y + 0.0420Z$; $Z' = -0.0485Y + 0.8390Z$. Talarach coordinates in the tables indicate the location(s) of peak activity within each region.

3. Results

3.1. Behavior

Data from three of the 15 participants were lost due to a problem with the response box. Mean reaction times (RTs) for the remaining participants were analyzed with repeated

measures ANOVA using three factors: block (runs 1–3, runs 4–6, runs 7–9), level (global, local) and distractor type (congruent, incongruent). As expected [21,22,25], RTs were significantly faster for congruent (520 ms) than for incongruent (579 ms) trials, $F(1,11) = 35.718$, $P < 0.001$. Consistent with prior findings [35], RTs were significantly faster for global (533 ms) than for local (567 ms) trials, $F(1,11) = 8.585$, $P < 0.02$. No other main effects or interactions reached significance ($P > 0.50$ in all cases).

An analogous ANOVA with percent correct as the dependent measure revealed that overall performance was quite high (90.7%). As in the RT analysis, there was a significant main effect of distractor type, $F(1,11) = 7.003$, $P < 0.025$, because responses were less accurate for incongruent (87.1%) than for congruent (94.2%) cue-plus-target trials. All other possible main effects and interactions failed to achieve statistical significance ($P > 0.16$ in all cases).

3.2. Imaging

We contrasted neural activity for attention-directing (i.e. global and local) cues to that for passive cues in order to functionally define left inferior parietal regions that were engaged by cued attentional orienting as well as other regions of interest (ROIs) in which we performed exploratory analyses (Table 1; Figs. 2 and 3). To investigate practice effects with sufficient statistical power, we combined data across groups of three runs. Specifically, we determined whether neural activity associated with cued attentional orienting varied across runs 1–3, runs 4–6, and runs 7–9. In line with predictions, there was a significant

