Abstract

Behavioral studies have shown that consistent practice of a cognitive task can increase the speed of performance and reduce variability of responses and error rate, reflecting a shift from controlled to automatic processing. This study examines how the shift from controlled to automatic processing changes brain activity. A verbal Sternberg task was used with continuously changing targets (novel task, NT) and with constant, practiced targets (practiced task, PT). NT and PT were presented in a blocked design and contrasted to a choice reaction time (RT) control task (CT) to isolate working memory (WM)-related activity. The three-dimensional (3-D) PRESTO functional magnetic resonance imaging (fMRI) sequence was used to measure hemodynamic responses. Behavioral data revealed that task processing became automated after practice, as responses were faster, less variable, and more accurate. This was accompanied specifically by a decrease in activation in regions related to WM (bilateral but predominantly left dorsolateral prefrontal cortex (DLPFC), right superior frontal cortex (SFC), and right frontopolar area) and the supplementary motor area. Results showed no evidence for a shift of foci of activity within or across regions of the brain. The findings have theoretical implications for understanding the functional anatomical substrates of automatic and controlled processing, indicating that these types of information processing have the same functional anatomical substrate, but differ in efficiency. In addition, there are practical implications for interpreting activity as a measure for task performance, such as in patient studies. Whereas reduced activity can reflect poor performance if a task is not sensitive to practice effects, it can reflect good performance if a task is sensitive to practice effects.

INTRODUCTION

People are capable of performing complex cognitive tasks where new information has to be manipulated and stored briefly in order to generate adequate responses. It has been shown that the storage and processing capacity of this system is limited (Miller, 1956). However, practice can improve task performance by making it faster, more accurate, less variable, and decrease effort to perform the task (Posner & Snyder, 1975). The different behavioral profiles of novel and practiced task processing have led Schneider and Shiffrin (1977) to introduce a dual-process theory of information processing. In this theory, a qualitative difference is made between two modes of processing. Novel performance requires controlled processing, which is typically easily established and modified but limited in capacity. After practice automatic processing may take over, which is typically faster and more invariant than controlled processing, less sensitive to capacity limits, but more difficult to alter or inhibit. As demonstrated in their study, an important prerequisite for automatic processing to occur is a consistent relation between a stimulus and a response. If stimulus–response relations are constantly changed, automatic processing cannot be established and there is little performance improvement, even after extensive periods of practice. Based on behavioral studies, in particular with using dual-task paradigms, various investigators have hypothesized that a shift from controlled to automatic processing relieves the capacity-limited working memory (WM) system (Carlson, Sullivan, & Schneider, 1989; Schneider & Fisk, 1982a, 1982b). The ability to automate task processing may therefore be essential for complex task execution, as it enables reallocation of limited attentional and processing resources. Furthermore, it enables learning of increasingly complex modes of processing by building upon acquired sequences (Logan, 1985).

Although behavioral studies convincingly demonstrate two modes of information processing, the functional anatomical correlates that underlie automatic and controlled processing are still debated. Some theories state that the shift from controlled to automatic processing involves a restructuring of the underlying processes. Restructuring theories argue that automation involves organizational changes, that is,
that different subsystems are involved in automatic and controlled task processing (e.g., Logan, 1988; Cheng, 1985). Logan, for instance, hypothesizes that automation reflects a transition from algorithm-based to memory-based task processing. Initially, computational processes mediate task processing, but since with each stimulus encounter a memory trace is formed, performance becomes increasingly dependent on memory retrieval processes with practice. Other theories state that a shift from controlled to automatic processing involves changes in the processes that were already initially involved in task processing. These “process-based” theories state that a task performance integrates various subsystems into a circuit. Practice enhances the efficiency of communication between the subsystems. As a consequence, some processes may become obsolete. Strengthened connections may, for instance, decrease the need for controlled attentional interference (LaBerge & Samuels, 1974).

