

Sustained involvement of a frontal–parietal network for spatial response selection with practice of a spatial choice–reaction task

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Abstract

With practice, performance on a task typically becomes faster, more accurate, and less prone to interference from competing tasks. Some theories of this performance change suggest it reflects a qualitative reorganization of the cognitive processing required for successful task performance. Other theories suggest this change in performance reflects a more quantitative change in the amount of processing required to perform the task. Neuroimaging research results provide some support for both of these broad theories. This inconsistency may reflect the complex nature of the effect of practice on cognitive and neural processing. Our current experiment addresses this issue by investigating the effect of practice of a relatively easy perceptual–motor task on the frontal–parietal brain network for a specific cognitive process (viz. spatial response selection). Participants were scanned during three functional magnetic resonance imaging sessions on separate days within 4 days while they performed a relatively easy spatial perceptual–motor task. We found sustained activity with practice in right dorsal prefrontal cortex; and sustained but decreasing activity in bilateral dorsal premotor, left superior parietal, and precuneus cortices, supporting a quantitative decrease in difficulty of response selection with practice. Conversely, we found a qualitative change in activity with practice in left dorsal prefrontal cortex. This brain region is outside the response selection network for this task and showed activity only during novel task performance. These results suggest that practice produces both qualitative and quantitative changes in processing. The particular effect of practice depends on the cognitive process in question.

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1. Introduction

“Practice makes perfect.” Despite its banality, this truism has been the focus of a great deal of experimental research in psychology and neuroscience. Practice improves performance on almost every task. For brevity we focus here on the performance of relatively easy perceptual–motor tasks like those involved in common tasks like driving a car and experimental ones often performed by volunteers in psychology experiments. These tasks typically require participants to make motor responses to perceptual

stimuli based on arbitrary stimulus–response (S–R) rules. For example, press the brake pedal when one sees a red light. With practice, mean reaction times (RTs) tend to decrease and accuracy rates tend to increase. This decrease in mean RTs roughly follows a power function (Crossman, 1959; Snoddy, 1926, also Heathcote, Brown, & Mewhort, 2000).

Some influential theories for this effect of practice postulate that performing novel tasks relies heavily on capacity-limited control processes; whereas performing well-practiced ones relies more heavily on automatic processes, which are not capacity limited. That is, with training on a task, there is a *qualitative* shift in processing such that automatic processes supplant controlled ones (Logan, 1988; Shiffrin & Schneider, 1977).

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Similarly, Anderson and co-workers (Anderson, 1976; Neves & Anderson, 1980) also postulate a qualitative change in information processing with extended task practice. In their model, the knowledge required for performing novel tasks is encoded as declarative facts in semantic memory, which is capacity limited and slow to interpret and apply. With practice, task knowledge becomes proceduralized (i.e., encoded into procedural memory), whose application is fast and requires little or no conscious interpretation.

Qualitative changes in processing are not the only way we may get better with practice, however. A different learning theory postulates *quantitative* changes in processing with practice (Newell & Rosenbloom, 1980). According to this theory, the same processes mediate both novel and skilled task performance. Mean RTs decrease with practice not through functional reorganization of processing, but through increased efficiency.

Both of these broad theories (i.e., qualitative versus quantitative processing changes with practice) have received some support from neuroimaging research. Several studies have found distinct brain regions involved in the performance of novel versus well-practiced tasks (Petersen, Van Mier, Fiez, & Raichle, 1998; Poldrack, Desmond, Glover, & Gabrieli, 1998; Raichle et al., 1994). For example, in one of the first investigations of the neural effect of practice, Raichle et al. had participants generate verbs to visually presented nouns. Brain activity in this task was compared to a control condition in which participants read the nouns. Novel performance of the task activated left dorsal prefrontal, left posterior temporal, and anterior cingulate cortices. After roughly 15 min of practice, activity in these regions significantly decreased whereas activity in left extrastriate and bilateral sylvian-insular cortices significantly increased. This change in the location of active brain regions with practice suggests a qualitative shift, or a functional reorganization, in the processes required to successfully perform this task and is consistent with theories emphasizing qualitative processing changes with practice (Anderson, 1976; Logan, 1988; Neves & Anderson, 1980; Shiffrin & Schneider, 1977).

Other studies, however, report only quantitative changes in brain activity with practice (Garavan, Kelley, Rosen, Rao, & Stein, 2000; Landau, Schumacher, Garavan, Druzgal, & D'Esposito, 2004; Milham, Banich, Claus, & Cohen, 2003). These studies report no functional reorganization with practice; only activity decreases without corresponding increases in other brain regions. These results suggest that we may get better with practice through increases in neural efficiency and are more consistent with theories emphasizing quantitative processing changes with practice (Newell & Rosenbloom, 1980).

Despite the computational rigor of these cognitive models, they, and the neural data supporting them, tend to be relatively abstract with regard to how practice affects particular cognitive processes. Another avenue of behavioral research has been to investigate the cognitive locus of the practice effect. Many behavioral studies have shown that, for choice–reaction

tasks, the effect of practice primarily decreases the duration of response selection (Pashler & Baylis, 1991; Welford, 1976).

Response selection is a cognitive process that chooses (i.e., activates above threshold) one response representation over competing ones (Dutta & Proctor, 1992; Hommel, 1998; Kornblum, Hasbroucq, & Osman, 1990; Rosenbloom & Newell (1987)). The duration of this process may be based on a number of factors, including the ease of the S-R mappings and the amount of practice with the task.

Rosenbloom and Newell (1987) developed a theory of response selection using their GOMS (i.e., goals, operators, methods, selection rules) computational architecture. Their algorithm identified a number of operations required to successfully compute the correct response to a currently presented stimulus. According to this model, response selection difficulty increases with the number of operations required. Additionally, the number of required operations decreases with practice through a *chunking* mechanism that quantitatively increases the efficiency of the operators.