Cued Attentional Orienting: Frontal and Parietal ROIs

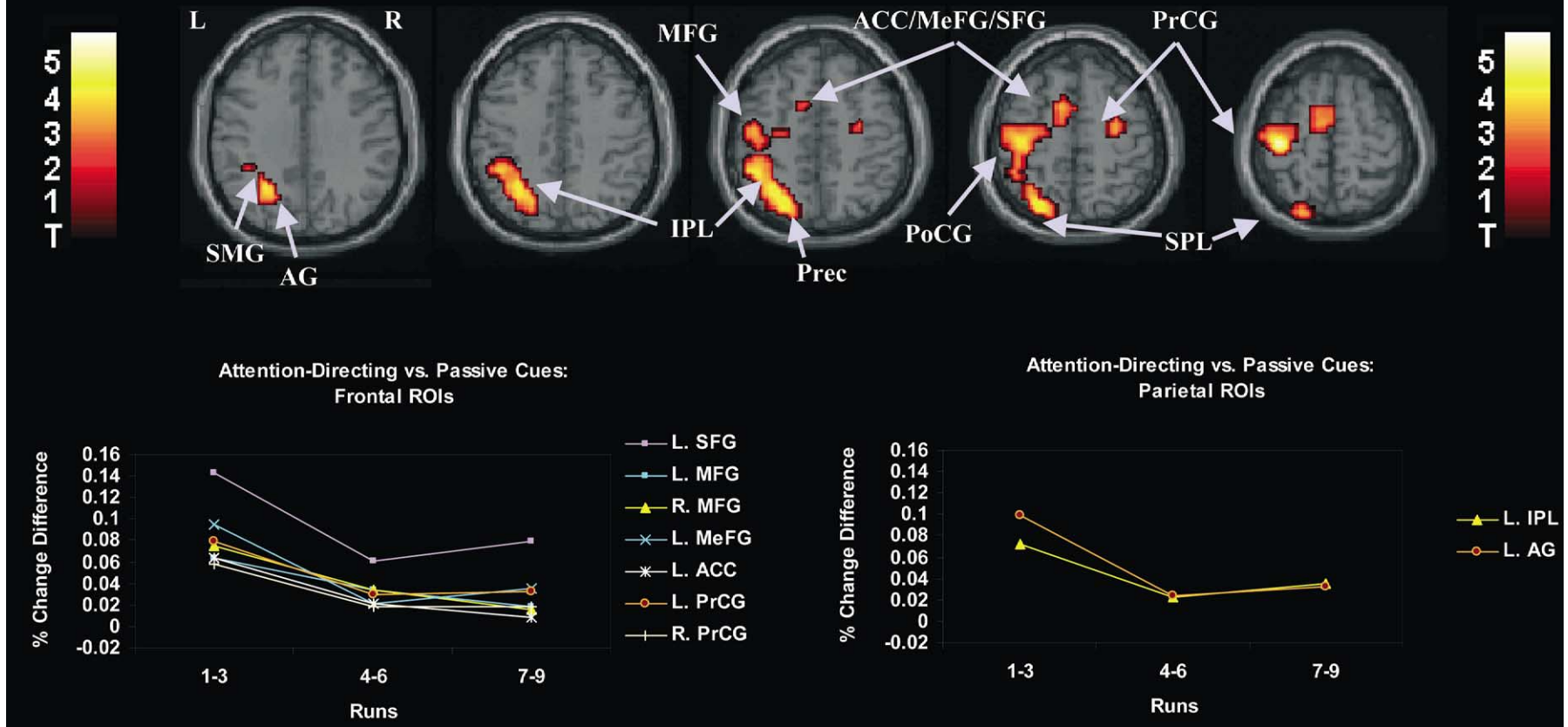


Fig. 2. Effects of practice on neural activity associated with cued attentional orienting in frontal and parietal regions of interest (ROIs). As shown in the figure, cued attentional orienting activated regions of frontal and parietal cortex (see also Table 1). ROI analyses revealed that practice significantly reduced the size of the hemodynamic response evoked by cued attentional orienting in several ROIs including the left inferior parietal lobe. This reduction is illustrated in separate insets for frontal and parietal ROIs. In each graph, the difference in peak percent signal change between attention-directing and passive cues is depicted as a function of practice (runs 1-3, runs 4-6, runs 7-9) for individual brain ROIs (see Table 2 for a list of abbreviations for these ROIs). These differences in peak percent signal change were derived from the time-locked average responses to global and local cue-only and passive cue-only trials. In most of these ROIs, there was a large and significant decrease in neural activity associated with cued attentional orienting after runs 1-3 that was sustained throughout the remainder of the experiment (see Table 2 for relevant statistics performed on parameter estimates). All activations are overlaid on the canonical MNI normalized anatomical template provided by SPM'99. Anatomical slices range from Z=35 mm (top left) to Z=63 mm (top right). L, left; R, right.