Recently, the functional anatomical changes related to cognitive practice have been examined by using brain imaging methods such as positron emission tomography (PET) and functional magnetic resonance imaging (fMRI). Several studies have indicated that learning a new skill such as visuomotor sequences (Hikosaka, Miyashita, Miyachi, Sakai, & Lu, 1998), mirror reading (Poldrack, Desmond, Glover, & Gabrieli, 1998), and reversed reciting of the months of the year (Wildgruber, Kischka, Ackermann, Klose, & Grodd, 1999) involves a functional anatomical shift of activation. Practice of cognitive tasks such as word generation (associating a verb with a given noun) (Petersen, van Mier, Fiez, & Raichle, 1998; Raichle et al., 1994), recall of simple abstract line drawings (Petersson, Ellgren, & Ingvar, 1999a, 1999b), and recall of faces (Wiser et al., 2000) also demonstrated a spatial shift in brain activity, indicating a restructuring of involved processes. The relevance of these studies for controlled and automatic processing, and the role of WM therein, is not clear because none of the used tasks were designed to address WM selectively. As a result, restructuring may be attributed to changes in task characteristics after practice, rather than to automation. Two recent studies on effects of cognitive practice that used a visuospatial WM task showed evidence for process-based practice effects but not for restructuring (Garavan, Kelley, Rosen, Rao, & Stein, 2000; Buchel, Coull, & Friston, 1999). Garavan et al. (2000) used a task where the location of three briefly presented dots has to be matched to a subsequently presented circle. Practice on this task predominantly reduced activity in frontal, parietal, and cingulate regions, indicating process-based changes, although increased activity after practice was also found in the posterior cingulate. Buchel et al. (1999) specifically addressed the question of the effects of practice on connectivity between brain systems using an object-location task. Results showed reduced activity but increased connectivity between posterior and temporal regions after practice.

Although these studies convincingly showed that practice reduces activity in WM-related regions, the effects cannot specifically be attributed to a shift from controlled to automatic processing, as the visuospatial tasks used in these studies did not contrast consistent versus varied stimulus–response relations. Consequently, the reported changes in brain activity may also reflect other practice-related effects—for instance, learning of skills involved in the visuospatial task. Since the concepts of controlled and automatic processing form the basis of many cognitive theories and hypotheses of information processing, the underlying functional substrates of controlled and automatic processing deserve specific attention from the neuroimaging field.

In the present study, a Sternberg task was used to examine the functional anatomical changes that are correlated with a shift from controlled to automatic processing (Sternberg, 1966). In addition, the present study tests the hypothesis that consistent practice of a cognitive task relieves WM, which is until now primarily based on behavioral evidence. Performance and brain activity are compared between a practiced task (PT) with a constant stimulus–response relationship and a novel task (NT) in which the stimulus–response relationship is continuously changed by using novel target sets. As this study focuses on practice-related effects in WM, activity in the Sternberg task is contrasted with a choice reaction time (RT) task, which does not require memorization of stimuli. The three-dimensional (3-D) PRESTO fMRI (Gelder et al., 1995) technique is used to visualize brain activity related to the execution of the cognitive tasks.

RESULTS

Behavioral Data

All subjects practiced the Sternberg task with one constant target set and nontarget set before the fMRI session. Figure 1 illustrates the decrease of RT during the practice session outside the scanner (see Materials and Method section for a detailed description of the used tasks). The average RT over the first 10 trials in the practice session is 719 msec. The RT over the last 10 trials in the practice session is 557 msec.

Performance data collected during the scan session are illustrated in Figure 2. The RT on the PT was decreased compared to the NT, in which the target set changed every 10 trials, \( t = 11.2, df = 14, p < .001 \). The standard deviation of the responses in the PT was also reduced compared to the NT, \( t = 6.9, df = 14, p < .001 \), indicating a more stereotyped response profile. Performance on the PT was more accurate than on the NT, as the percentage incorrect responses was reduced compared to the NT, \( t = 2.5, df = 14, p < .05 \).
There was no difference in the percentage misses made in the NT and the PT.

RT on the PT was not as short as on the choice RT control task (CT, responding to an arrow pointing left or right in the PT, \( t = 8.5, p < .001 \)). There was no difference between the PT and the CT on standard deviation of correct responses, incorrect responses, and misses.

**fMRI Data**

Table 1 gives an overview of regions activated in the NT, the PT and the CT. Task activity was contrasted with a resting state (RS). The descriptive names are no more than approximations of the anatomical locations of the activated area, as the activation maps are based on group averages, and hence cannot be mapped reliably onto specific gyri or sulci (Mandl, Jansma, Slagter, Collins, & Ramsey, 2000). Table 2 gives the Talairach coordinates of the voxel within each activated region that contains the highest \( t \) value. These coordinates show that the locations of peak activity vary little across tasks, indicating a consistent pattern of activation across tasks (see also Figure 3).