Other theories of response selection propose multiple processing pathways for response selection (Eimer, Hommel, & Prinz, 1995; Kornblum et al., 1990). According to these theories, there is a relatively slow route requiring S-R translation algorithms and a faster process that automatically activates potential responses. Response selection is more difficult both to the extent that the algorithmic process is required for successful performance and to the extent that the algorithmic and automatic processes lead to competing responses. Additionally, one reason the duration of response selection may decrease with practice is that there is a qualitative change in the processes required for successful task performance. That is, with training automatic processes may supplant algorithmic ones (Van Selst, Ruthruff, & Johnston, 1999). Thus, even for theories specific to response selection, there is disagreement about whether practice produces quantitative or qualitative processing changes.

Unfortunately, our knowledge of how the brain mediates response selection does not yet provide compelling evidence for how this process changes with practice. The neural mechanisms for response selection have recently been investigated with neuroimaging techniques (Bunge, Hazeltine, Scanlon, Rosen, & Gabrieli, 2002; Dasonville et al., 2001; Deiber et al., 1991, 1997; Iacoboni, Woods, & Mazziotta, 1996; Jiang & Kanwisher, 2003; Rowe, Toni, Josephs, Frackowiak, & Passingham, 2000; Schumacher & D'Esposito, 2002; Schumacher, Elston, & D'Esposito, 2003; Toni, Rushworth, & Passingham, 2001). Some of this research suggests that different neural mechanisms may mediate response selection depending on stimulus type, response type, and modality (Hazeltine, Bunge, Scanlon, & Gabrieli, 2003; Schumacher et al., 2003; Toni et al., 2001). Many of these studies show that increasing spatial response selection produces a corresponding increase in brain activity in a number of frontal–parietal brain regions (e.g., dorsal prefrontal, dorsal premotor, superior parietal, and precuneus).

The effect of practice on the processing mediated by these brain regions is unclear because the few studies of this issue have focused on practice across only one session and have produced inconsistent results. In one study, participants learned to associate four spatial locations with four different movements of a joystick (Deiber et al., 1997). This study found practice related decreases in activity in right dorsal prefrontal, premotor, and parietal cortices. In another study, spatial cues appeared to the participants' left or right and they made compatible or incompatible responses with their left and right hands (Iacoboni et al., 1996). This study found practice related increases in activity in left dorsal prefrontal, premotor, primary motor cortices. Finally, our previous studies provide indirect evidence that activation related to response selection does not change with practice. Two of our recent studies implicate these frontal–parietal brain regions for response selection both when participants practiced the tasks for a session on a day prior to scanning (Schumacher & D'Esposito, 2002), as well as when they performed the tasks with minimal pre-scan practice prior to scanning (Schumacher et al., 2003).

Despite the many differences between these studies, the discrepancy among them (i.e., right hemisphere decreases with practice, left hemisphere increases with practice, or no change with practice) warrants further investigation. Additionally, no study has directly investigated the effect of more than one session of practice on brain activity for choice–reaction task performance. This is surprising given that cognitive theories account for practice related changes over thousands of trials across multiple experimental sessions (Anderson, 1976).

Our current study addresses these limitations in several ways. In it, participants perform a visual-manual choice–reaction task in which they press buttons to the location of a spatial cue based on arbitrary S-R rules. This task places large demands on response selection due to the computation required to translate the current stimulus position to the correct response key and to the competition between the response activation for the correct response and that of the response directly corresponding to the current stimulus location (Dutta & Proctor, 1992; Eimer et al., 1995; Fitts & Seeger, 1953; Kornblum et al., 1990; Rosenbloom & Newell, 1987). Additionally, in a previous experiment, we used this task and easier ones to parametrically vary response–selection difficulty (Schumacher et al., 2003). In that study, we found that activation in right dorsal prefrontal, bilateral dorsal premotor, left superior parietal, and precuneus cortices increased monotonically with response–selection difficulty. This provides us with direct evidence for the brain regions mediating response selection for this task. Thus, comparing the pattern of activity produced by this task across levels of practice in these regions may allow us to identify the neural effect of practice in brain regions specifically related to spatial response selection. Finally, we performed both univariate and multivariate tests on these data. In this way we may discover

the effect of practice on the network of brain regions mediating the specific cognitive process of spatial response selection.

2. Materials and methods

2.1. Participants

Six healthy right-handed volunteers (ages 23–33 years; three females) participated in this experiment. All participants were recruited from the University of California community and gave their informed consent.

2.2. Behavioral procedure

Stimuli were projected onto a screen viewed by participants through a mirror mounted on the head radiofrequency (RF) coil while lying prone in a magnetic resonance scanner. Participants made their responses with the index and middle fingers of their left and right hands using a four-button response pad.

Participants performed a choice–reaction task. At the beginning of each trial a fixation-cross (+) appeared in the center of the fixation display. The display consisted of a horizontal array of four circles, two on either side of the fixation cross. The fixation and circles appeared in white on a black background. The circles were equidistant from each other and the entire display subtended roughly 3° visual angle horizontally. This fixation display remained onscreen for a variable foreperiod of 400 ms (53% of the trials), 500 ms (27% of the trials), 600 ms (13% of the trials), or 700 ms (7% of the trials). After the foreperiod, the cue stimulus (viz. a filled white disk) replaced one of the display circles for 200 ms; after which the original fixation display returned and remained onscreen for an additional 500 ms. The circles then disappeared and the fixation cross remained onscreen for either 800, 900, 1000, or 1100 ms, such that the entire trial lasted 2200 ms. Participants responded to the location of the stimulus cue based on an arbitrary, incompatible S-R mapping. The cue appeared equally often on the far left, middle left, middle right, and far right position and participants pressed a button with their right index, left middle, right middle, and left index finger to each cue, respectively. Prior to the first scan, participants were told about the task. They were shown the display and verbally and visually instructed about the correct S-R pairings. They did not practice the task prior to scanning.