Cued Attentional Orienting: Occipital ROIs

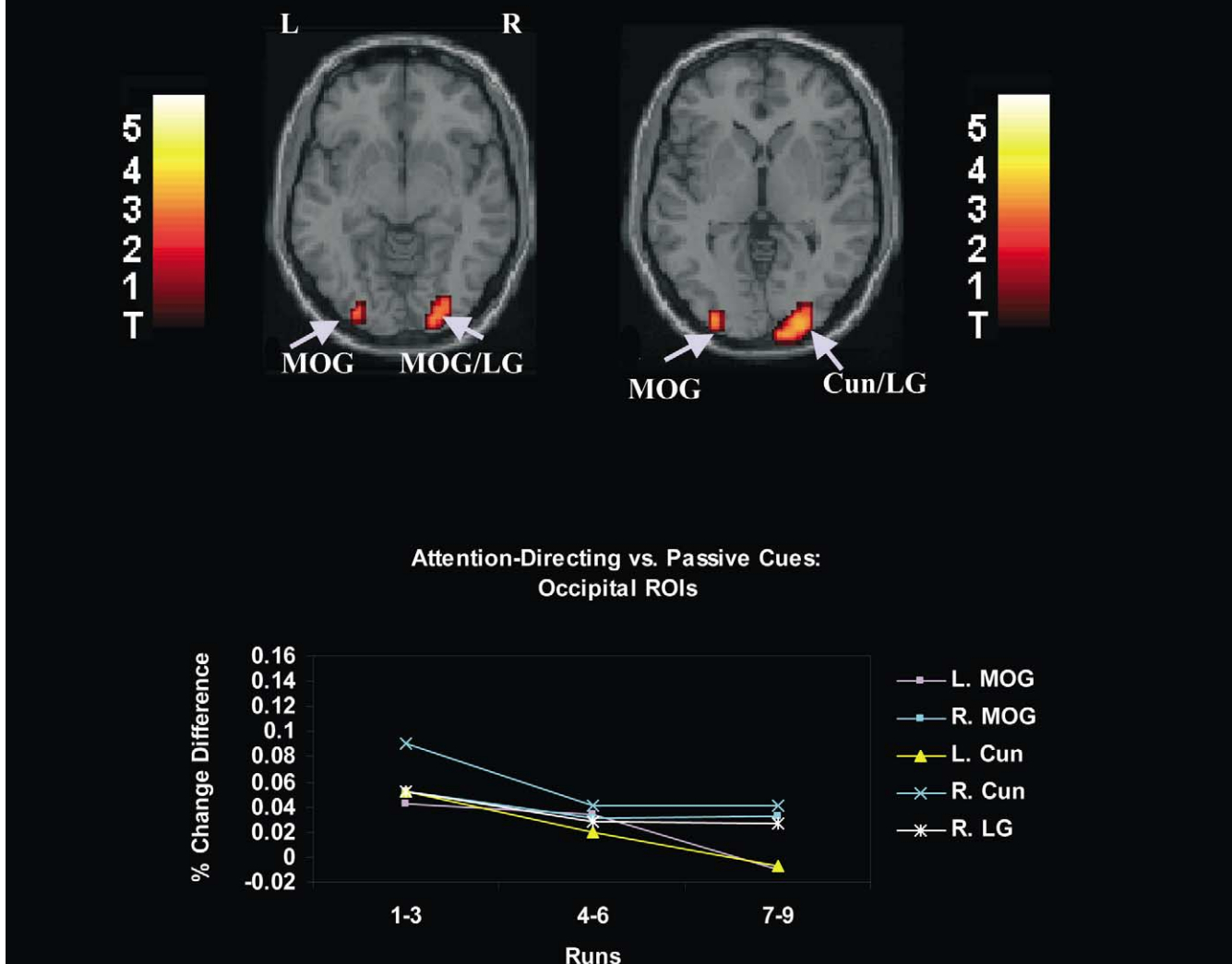


Fig. 3. Effects of practice on neural activity associated with cued attentional orienting in occipital regions of interest (ROIs). As shown in the figure, cued attentional orienting activated regions of occipital cortex (see also Table 1). ROI analyses revealed that practice significantly reduced the size of the hemodynamic response evoked by cued attentional orienting in several occipital ROIs. In the inset graph, the difference in peak percent signal change between attention-directing and passive cues is depicted as a function of practice (runs 1–3, runs 4–6, runs 7–9) for individual brain ROIs (see Table 2 for a list of abbreviations for these ROIs). These differences in peak percent signal change were derived from the time-locked average responses to global and local cue-only and passive cue-only trials. In most of these ROIs, there was a large and significant decrease in neural activity associated with cued attentional orienting after runs 1–3 that was sustained throughout the remainder of the experiment (see Table 2 for relevant statistics performed on parameter estimates). All activations are overlaid on the canonical MNI normalized anatomical template provided by SPM'99. Anatomical slices range from -7 mm (top left) to 0 mm (top right) in intervals of 7 mm. L, left; R, right.

decrease ($t > 2.15$, $P < 0.025$) of neural activity associated with cued attentional orienting between runs 1–3 and runs 4–6 for the left inferior parietal cortex with no further significant changes between runs 4–6 and runs 7–9 (Table 2; Fig. 2). Exploratory analyses revealed similar effects in several other frontal and parietal ROIs (Table 2; Fig. 2) as

well as several occipital ROIs (Table 2; Fig. 3). Thus, the pattern of effects observed in all ROIs indicates an early reduction in the recruitment of executive mechanisms following runs 1–3 that was sustained throughout the remainder of the experiment. We make no strong conclusions regarding statistical significance in ROIs identified

by the exploratory analyses, however, since they were not predicted at the outset of the study. Finally, no ROIs showed increases of neural activity associated with cued attentional orienting.