**Description of Activity Patterns for Examined Contrasts**

Novel task. The NT (NT–RS contrast, see Materials and Method section for details) induced an extensive pattern of activity in the frontal cortex, mostly left-lateralized at the junction of the middle frontal sulcus and precentral sulcus (denoted as dorsolateral prefrontal cortex or DLPFC), in the middle frontal and superior gyrus (denoted as superior frontal cortex or SFC), bilaterally in the operculum, and in an area partly covering the anterior cingulate cortex and the supplementary motor area (ACC/SMA). Parietal activation was found in the region of the intraparietal sulcus bilaterally (denoted as superior parietal cortex or SPC). Furthermore, activity was detected in the left primary sensorimotor cortex (PSMC), left premotor cortex (PrMC), bilaterally in the visual cortex (VC), and in a region covering the precuneus (see Table 1).

Practiced task. The PT (PT–RS contrast) elicited left-lateralized activity in DLPFC, the ACC/SMA, the operculum (bilaterally), and the SPC (right lateralized). Furthermore, the left PSMC, left PrMC, and VC (bilateral) were activated. Additional activation in the PT compared to the NT was found in the left medial PrMC and in the right PSMC (see Table 1).

Control task. The CT (CT–RS contrast) elicited left-lateralized activity in the DLPFC and the operculum. The CT also activated left PSMC, left PrMC, and VC (bilateral).

**Figure 1.** Behavioral data: RT during the practice session averaged over all subjects. Each point reflects the average RT over 10 consecutive trials.

**Figure 2.** Behavioral data. (a) Mean RT (±SEM) of correct responses (on targets and nontargets) averaged over all subjects. (b) Mean standard deviation (±SEM) of correct responses (on targets and nontargets) averaged over all subjects. (c) Misses and incorrect responses as percent of all 80 trials (±SEM) averaged over all subjects. ***p < .001; *p < .05.
erally). Additional activation in the CT compared to the NT was found in the right PSMC (see Table 1).

### Novel task versus control task

Regions specifically involved in WM were selected by contrasting the NT activity map with the CT activity map (NT–CT contrast). Regions of increased activity in this contrast are denoted as WM-specific regions. This analysis yielded seven regions: the left and right DLPFC, the right frontalopolar area, the SMA, the right SPC, and regions covering the cuneus and the precuneus. Details are shown in Table 3.

### Effects of Practice in WM-Specific Regions

To test the hypothesis that practice reduces the load on WM, the WM-specific regions that were identified in the NT–CT contrast were further analyzed. The selected regions showed a significant overall effect of practice, $F(1,14) = 12.02, p = .004$, and no significant interaction effect of practice and region-of-interest, $F(6,9) = 1.07, p = .45$. Follow-up analysis of the 7 regions revealed a significant effect of practice in the left DLPFC, $t = 2.40; df = 14, p = .02$, right DLPFC, $t = 3.19, df = 14, p = .004$, right frontopolar area, $t = 2.87, df = 14, p = .006$, the SMA, $t = 2.07, df = 14, p = .03$, and the right SPC, $t = 2.32, df = 14, p = .02$ (see Figure 4). The other two clusters that were identified in the NT–CT contrast, regions covering the cuneus and precuneus, did not show an effect of practice (see Figure 4).

### Effects of Practice in Other Contrasts

Additional effects of practice may show in regions that are not WM-specific, or in regions that are not fully overlapping with WM-specific regions. Therefore, selected active regions in the NT were separately analyzed for effects of practice. Fourteen regions of activity were identified in the NT (described in Table 2). Multivariate