Participants were paid US \$8 an hour plus a monetary bonus based on points earned for their performance. Three hundred points were awarded for each correct response and 1 point was deducted for every 10 ms taken to respond correctly; 300 points were deducted per incorrect response. Participants earned US \$1 for every 10,000 points they scored. They were fully informed about the reward system before the experiment began.

2.3. fMRI procedure

Each participant was scanned three times on separate days. Four participants completed all scans on consecutive days. No more than one day separated consecutive scans for the other two participants. Each functional magnetic resonance imaging (fMRI) scanning session consisted of eight runs per session. Each run consisted of three condition blocks lasting 33 s each. The choice–reaction task consisted of 15 trials each. The second condition was a fixation baseline block in which participants fixated on a centrally presented cue (+) for 33 s. Participants also performed a third unrelated non-spatial task condition for 33 s, which is not presented here. Each condition block was presented four times per run. The order of presentation was randomized such that each participant received four of the six possible condition block orders during each run.

Text displaying the instructions for the upcoming block type appeared for 2.2 s prior to the beginning of each block. Feedback, including mean accuracy and RT for the block and overall points earned for the run, was displayed for 2.2 s after choice–reaction task blocks. Overall accuracy and mean RT, as well as total points earned for the experiment were displayed at the end of each run for at least 4.4 s.

Imaging was performed using a 4.0 Tesla Varian Inova scanner equipped with a fast gradient system for echoplanar imaging. A standard RF head coil was used with foam padding to restrict head motion comfortably. A 2-shot gradient echo, echoplanar sequence (TR = 2200 ms, TE = 28 ms, matrix size = 64 × 64, FOV = 22.4 cm) was used to acquire data sensitive to the blood oxygen level dependent signal. Each functional volume contained 20–0.5 mm axial slices with a 0.5 mm gap between slices. Each fMRI run began with 22 s of dummy gradient RF pulses to achieve a steady state of tissue magnetization. Each run lasted 7 min 47 s (212 volumes/run). Two high-resolution structural T1-weighted scans were also acquired. The first collected 20 axial slices in the same plane as the echoplanar images (TR = 200 ms, TE = 5 ms, matrix size = 256 × 256, FOV = 22.4 cm). The second was a 3D MPFLASH scan (TR = 9 ms, TE = 4.8 ms, TI = 300 ms).

2.4. fMRI data processing

Data processing and analyses on each participant were performed using Voxbo software (www.voxbo.org). Before data were analyzed, they were corrected for head-motion artifacts using a six-parameter, rigid-body transformation algorithm (Friston et al., 1995) and the time-series from each voxel was normalized by the mean signal value across the run to remove scaling differences.

Primary statistical analyses were performed on the data from all sessions using a modified general linear model (Worsley & Friston, 1995). We modeled the data separately for each participant and session. For each model, we created a design matrix including covariates for each condition

(e.g., choice task, instruction, and feedback) convolved with an idealized hemodynamic response function. A time-domain representation of the expected $1/f$ power structure and a notch filter that removed frequencies above the Nyquist frequency and below 0.005 Hz (i.e., the portions of highest power in the noise spectrum) were also included in the convolved design matrix (Zarahn, Aguirre, & D'Esposito, 1997).

A second analysis was performed to characterize the effect of practice within each session. For this analysis we included additional covariates separating the first half from the second half of each session. We have used this analysis technique in previous studies (Landau et al., 2004) to successfully reveal within-session changes in activation.

Each participant's brain was normalized to the Montreal Neurological Institute reference brain using SPM99. Statistical parametric maps of β -values for the choice task versus fixation baseline were calculated for each session for each participant. These contrasts were spatially smoothed with a 6 mm full-width half-maximum Gaussian kernel to account for between-subject anatomical variability and analyzed with separate t -tests for each session.

To more specifically characterize the task-related changes within and across sessions, we conducted a block-wise analysis on the data from Sessions 1 and 3 separately. The modified general model for this analysis was identical to the previous ones except that it included separate covariates for each experimental block. The β -values from this analysis reflect the activation in each block of trials of the choice–reaction task relative to the fixation baseline condition.

2.5. Primary region-of-interest (ROI) analyses of fMRI data

The contrast described above (i.e., choice–reaction task versus baseline) includes all task-related processes (e.g., stimulus encoding, response selection, response programming, etc.). To characterize the effect of practice across all sessions on regions specifically related to response selection, we investigated the effect of practice on brain activity in ROIs from a previous study with the same and other similar spatial choice–reaction tasks (Schumacher et al., 2003).

In Schumacher et al. (2003), participants performed spatial choice–reaction tasks that differed across four levels of response–selection difficulty. We conducted whole-brain statistical analyses and found five brain regions (i.e., right dorsal prefrontal, bilateral dorsal premotor, left superior parietal lobule, and precuneus) to be monotonically affected by our parametric manipulation of spatial response–selection difficulty. No other response–selection related regions were found.

For the current analyses, ROIs for each of the areas identified from Schumacher et al. (2003) included the sites of peak activity and contiguous voxels with a t -value corresponding to $p < 0.01$ from that study. An additional ROI for the left dorsal prefrontal cortex (homologous to activity in the right hemisphere) was also included to investigate the effect of

practice with a spatial compatibility task in this region because it has produced inconsistent patterns of activity in previous studies of spatial response selection (Deiber et al., 1991; Iacoboni et al., 1996; Jiang & Kanwisher, 2003; Schumacher & D'Esposito, 2002).