We next contrasted neural activity for incongruent targets with that to congruent targets (averaged across the global and local tasks to increase statistical power) in order to functionally define medial frontal and anterior cingulate regions that were activated by interference (Table 3; Figs. 4 and 5). As for the analysis of cue-related practice effects, we divided the experiment into three parts (runs 1–3, runs 4–6, and runs 7–9). In line with predictions (and opposite to the findings for cued attentional orienting), practice significantly ($t > 2.15$, $P < 0.025$) increased interference-related activity between runs 1–3 and runs 4–6 in bilateral regions of the medial frontal gyrus (Table 4; Fig. 4), with no further changes between runs 4–6 and runs 7–9. Exploratory analyses revealed similar effects in several other frontal ROIs (Table 4; Fig. 4) and in some subcortical ROIs (Table 4; Fig. 5). We make no strong conclusion regarding statistical significance in these regions, though,

because they were not predicted at the outset of the study. Finally, no ROIs showed decreases of interference-related activity.

4. Discussion

We investigated a key prediction of various models of executive control [10,36], which is that practice strengthens associations between task stimuli and task-relevant processes and responses. To do so, we determined whether practice affects the recruitment of brain regions that are engaged by (a) cued attentional orienting and (b) interference between target and distractor stimuli. As predicted, practice reduced neural activity associated with cued attentional orienting in left inferior parietal regions and increased interference-related activity in medial frontal regions. Both of these findings support models in which practice strengthens schemas as we describe below.

4.1. Effects of practice on cue-related activity

Attention-directing cues engage processes that interpret the meaning of cues [47,53,54], orient attention [41], and activate task-relevant stimulus–response mappings [44]. If practice strengthens associations between cues and these processes, then cues should become able to evoke these processes more automatically, with less intervention by the supervisory system. Practice should therefore reduce the recruitment of executive brain mechanisms that are engaged by cued attentional orienting (i.e. attention-directing cues versus passive sensory/semantic control cues).

Consistent with this prediction, practice reduced neural activity that was associated with cued attentional orienting in left inferior parietal regions that have been specifically linked to the control of attention toward global and local aspects of hierarchical stimuli [43]. In addition, this effect occurred relatively quickly. Neural activity associated with cued attentional orienting was greatest in runs 1–3, significantly lower in runs 4–6, and remained low in runs 7–9. Exploratory analyses suggested that the same pattern of effects was present in several other brain areas, including regions of frontal, parietal and occipital cortex. Given that we controlled for basic sensory and semantic processing of attention-directing cues with passive cues, our findings provide support for the view that practice strengthens cue schemas, thereby allowing cues to activate appropriate processes with less intervention from executive brain mechanisms.

Definitive interpretations of the decreased cue-related activity in frontal, parietal and occipital cortices must await further investigation, but the existent literature suggests several possibilities. Practice may engender more efficient focusing of attention on task-relevant information, thereby leading to decreased activity within inferior parietal regions that orient attention [12,13,19,26,42,51]. It may

Table 3
Major foci activated by interference

Region	BA	x	y	z	T	P
Frontal						
L. MFG	8	−52	6	45	7.26	<0.0001
R. MFG	6	41	6	51	5.91	<0.0001
L. SFG	6	−8	10	51	5.08	0.0001
R. ACC	32	8	21	44	4.81	0.0001
L. PrCG	4	−41	−12	52	4.77	0.0001
R. IFG	47	34	29	−7	4.11	0.0005
L. IFG	9	−45	16	25	3.84	0.0009
R. MedFG	32	8	6	51	3.72	0.0011
Parietal						
L. IPL	40	−45	−35	47	5.86	<0.0001
R. Prec	19	30	−71	36	5.12	0.0001
L. SPL	7	−26	−67	48	5.01	0.0001
R. SPL	7	34	−52	48	3.72	0.0011
Temporal						
R. FFG	37	45	−55	−15	6.86	<0.0001
L. ITG	20	−49	−52	−15	5.98	<0.0001
Occipital						
L. FFG	19	−41	−69	−8	4.89	0.0001
L. MOG	37	−52	−63	−9	4.36	0.0003
R. MOG	19	38	−77	−2	4.23	0.0004
Subcortical						
L. Cereb.		0	−68	−32	4.73	0.0002
R. Thal		4	−11	1	4.49	0.0003
L. Pulv.		−15	−25	1	2.75	0.0078
L. PhG	30	−23	−37	2	3.72	0.0011

BA, Brodmann area; x, y, z, coordinates of peak activation from Talaraich and Tournoux's (1988) atlas [49]. T, peak voxel T-score within a region; P, probability that a voxel T-score occurred by chance. L, left; R, right; SFG, superior frontal gyrus; MFG, middle frontal gyrus; MeFG, medial frontal gyrus; ACC, anterior cingulate cortex; PrCG, precentral gyrus; IFG, inferior frontal gyrus; SPL, superior parietal lobule; IPL, inferior parietal lobule; Prec, precuneus; FFG, fusiform gyrus; ITG, inferior temporal gyrus; PhG, parahippocampal gyrus; MOG, middle occipital gyrus; Cereb, cerebellum; Thal, thalamus; Pulv, pulvinar nucleus of the thalamus.