---

Table 1. Results for the Group-Averaged Activity Patterns

<table>
<thead>
<tr>
<th>Region</th>
<th>BA</th>
<th>NT</th>
<th>PT</th>
<th>CT</th>
<th>NT</th>
<th>PT</th>
<th>CT</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Frontal cortex</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Left DLPFC</td>
<td>6/8</td>
<td>51</td>
<td>13</td>
<td>11</td>
<td>7.20</td>
<td>5.69</td>
<td>5.10</td>
</tr>
<tr>
<td>Right DLPFC</td>
<td>6/8</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>4.00</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Left SFC</td>
<td>6</td>
<td>8</td>
<td>8</td>
<td>8</td>
<td>6.57</td>
<td>5.34</td>
<td>7.02</td>
</tr>
<tr>
<td>Right SFC</td>
<td>6</td>
<td>40</td>
<td>38</td>
<td>37</td>
<td>5.69</td>
<td>5.62</td>
<td>6.54</td>
</tr>
<tr>
<td>ACC/SMA</td>
<td>24/6</td>
<td>357</td>
<td>341</td>
<td>244</td>
<td>12.38</td>
<td>12.87</td>
<td>11.75</td>
</tr>
<tr>
<td>Left operculum</td>
<td>44</td>
<td>31</td>
<td>14</td>
<td>15</td>
<td>5.84</td>
<td>5.86</td>
<td>5.21</td>
</tr>
<tr>
<td>Right operculum</td>
<td>44</td>
<td>36</td>
<td>4</td>
<td>0</td>
<td>4.71</td>
<td>4.21</td>
<td>–</td>
</tr>
<tr>
<td><strong>Parietal cortex</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Left SPC</td>
<td>7</td>
<td>6</td>
<td>0</td>
<td>7</td>
<td>4.30</td>
<td>–</td>
<td>4.92</td>
</tr>
<tr>
<td>Right SPC</td>
<td>7</td>
<td>74</td>
<td>14</td>
<td>0</td>
<td>5.49</td>
<td>4.12</td>
<td>–</td>
</tr>
<tr>
<td>Precuneus</td>
<td>7</td>
<td>9</td>
<td>0</td>
<td>0</td>
<td>4.24</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td><strong>Visual cortex</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Left</td>
<td>18</td>
<td>45</td>
<td>52</td>
<td>33</td>
<td>10.68</td>
<td>11.87</td>
<td>10.78</td>
</tr>
<tr>
<td>Right</td>
<td>18</td>
<td>195</td>
<td>200</td>
<td>136</td>
<td>15.43</td>
<td>16.5</td>
<td>15.9</td>
</tr>
<tr>
<td><strong>Motor cortex</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Left PSMC</td>
<td>1–5</td>
<td>446</td>
<td>451</td>
<td>518</td>
<td>9.44</td>
<td>10.2</td>
<td>10.6</td>
</tr>
<tr>
<td>Right PSMC</td>
<td>1–5</td>
<td>0</td>
<td>2</td>
<td>19</td>
<td>–</td>
<td>4.6</td>
<td>5.37</td>
</tr>
<tr>
<td>Left PrMC</td>
<td>6</td>
<td>5</td>
<td>7</td>
<td>29</td>
<td>4.01</td>
<td>4.43</td>
<td>5.21</td>
</tr>
</tbody>
</table>

This shows the number of active voxels ($t > 3.88$), followed by the peak $t$ value within each volume of interest. BA = Brodmann’s area; NT = novel task; PT = practiced task; CT = control task, see text for abbreviations of regions of interest.
testing showed no overall effect of practice, $F(1,14) = 2.38, p = .15$, and no interaction effect of practice and region-of-interest, $F(13,2) = 2.22, p = .66$. Post hoc analysis of the selected regions revealed a significant signal decrease in the right DLPFC, $t = 2.11, df = 13, p = .03$, the left DLPFC, $t = 1.87, df = 13, p = .04$, the right operculum, $t = 2.09, df = 13, p = .03$, and the right SPC, $t = 1.81, df = 13, p = .05$, uncorrected for multiple comparisons. None of the regions passed the test for significance after correction for multiple comparisons (Bonferroni, 14 comparisons) (Figure 5).

To examine whether practice also induced increased activity, regions of activity in the PT (PT–RS contrast) were further examined. In this contrast, 12 regions of activity were identified, which are described in Table 2. Multivariate testing showed no overall effect of practice, $F(1,14) = 0.01, p = .93$, and no significant interaction effect of practice with region-of-interest, $F(11,4) = 0.86, p = .62$. Post hoc analysis revealed a significant signal increase after practice only in the right PSMC ($t = 3.49, df = 14, p = .002$, significant after Bonferroni correction for 12 comparisons) (Figure 6).