2.6. Secondary correlation analyses of fMRI data

The effect of practice on dorsal prefrontal cortex was further investigated through a number of separate correlational analyses. We focused on dorsal prefrontal cortex for several reasons. Firstly, this region has been hypothesized to be involved in cognitive control processes responsible for S-R translation (Baddeley, 1986; Miller & Cohen, 2001; Norman & Shallice, 1986; Schneider & Chein, 2003). Accordingly, activity in this region may be susceptible to practice related changes, especially if there is a qualitative shift in the processing required for successful task performance. Additionally, it is controversial whether the left and right dorsal prefrontal cortex mediate response selection for different types of stimuli (Jiang & Kanwisher, 2003; Schumacher et al., 2003); thus, an investigation of the laterality of the effect of practice in this region may provide evidence supporting unimodal or multimodal hypotheses for the neural mechanisms of response selection. Finally, left and right dorsal prefrontal cortices show different patterns of activity with practice (Deiber et al., 1997; Iacoboni et al., 1996). Therefore, the data from these regions may provide direct evidence for the nature of neural processing in this important brain area. Finally, we further restricted these correlational analyses to the data from Sessions 1 and 3 where there is likely to be the greatest change between the processes required to perform the task.

2.6.1. Inter-regional correlational analysis

The block-wise β -values, which reflect activation separately for each choice–reaction block, were used as dependent measures for several correlation analyses. These correlations investigated whether the frontal–parietal ROIs function as a network mediating response selection and whether this network changes with practice. We hypothesized that if the regions function as a network, then their activity should correlate across blocks.

To investigate this we computed the correlation between the mean activity in each dorsal prefrontal ROI across blocks and the activity in each brain voxel across blocks. For example, mean activity was computed for each choice–reaction block in the right dorsal prefrontal ROI by averaging together the β -values within the ROI separately for each block. These averaged β -values were then correlated with the β -values for each block independently across all voxels. We computed this correlation for both the left and right dorsal prefrontal ROIs in both Session 1 and Session 3. From these whole-brain correlation maps, we computed the average correlation within each ROI (i.e., bilateral premotor, superior parietal, and precuneus).

2.6.2. Brain-behavior analysis

We investigated how different behavioral measures of performance correlated with dorsal prefrontal activity to test two hypotheses. First, Pashler and Baylis (1991) suggest that the decrease in RTs with practice is due primarily to a decrease in the duration of response selection. Therefore, activity in the left and right dorsal prefrontal cortex should show a corresponding decrease if these regions mediate response selection. To investigate this, we correlated mean RT across the 32 choice–reaction task blocks with mean activity from the ROIs in these blocks for each participant in Session 1. This correlational analysis focused on the effect of practice in Session 1 because only that session showed a large practice effect on mean RTs.

For the second hypothesis, we were interested in how brain activity relates to overall performance once a task is well learned. We hypothesized that, after practice, some participants may have more difficulty performing the task than others because they continue to rely on slow algorithmic processes required during novel task performance. A relationship between overall task performance and dorsal prefrontal activity may provide insight into the nature of the processes mediated by these regions.

We used mean RT from Session 3 as a measure of each participant's overall performance. We assumed that slower performers had more difficulty with the task than faster ones. This assumption seems warranted given the relatively high levels of accuracy in the task across sessions. Furthermore, there was no correlation between mean RT and accuracy across participants in Session 3 ($r = 0.15, p > 0.75$). Thus, it is unlikely that our participants were trading speed for accuracy and mean RT may be a reasonable measure of overall task performance.

Before assessing the significance of the correlational data, we applied an arc-hyperbolic tangent transform (Fisher's- z) to them, so that the difference of the coherency magnitudes approached a zero-centered normal distribution. Group means and t -tests were computed on these transformations. The Fisher's- z score means were then transformed back to correlations for display in the table and figure.

3. Results

3.1. Behavioral data

Mean RTs for the choice–reaction tasks are shown for each block across the three sessions in Fig. 1.

A within-subjects analysis of variance (ANOVA) showed a significant effect of Session on mean RTs from correct trials for the choice–reaction task [$F(2,10) = 41.33, p < 0.001$].¹

¹ Left index finger responses were slower than other finger responses. There were no significant differences between the other finger responses. Because our blocked experimental design cannot distinguish brain activity for each response individually, the data have been combined across finger.

Table 1

Coordinates for peak activation voxel and cluster size for each region-of-interest and the correlations between mean activity in these regions and mean activity in left and right dorsal prefrontal cortices in Sessions 1 and 3

Region-of-interest	MNI coordinates			Cluster size	Correlation with left dorsal prefrontal		Correlation with right dorsal prefrontal	
	x	y	z		Session 1	Session 3	Session 1	Session 3
Left dorsal prefrontal cortex	−42	32	24	215	−	−	0.50	0.44
Right dorsal prefrontal cortex	42	32	24	215	0.52	0.43	−	−
Premotor cortex					0.43	0.29	0.48	0.43
Left premotor cortex	−30	−8	58	730				
Right premotor cortex	18	4	58	304				
Parietal cortex					0.49	0.30	0.50	0.41
Left superior parietal lobule	−16	−70	44	730				
Precuneus cortex	−8	−54	48	922				

All correlations are significant at $p < 0.05$.

Mean accuracies increased with session (Fig. 1). An arcsine transformation was applied to the proportion correct in each session (Howell, 1987). An analysis of variance on these data showed that the accuracy increase was not significant [$F(2,10) = 2.33$, $p > 0.10$]. The decrease in mean RTs and increase in mean accuracy across session suggests that participants were not trading speed for accuracy in this task.

3.2. fMRI data

3.2.1. Primary ROI analyses

The early versus late within-session analysis produced no significant differences in the ROIs in any session, therefore given the decrease in signal-to-noise and corresponding loss of statistical power caused by dividing the data in half, we focus our analysis and interpretation on the statistical model without these covariates.

The coordinates of the activation peaks and number of contiguous voxels for each ROI are shown in Table 1.

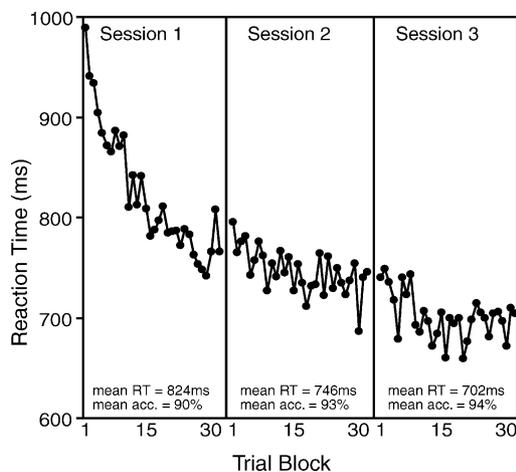


Fig. 1. Mean reaction times for the choice task for each experimental block across session and mean reaction time and accuracy for each session overall.