Interference: Frontal and Parietal ROIs

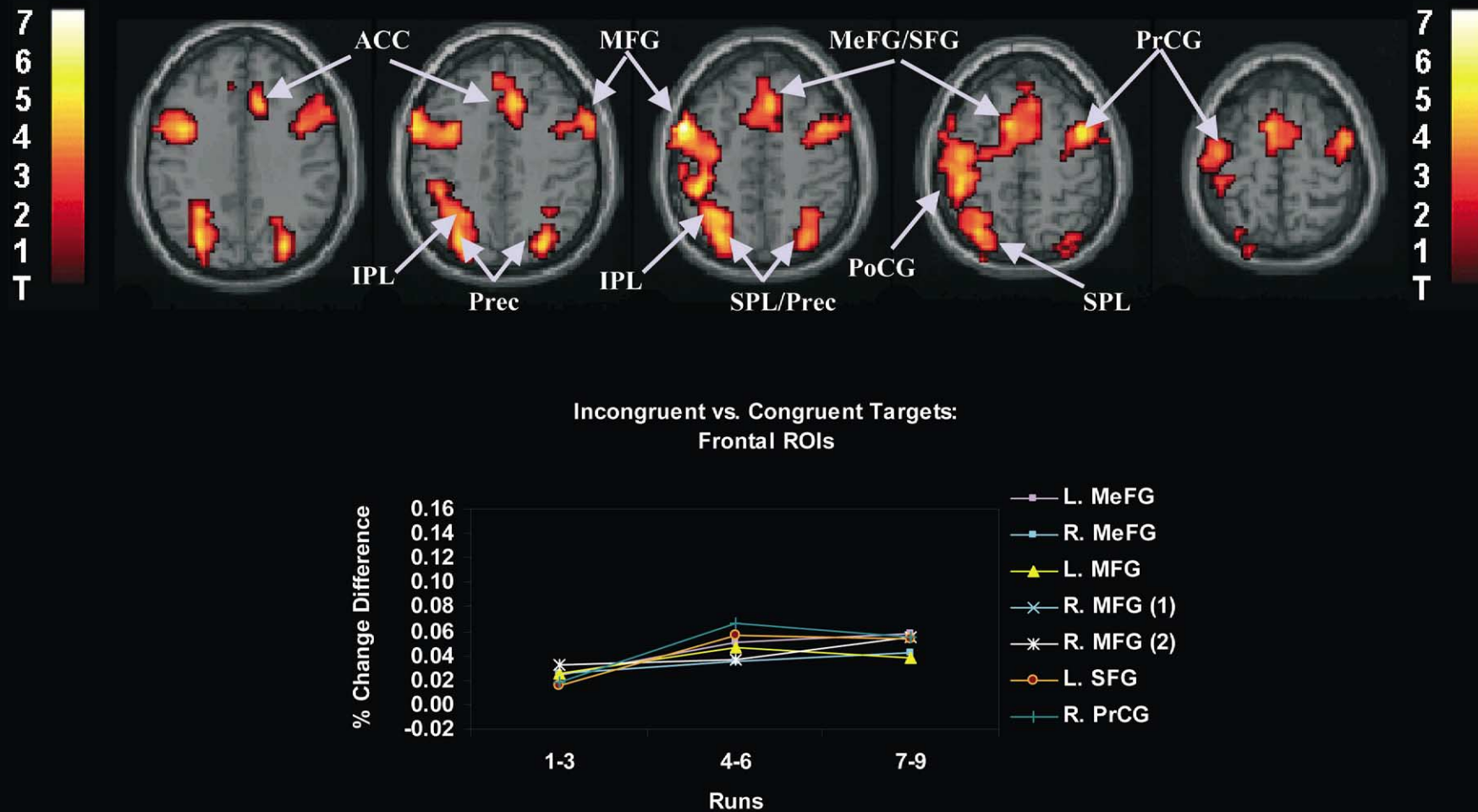


Fig. 4. Effects of practice on neural activity associated with interference in frontal and parietal regions of interest (ROIs). Interference activated regions of frontal and parietal cortex (see also Table 3). ROI analyses revealed that practice significantly increased the size of the hemodynamic response evoked by interference in several frontal ROIs including the medial frontal gyrus. This increase is illustrated in the inset graph. In this inset, the difference in peak percent signal change between incongruent and congruent targets is depicted as a function of practice (runs 1–3, runs 4–6, runs 7–9) for individual brain ROIs (see Table 4 for a list of abbreviations for these ROIs). These differences in peak percent signal change were derived from the time-locked average responses to cue-plus-incongruent and cue-plus-congruent trials, averaged across the global and local tasks. In most ROIs, there was a large and significant increase in neural activity associated with interference after runs 1–3 that was sustained throughout the remainder of the experiment (see Table 4 for relevant statistics performed on parameter estimates). All activations are overlaid on the canonical MNI normalized anatomical template provided by SPM'99. Anatomical slices range from $Z=35$ mm (top left) to $Z=63$ mm (top right). L, left; R, right.