DISCUSSION

The current study examined the functional anatomical correlates associated with practice-related changes in task performance. Brain activity evoked by a Sternberg task with a continuously changed stimulus–response relation was compared to activity evoked by a practiced Sternberg task with a consistent stimulus–response relation. We postulated that consistent practice of a Sternberg task is associated with a reduction of brain activity specifically related to WM, as a consequence of

Table 2. Results for the Group-Averaged Activity Patterns

<table>
<thead>
<tr>
<th>Region</th>
<th>BA</th>
<th>NT</th>
<th>PT</th>
<th>CT</th>
</tr>
</thead>
<tbody>
<tr>
<td>Frontal cortex</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Left DLPFC</td>
<td>6/8</td>
<td>-59</td>
<td>-7</td>
<td>-59</td>
</tr>
<tr>
<td>Right DLPFC</td>
<td>6/8</td>
<td>52</td>
<td>24</td>
<td>28</td>
</tr>
<tr>
<td>Left SPC</td>
<td>6</td>
<td>-10</td>
<td>0</td>
<td>73</td>
</tr>
<tr>
<td>Right SPC</td>
<td>6</td>
<td>14</td>
<td>0</td>
<td>73</td>
</tr>
<tr>
<td>ACC/SMA</td>
<td>24/6</td>
<td>-3</td>
<td>3</td>
<td>56</td>
</tr>
<tr>
<td>Left operculum</td>
<td>44</td>
<td>-59</td>
<td>10</td>
<td>0</td>
</tr>
<tr>
<td>Right operculum</td>
<td>44</td>
<td>42</td>
<td>17</td>
<td>0</td>
</tr>
<tr>
<td>Parietal cortex</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Left</td>
<td>7</td>
<td>-21</td>
<td>-70</td>
<td>59</td>
</tr>
<tr>
<td>Right</td>
<td>7</td>
<td>35</td>
<td>-59</td>
<td>56</td>
</tr>
<tr>
<td>Precuneus</td>
<td>7</td>
<td>3</td>
<td>-66</td>
<td>49</td>
</tr>
<tr>
<td>Visual cortex</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Left</td>
<td>18</td>
<td>-24</td>
<td>-98</td>
<td>-3</td>
</tr>
<tr>
<td>Right</td>
<td>18</td>
<td>24</td>
<td>-98</td>
<td>-3</td>
</tr>
<tr>
<td>Motor cortex</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Left PSMC</td>
<td>1–5</td>
<td>-56</td>
<td>-24</td>
<td>56</td>
</tr>
<tr>
<td>Right PSMC</td>
<td>1–5</td>
<td>49</td>
<td>-28</td>
<td>59</td>
</tr>
<tr>
<td>Left PrMC</td>
<td>6</td>
<td>-31</td>
<td>-3</td>
<td>59</td>
</tr>
</tbody>
</table>

This shows the MRI–Talairach coordinates of the voxel within each volume of interest with maximum $t$ value for each task. BA = Brodmann’s area; NT = novel task; PT = practiced task; CT = control task, see text for abbreviations of regions of interest.
Table 3. Activation Results for the Novel Task Versus Control Task (NT–CT) Contrast: Number of Active Voxels ($t > 3.88$), Peak $t$ Value, and Location of the Voxel With the Peak $t$ Value in MNI–Talairach Coordinates

<table>
<thead>
<tr>
<th>Region</th>
<th>BA</th>
<th>Number of Voxels</th>
<th>Peak $t$ Value</th>
<th>$x$</th>
<th>$y$</th>
<th>$z$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Frontal cortex</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Left DLPFC</td>
<td>BA 9</td>
<td>25</td>
<td>5.04</td>
<td>−56</td>
<td>21</td>
<td>31</td>
</tr>
<tr>
<td>Right DLPFC</td>
<td>BA 9</td>
<td>4</td>
<td>4.08</td>
<td>35</td>
<td>14</td>
<td>28</td>
</tr>
<tr>
<td>Right frontopolar area</td>
<td>BA 10</td>
<td>13</td>
<td>5.35</td>
<td>38</td>
<td>59</td>
<td>10</td>
</tr>
<tr>
<td>SMA</td>
<td>BA 6</td>
<td>42</td>
<td>5.16</td>
<td>−3</td>
<td>17</td>
<td>52</td>
</tr>
<tr>
<td>Parietal cortex</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Right SPC</td>
<td>BA 7</td>
<td>45</td>
<td>5.34</td>
<td>35</td>
<td>−63</td>
<td>52</td>
</tr>
<tr>
<td>Precuneus</td>
<td>BA 7</td>
<td>2</td>
<td>3.93</td>
<td>0</td>
<td>−70</td>
<td>45</td>
</tr>
<tr>
<td>Visual cortex</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cuneus</td>
<td>BA 18</td>
<td>19</td>
<td>4.78</td>
<td>10</td>
<td>−87</td>
<td>7</td>
</tr>
</tbody>
</table>

BA = Brodmann’s area.
a shift from controlled to automatic processing. The results obtained with this study support the hypothesis that automation of cognitive processes, namely, the shift from controlled to automatic processing, is associated with a reduced demand on the WM system.