The mean activation relative to the fixation baseline for each of the response–selection regions is shown for each session in Fig. 2. A one-way within-subjects ANOVA with Session as a factor was conducted on the data for each task and ROI separately.²

3.2.1.1. Left dorsal prefrontal cortex. As shown in Fig. 2, activity in left dorsal prefrontal cortex decreased across session. Collapsing across session, there was no significant activity in left dorsal prefrontal cortex, $F[1,5] = 3.17$, $p = 0.14$. There was, however, a significant linear trend in the data, $F[1,5] = 8.69$, $p < 0.05$; and the main effect of Session approached significance, $F[2,10] = 3.03$, $p < 0.10$. Activity was significant in Session 1 only, $t(5) = 3.13$, $p < 0.05$.

3.2.1.2. Right dorsal prefrontal cortex. As shown in Fig. 2, activity in right dorsal prefrontal cortex was active across all sessions. Collapsing across session, there was significant activity in right dorsal prefrontal cortex, $F[1,5] = 9.47$, $p < 0.05$. There was no significant linear trend or effect of Session on mean activity in right prefrontal cortex, $F[1,5] = 0.01$, and $F[2,10] = 0.09$, respectively.

3.2.1.3. Premotor cortex. Because there was no significant difference of the effect of Session on activity in left and right dorsal premotor ROIs, $F[2,10] = 2.46$, $p > 0.10$ and we have no hypotheses regarding hemispheric differences in premotor cortex, we averaged together the data from both premotor ROIs for the following analyses. As shown in Fig. 2, activity in premotor cortex decreased across sessions but remained active across all sessions. Collapsing across session, there was significant activity in premotor cortex, $F[1,5] = 22.01$, $p < 0.01$. There was also a significant linear trend and nearly significant effect of Session on mean activity in premotor cortex, $F[1,5] = 6.85$, $p < 0.05$ and $F[2,10] = 3.95$, $p = 0.05$, respectively.

² Additional native-space ROI analyses yielded the same results as the normalized-group analyses presented here.

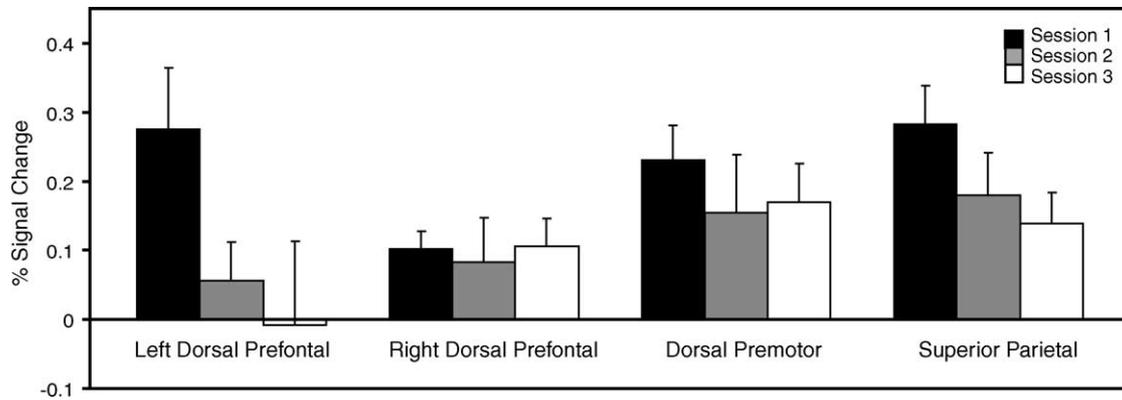


Fig. 2. Mean activity and standard error bars for the choice task relative to the fixation baseline task for each region-of-interest in each session.

3.2.1.4. Parietal cortex. Because there was no significant difference of the effect of Session on activity in our two parietal ROIs, $F[2,10]=0.61$, $p>0.55$ and we have no hypotheses regarding functional differences in these regions, we averaged together the data from both parietal ROIs for the following analyses. Collapsing across session, there was significant activity in parietal cortex, $F[1,5]=25.52$, $p<0.005$. There was also a significant linear trend and a trend toward a significant effect of Session on mean activity in parietal cortex, $F[1,5]=7.91$, $p<0.05$ and $F[2,10]=2.66$, $p=0.12$, respectively. As shown in Fig. 2, activity in parietal cortex decreased across sessions but remained active across all sessions.

3.2.2. Session 3 analysis

There was significant activity in Session 3 in the right dorsal prefrontal, premotor, and parietal ROIs ($p<0.05$ in all cases). Activity in the left dorsal prefrontal ROIs, conversely, did not significantly differ from zero ($p>0.45$) by Session 3.

The significant Session 3 activity in the right dorsal prefrontal ROI and the lack of activity in the left dorsal prefrontal ROI suggests that these hemispheres are differ-

entially affected by practice. This difference was tested by comparing the mean difference between Session 1 and 3 activity across participants. This comparison showed that activity decreased from Session 1 to 3 more in the left than the right dorsal prefrontal ROI, $t(5)=2.12$, $p<0.05$. Statistical parametric maps showing the dissociation between sustained activity with practice in right dorsal prefrontal and transient activity in left dorsal prefrontal cortices are shown in Fig. 3.