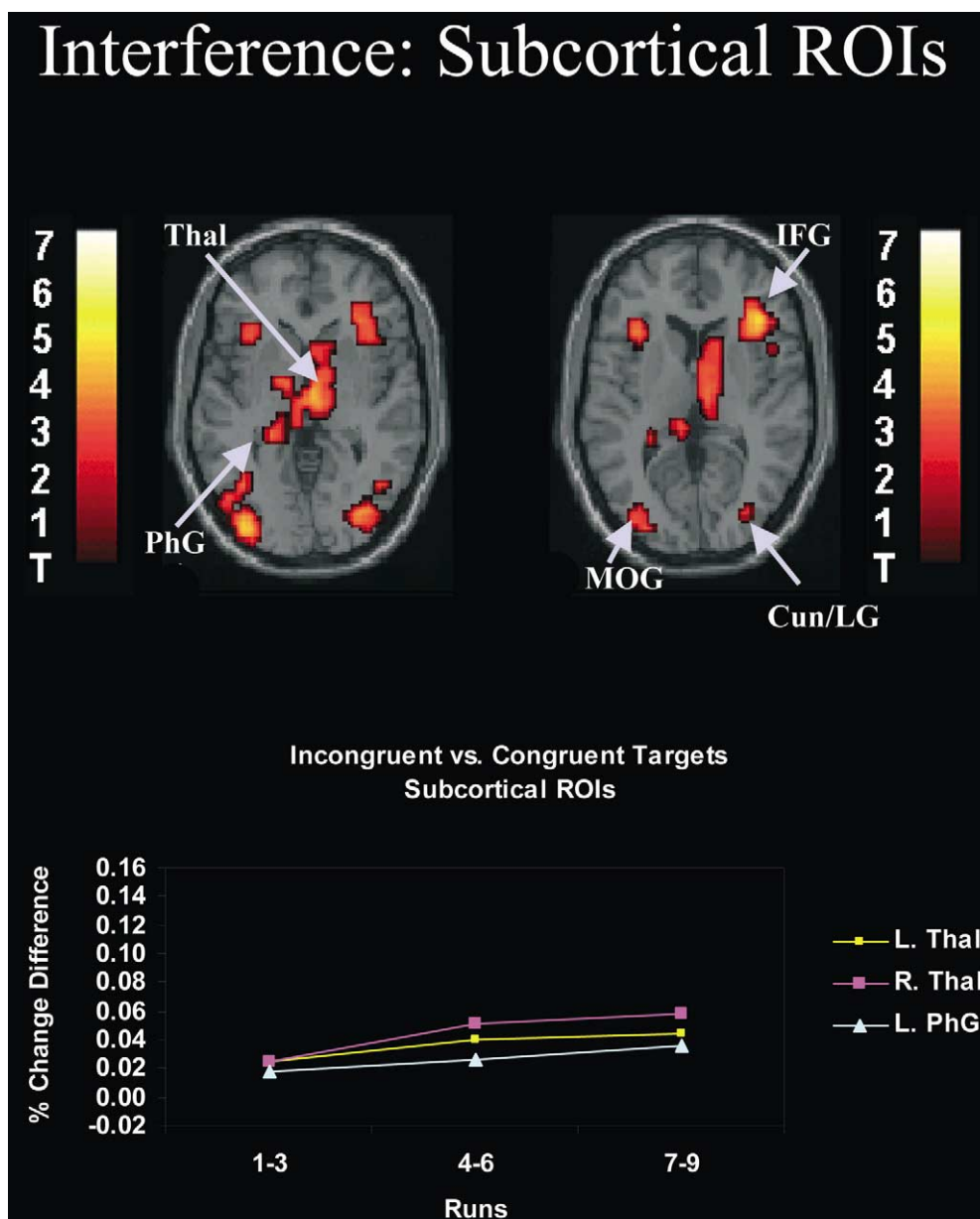


Fig. 5. Effects of practice on neural activity associated with interference in subcortical regions of interest (ROIs). As shown in the figure, interference activated subcortical regions including the thalamus and parahippocampal gyrus (see also Table 3). ROI analyses revealed that practice significantly increased the size of the hemodynamic response evoked by interference in several ROIs. This increase is illustrated in the inset graph. In this inset, the difference in peak percent signal change between incongruent and congruent targets is depicted as a function of practice (runs 1–3, runs 4–6, runs 7–9) for individual brain ROIs (see Table 4 for a list of abbreviations for these ROIs). These differences in peak percent signal change were derived from the time-locked average responses to cue-plus-incongruent and cue-plus-congruent trials, averaged across the global and local tasks. In most ROIs, there was a large and significant increase in neural activity associated with interference after runs 1–3 that was sustained throughout the remainder of the experiment (see Table 4 for relevant statistics performed on parameter estimates). All activations are overlaid on the canonical MNI normalized anatomical template provided by SPM'99. Anatomical slices range from 0 mm (top left) to 7 mm (top right) in intervals of 7 mm. L, left; R, right.