3.2.3. Secondary correlation analyses

3.2.3.1. Inter-regional correlational analysis. As shown in the Table, both the left and the right dorsal prefrontal cortices correlated with the activity in the premotor and parietal ROIs in Sessions 1 and 3. This suggests that both left and right dorsal prefrontal cortices function as a network with posterior brain regions (e.g., premotor and parietal cortex) to mediate task performance. We conducted an additional analysis to assess the effect of practice on these frontal–parietal networks. For this analysis, we first combined the Fisher's- z scores for the premotor and parietal ROIs for each dorsal prefrontal ROI. Thus, each score represented the activity

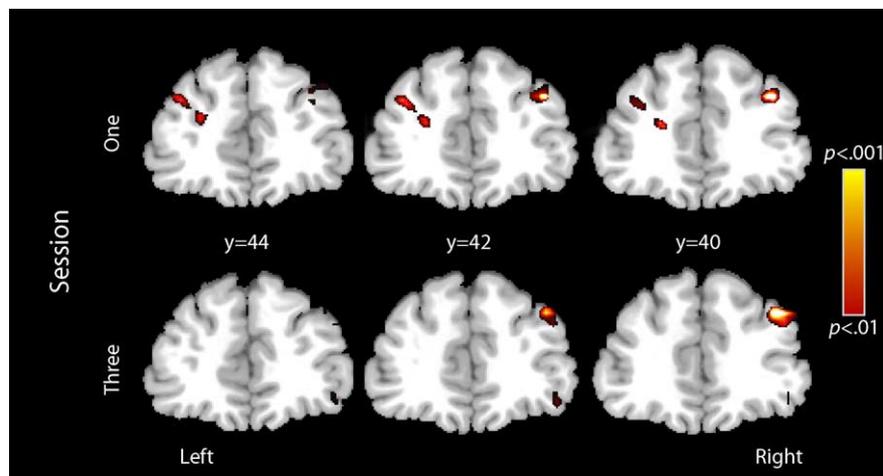


Fig. 3. Statistical parametric maps of activity in left and right dorsal prefrontal cortices in Sessions 1 and 3 overlaid on three spatially normalized coronal slices.

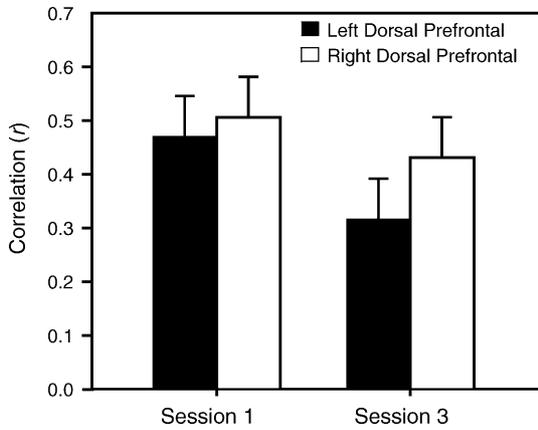


Fig. 4. Average correlation between the combined activity in the parietal and premotor regions-of-interest and the left and right dorsal prefrontal cortices for Sessions 1 and 3.

relationship between the left or right dorsal prefrontal cortex and the posterior brain ROIs. We then compared the decrease from Session 1 to 3 in these Fisher's-z scores for the left and right dorsal prefrontal ROIs. As shown in Fig. 4 and similar to the univariate activation patterns overall (Figs. 2 and 3), the correlation between mean activity in the combined posterior ROIs and the left dorsal prefrontal cortex decreased more from Session 1 to 3 than the correlation between the posterior ROIs and the right dorsal prefrontal cortex, $t(5) = 1.97$, $p = 0.05$.

3.2.3.2. *Brain-behavior relationship.* As shown in Fig. 5, there was a significant positive relationship between mean RT across Session 1 and activity in right ($r = 0.65$, $p < 0.05$), but not left ($r = 0.27$, $p > 0.05$), dorsal prefrontal cortex. In fact, this correlation was significantly greater in right dorsal prefrontal cortex than in left dorsal prefrontal cortex, $z = 1.93$, $p < 0.05$.

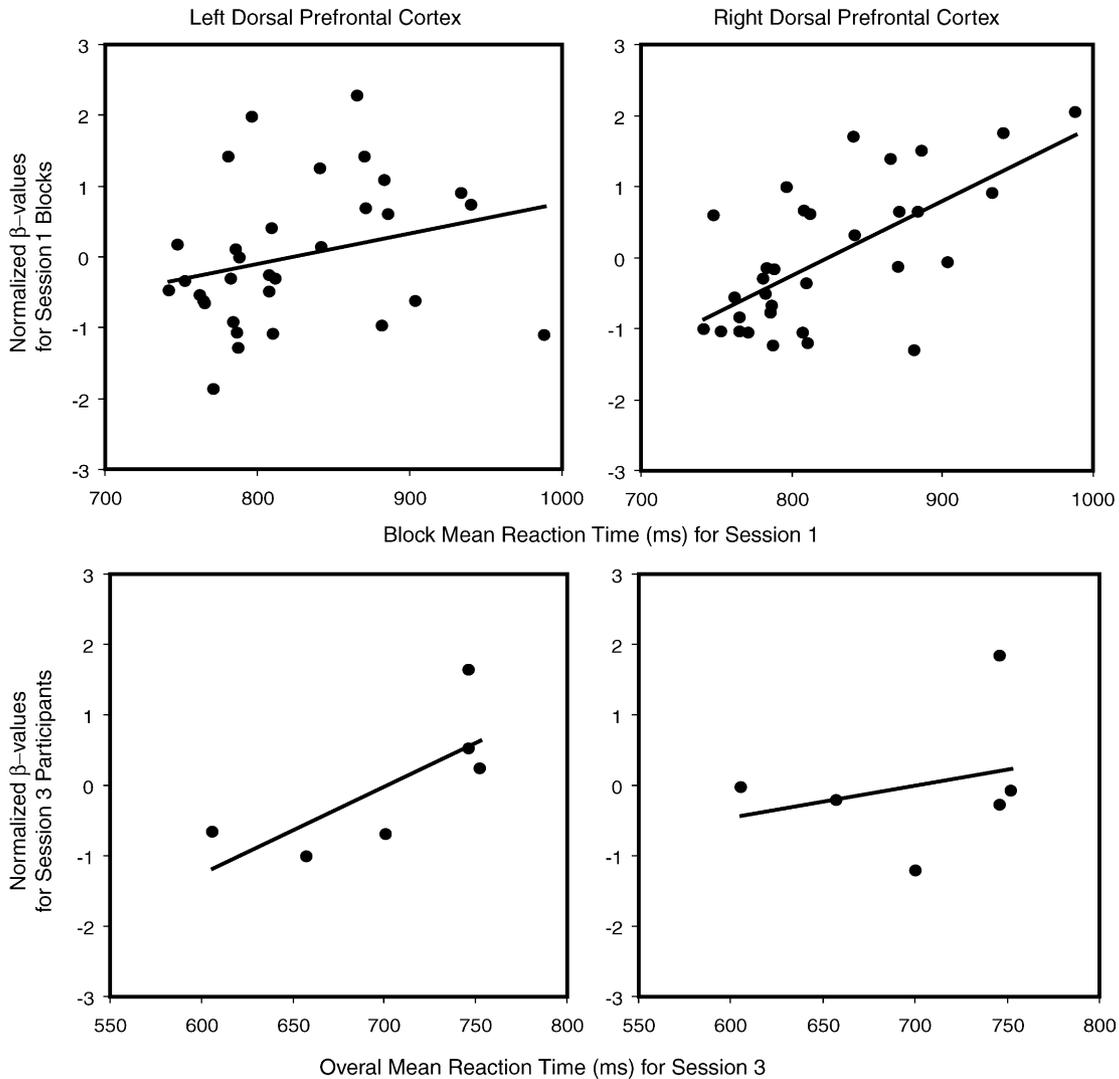


Fig. 5. Plots of the relationship between activity in left and right dorsal prefrontal cortices and mean block reaction time in Session 1 and mean overall reaction time in Session 3.

Conversely, for the correlation with overall performance in Session 3 there was a significant positive relationship between mean RT and activity in left ($r = 0.73$, $p < 0.05$), but not right ($r = 0.27$, $p > 0.30$) dorsal prefrontal cortex. This analysis yielded only one pair of numbers (mean RT and activation) for each ROI for each participant, and therefore suffers from relatively low power. Drawing conclusions from regression analyses based on only six data points is necessarily tentative. Nonetheless, the positive correlation in left dorsal prefrontal cortex was significantly greater than the correlation in right dorsal prefrontal cortex ($z = 4.84$, $p < 0.005$).

4. Discussion

Our current experiment investigates the effect of practice on the neural mechanisms underlying response selection and other cognitive processes during the performance of a choice–reaction task. As shown in Fig. 2, three patterns for the effect of practice on brain activity emerged in the ROIs investigated. Firstly, there was no effect of practice on activity in right dorsal prefrontal cortex. It was significantly active across all sessions. Secondly, there was a quantitative decrease with practice on activity in premotor and superior parietal cortices. Activity in these regions decreased with practice, but remained significantly above baseline across all three sessions. Thirdly, there was a qualitative decrease with practice on activity in left dorsal prefrontal cortex. Left dorsal prefrontal cortex was active only during Session 1 and produced no activity whatsoever by Session 3.

These results are consistent with previous studies showing activity in right dorsal prefrontal, premotor, and superior parietal cortices for manipulations of spatial response selection (Dassonville et al., 2001; Deiber et al., 1991; Iacoboni et al., 1996; Jiang & Kanwisher, 2003; Merriam et al., 2001; Schumacher & D’Esposito, 2002; Schumacher et al., 2003). Furthermore, our current data show that these regions mediate spatial response selection both during novel and well-practiced task performance. Our data additionally show that there is a quantitative decrease in activity with practice in premotor and parietal cortices. This decrease may reflect a habituation to the task stimuli and responses or it may reflect a practice related increase in the efficiency for the particular response selection subprocesses carried out by these regions.

We also found that the frontal–parietal network for spatial response selection remains involved in task performance even after substantial practice. This result is consistent with the multivariate results from a study of the learning of non-spatial visual-manual S-R rules (Toni, Rowe, Stephan, & Passingham, 2002). That study used structural equation modeling to show that the connectivity between frontal and parietal cortices did not change for the performance of novel and well-practiced non-spatial choice–reaction tasks.

A very different effect of practice emerged in left dorsal prefrontal cortex. It was active only during Session 1.

Consistent with our previous research, the hemispheric dissociation between the effects of practice on activity in dorsal prefrontal cortex suggests that these regions mediate distinct cognitive processes. Using parametric techniques, we previously showed that, although both hemispheres were active, only right dorsal prefrontal cortex mediated response selection for spatial material (Schumacher et al., 2003). Here we show an additional, practice-related, dissociation between the hemispheres for the performance of a spatial compatibility task.

The decrease in activity in left dorsal prefrontal cortex reflects a qualitative change in processing. The process mediated by left dorsal prefrontal cortex was involved in the performance of the spatial response selection task only during the early stages of learning. This pattern is different than the quantitative change found in premotor and parietal cortices because, although activity decreased with practice in each of these regions, both premotor and parietal cortices remained active even after substantial practice. Only left dorsal prefrontal cortex changed from active to non-active with practice. These data suggest that left dorsal prefrontal cortex may mediate control processes for learning the task, organizing performance in a novel task environment, or other control processes necessary for the successful performance of a novel task.

Our multivariate correlational analyses substantially augment the findings of the univariate brain activation data. Dorsal prefrontal activity in both hemispheres correlates with activity in both posterior ROIs. These correlations suggest that dorsal prefrontal, premotor, and parietal cortices work in concert to successfully perform the spatial compatibility task.