also increase the efficiency of encoding processes in occipital regions [5], where attention can facilitate the encoding of task-relevant stimuli [19,30], such that less attention is necessary during cue processing to prepare for upcoming task stimuli. In addition, repeated performance of a task may strengthen associations between task cues and the processes they activate at non-supervisory levels

[36], such that brain regions that interpret the meaning of linguistic (cue) stimuli, such as the angular gyrus [4], become less recruited by executive mechanisms. Task repetition may also lead to more efficient maintenance of task-relevant representations [46], thereby reducing activity in brain regions that keep currently relevant representations active in working memory, such as the middle frontal

Table 4
ROIs for which practice significantly increased activity associated with interference

Region	<i>N</i>	BA	<i>x</i>	<i>y</i>	<i>z</i>	<i>T</i> -1	<i>T</i> -2	<i>T</i> -3	<i>T</i> -1 vs. 2	<i>T</i> -2 vs. 3
Frontal										
L. MeFG	50	6/32	−5	10	49	0.79	3.90	1.99	2.39	0.91
R. MeFG	42	6	7	17	45	1.32	3.65	2.03	2.33	0.75
R. ACC	29	24/32	10	19	37	1.50	3.13	2.26	1.96	0.12
L. MFG	44	6	−42	2	45	1.07	6.52	2.70	2.75	0.25
R. MFG(1)	54	6	44	4	49	0.13	4.63	2.84	3.28	0.44
R. MFG(2)	7	8	51	12	40	0.29	3.07	1.89	2.27	0.37
R. PrCG	44	6	45	−2	50	0.37	2.91	2.33	2.41	0.31
L. SFG	37	6/8	−4	14	55	0.81	4.11	2.61	2.26	0.35
Subcortical										
L. Thal	28		−9	−24	3	0.2	2.87	2.61	2.27	0.38
R. Thal	47		9	−12	5	0.26	2.96	2.93	2.66	0.37
L. PhG	14	27	−17	−28	−3	0.15	2.79	2.77	2.34	0.78