It is somewhat surprising that activity in left dorsal prefrontal cortex correlated with activity in premotor and parietal cortices in Session 3, where mean activity in left dorsal prefrontal cortex was no greater than baseline. However, frontal and parietal cortices show correlated activity even in participants at rest (Horwitz, 1991). Thus, it is the significant decrease in the correlation between premotor and parietal cortices and left, relative to right, dorsal prefrontal cortex (Fig. 4) that supports the claim that right, but not left, dorsal prefrontal cortex mediates spatial response selection even after practice.

The univariate and multivariate data presented thus far, and our previous study (Schumacher et al., 2003), suggest that left and right dorsal prefrontal cortex mediate different processes during the performance of choice–reaction tasks. This claim is supported by practice related hemispheric asymmetries in dorsal prefrontal cortex reported in other task domains (Fletcher, Buchel, Josephs, Friston, & Dolan, 1999; Seger et al., 2000), as well as by our brain-behavioral correlations (Fig. 5).

Pashler and Baylis (1991) suggest that the decrease in mean RT with practice in the performance of choice–reaction tasks is due primarily to a decrease in the duration of response selection. Although we found no decrease in average activity

in right dorsal prefrontal cortex in Session 1, we found a correlation between activity in this region and mean RTs across blocks, and no corresponding relationship in left dorsal prefrontal cortex.

On the other hand, overall mean RTs for Session 3, which may reflect the difficulty participants had learning the task, correlated with activity in left, but not right, dorsal prefrontal cortex. Thus, participants who had not successfully proceduralized the task may still have been relying on a processing strategy involving left dorsal prefrontal cortex in Session 3, whereas participants who had successfully learned the task no longer required this process for successful task performance.

Taken together, these results suggest that right dorsal prefrontal, premotor, and superior parietal cortices mediate the application of S-R rules across levels of practice, whereas left dorsal prefrontal cortex may mediate the learning and organization of the task or the task situation. The presence of these correlations (i.e., between block RTs in Session 1 and right dorsal prefrontal cortex and overall RTs in Session 3 and left dorsal prefrontal cortex) in the absence of any measurable activity differences underscore the usefulness of these techniques for understanding the neural mechanisms underlying cognitive processing.

Many theories of prefrontal function implicate this region in cognitive control (Baddeley, 1986; Miller & Cohen, 2001; Norman & Shallice, 1986; Schneider & Chein, 2003). According to these theories, prefrontal cortex acts as part of the central executive system, supervisory attentional system, or other control mechanisms to organize one's processing to successfully perform goal-directed behavior. Although these theories differ in their specifics, common to them is the view that prefrontal cortex modulates processing carried out in other brain regions when control is necessary (e.g., under situations in which the correct response is unclear). Accordingly, more control should be required when a task is novel and the correct S-R associations are new, than when it is well learned. Therefore, prefrontal cortex should mediate task performance more for novel than well-practiced tasks.

Our finding that left dorsal prefrontal cortex is active only in Session 1 (Figs. 2 and 3) provides some support for this view. The sustained activity in right dorsal prefrontal cortex, on the other hand, may suggest that these theories are imprecise. The nature of the neural effect of practice depends on the nature of the cognitive process mediated by the region in question.

During the performance of this task, some processes show a functional reorganization with practice (e.g., processes mediated by left dorsal prefrontal cortex); whereas other processes (e.g., response selection, mediated by right dorsal prefrontal, premotor, and parietal cortices) show little or no change with practice.

The sustained activity in this frontal-parietal network suggests that it mediates response selection both when response selection requires controlled processing and declarative knowledge and after processing becomes more automatic

and proceduralized. It is especially interesting that right dorsal prefrontal cortex shows almost no change in activity with practice, given that prominent theories of frontal lobe function hypothesize that prefrontal cortex should be most sensitive to practice related processing changes (Baddeley, 1986; Miller & Cohen, 2001; Norman & Shallice, 1986).

Unfortunately, the dorsal prefrontal pattern of activity in Session 1 is only partially consistent with the literature. Deiber et al. (1997) reported that activity in right dorsal prefrontal cortex decreased across one session of practice with a spatial perceptual-motor task. On the other hand, Iacoboni et al. (1996) found increases in activity in left dorsal prefrontal cortex across one session of practice with a similar task. We did not replicate either of these findings, although the brain-behavior correlation in Session 1 suggests that there was a small decrease in activity in right dorsal prefrontal cortex and no change in the left hemisphere.

Perhaps particular aspects of the tasks and procedures used in these experiments contributed to the activation differences. Although it is unclear why these three relatively similar studies produced somewhat discrepant results, it is clear that left and right dorsal prefrontal cortices behave differently under practice with a spatial compatibility task, supporting the claim that these regions mediate distinct cognitive processes.

Our participants achieved a high level of performance on a relatively easy perceptual-motor task that did not require working memory in the strictest sense (D'Esposito, Ballard, Aguirre, & Zarahn, 1998). That is, they did not have to maintain or manipulate information across a temporal delay. Yet we show distinct patterns of task-related activity in prefrontal cortex. These data not only identify the distinct processes carried out by left and right dorsal prefrontal cortices; they also support the hypothesis that dorsal prefrontal cortex mediates processes not related to working memory maintenance (Curtis & D'Esposito, 2003).

Our data not only suggest that theories of frontal lobe function are imprecise but so may be computational theories of practice more generally. We show that practice produces both qualitative and quantitative processing changes, and that the prefrontal cortex is involved in both controlled and automatic processing. For example, left dorsal prefrontal cortex may mediate processes related to the acquisition of the rules for general task performance. These processes show a qualitative change with practice. That is, they are only involved during novel task performance. On the other hand, right dorsal prefrontal, bilateral premotor, and superior parietal cortices mediate spatial response selection, which shows a quantitative change with practice. That is, response selection (and the regions mediating it) is involved in successful task performance both during the declarative and procedural stages of task performance. These brain data support the hypothesis that practice affects specific cognitive processes differently (Pashler & Baylis, 1991) and highlight the utility of using functional neuroimaging data to inform conceptual models of human cognition.

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