T-1, 2, 3 = *T*-score indicating reliability of activation for runs 1–3, runs 4–6, and runs 7–9. *T*-1 vs. 2 = *T*-score testing whether activity was smaller for runs 1–3 than runs 4–6 ($t > 2.15$, $P < 0.025$). *T*-2 vs. 3 = *T*-score testing whether activity was smaller for runs 4–6 than runs 7–9 ($t > 2.15$, $P < 0.025$). ROI, region of interest; *N*, number of voxels; BA, Brodmann area; *x*, *y*, *z*, geographic center of mass coordinates from Talaraich and Tournoux's (1988) atlas [49]. L, left; R, right; MeFG, medial frontal gyrus; MFG, middle frontal gyrus; PrCG, precentral gyrus; SFG, superior frontal gyrus; PhG, parahippocampal gyrus; Thal, thalamus.

gyrus [40]. Finally, practice may strengthen associations between target stimuli and their appropriate responses. Such effects may reduce neural activity in midline frontal regions that is related to motor preparation following cue presentation [39]. These interpretations are highly consistent with current views on the functional neuroanatomy of cued attentional orienting.

4.2. Effects of practice on interference-related activity

Target stimuli engage processes that select, identify and respond to task-relevant stimulus features. If practice strengthens associations between targets and such processes, then targets should come to evoke identification and response processes relatively automatically, with less intervention by the supervisory system. In the present experiment, we used a cued attention paradigm in which participants became increasingly practised at selecting, identifying and responding to every possible target stimulus (e.g. global H, global S, local H, local S). We therefore predicted that practice would increase the recruitment of brain regions that implement conflict detection and/or resolution processes when those same stimuli served as incongruent distractors.

Consistent with this prediction, practice significantly increased interference-related activity in the medial frontal gyrus (just dorsal to the anterior cingulate cortex), which has previously been linked to the detection of response conflict [34]. This effect occurred relatively quickly in that interference-related activity was quite low in runs 1–3, significantly higher for runs 4–6, and remained high (possibly at ceiling) for runs 7–9. Exploratory analyses revealed similar effects in a number of other regions including the middle frontal gyrus and the thalamus. The middle frontal gyrus is engaged when the presence of conflicting distractor stimuli increases demands on pro-

cesses that keep track of current task goals [3,15]. In the present study, practice at associating distractor stimuli with motor responses that conflicted with those required by targets on incongruent trials may have increased the demands on such working memory processes. Practice effects in thalamic regions, which included the left pulvinar, may indicate that strengthening associations between distractors and specific motor responses leads to increased focusing of attention on target features [24] during incongruent trials. Therefore, the present findings support the view that practice at associating distractor stimuli with specific responses increases the recruitment of executive brain systems that detect/resolve interference on incongruent trials.

One may wonder why, if our interpretation of the imaging data is correct, practice failed to increase *behavioral* measures of interference. One possibility is that practice increased the ability of distractors to evoke conflict, but that the increased conflict was resolved before it affected behavioral performance. From this perspective, at least some of the brain regions that showed increased interference-related activity with practice likely make a functional contribution to detecting/resolving interference rather than causing it.

5. Summary

The present findings make several important contributions to our understanding of executive brain mechanisms. Firstly, to our knowledge, they constitute the first direct evidence from functional neuroimaging that practice decreases the recruitment of executive brain mechanisms engaged by cued attentional orienting. Secondly, our results are the first to show that practice increases the recruitment of executive brain mechanisms that are en-

gaged by interference when the task-relevance of distractor information is controlled. These findings illustrate that practice can decrease the recruitment of executive brain mechanisms for one component of a task (e.g. cued attentional orienting) while increasing it for another (e.g. detecting/resolving interference). This finding is more compatible with the theoretical view that practice strengthens task schemas than with alternative explanations related to arousal. For example, it is unclear how a uniform decrease in arousal over the course of the experiment would predict both an increase of interference-related activity and a decrease of activity associated with cued attentional orienting. The present results therefore demonstrate how functional neuroimaging studies of practice effects can be extremely useful for testing theoretical models of executive control.

Acknowledgements

This research was supported by a postdoctoral National Research Service Award to D.W. (1 F32 NS41867-01) and by NIMH grants to M.G.W. (MH60415) and G.R.M. (MH55714 and MH02019). We wish to thank Barry Giesbrecht, Kevin Wilson, Sean Fannon, Wayne Khoe, Laura Busse and Heleen Slagter for useful discussions. We also wish to thank Linsay Warner for her careful proof-reading of the manuscript.

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