Important behavioral indications for automatic task processing are increased speed of processing, decreased variance in responses, and a more accurate performance (Jonides, Neveh-Benjamin, & Palmer, 1985). The paradigm successfully established these three behavioral changes in performance, as responses became faster, more stereotyped, and more accurate after practice.

Functional anatomical correlates of practice were examined in a set of WM-specific brain regions, a set of brain regions associated with NT activity, and a set of regions associated with PT activity. Reduced activation after practice was exclusively found in the set of WM-specific regions, indicating that automation of task processing specifically leads to a reduced claim on the capacity-limited WM system. In particular, automatic processing was associated with reduced activity in DLPFC (bilateral but predominantly left), right SPC, and SMA. These results indicate that automatic and controlled processing, although behaviorally distinct modes, have a similar functional anatomical representation but differ in efficiency of information processing in WM.

The present results do not support the notion that a shift from controlled to automatic processing is accompanied by restructuring of task processes. Practice was not related to additional activity except for the right PSMC. As the right PSMC is not involved in cognitive processing, nor in response execution, this signal increase is regarded as secondary to changes in performance. Furthermore, we found no indication that practice was related to a shift of foci of activity.

**Figure 4.** Group-averaged activity pattern projected onto an averaged anatomical background of all subjects for the NT–CT contrast. The active areas are in white (t > 3.88). Graphs present the change in activity from NT to PT, with activity in CT added as a reference (± SEM). Signals are averaged over voxels selected with the NT–CT contrast. The left and right DLPFC, right PC, and right frontopolar area show a decrease after practice. NT = novel task; PT = practiced task; CT = control task; z = location of transaxial slice in MNI–Talairach coordinates, see text for abbreviations of regions of interest. **p < .01; *p < .05.
within or across regions of the brain (see Table 1 and Figure 3). The imaging results therefore seem to be more in line with a process-based theory of automatic processing.

No indication was found that practice differentially affects brain regions involved in WM. All frontal and parietal WM-specific regions showed reduced activity after practice (see Figure 4), with the exception of the cuneus and the precuneus, which are generally not viewed as critical for WM. The region covering the cuneus appears to be deactivated in the CT and not active in the NT and PT.

An important question that follows from the findings pertains to the possible mechanisms by which practice induces a shift from controlled to automatic processing. NT execution relies on two basic WM processes: maintenance of information (the target set) and comparison of a displayed stimulus with each item of the target set in order to generate an adequate response. Consequently, a reduced claim on the WM system can be a consequence of changes in either one of these processes.

On the one hand, practice can change the efficiency of verbal short-term storage. Typically, human memory can

**Figure 5.** Graph presenting the change in activity from NT to PT averaged over voxels selected with the NT–RS contrast. Activity in CT is added as a reference (± SEM). The left and right DLPFC, right PC, and right operculum show a decrease after practice, uncorrected for multiple comparisons. NT = novel task; PT = practiced task; CT = control task; see text for abbreviations of regions of interest. *p < .05.

**Figure 6.** Graph presenting the change in activity from NT to PT averaged over voxels selected with the PT–RS contrast. Activity in CT is added as a reference (± SEM). The right PSMC shows an increase after practice, corrected for multiple comparisons. NT = novel task; PT = practiced task; CT = control task; see text for abbreviations of regions of interest. **p < .01.
retain only approximately 7 unrelated items (letters, digits, etc.) (Miller, 1956). A novel group of items, such as the five random consonants in the varied target set, expectedly uses a large part of this capacity, as they are not associated with one another in a unique way. However, after practice, the unrelated items can form a new association and consequently decrease the load on short-term storage, just as one can maintain one known word in WM without having to keep all the characters on-line. On the other hand, practice can change the efficiency of the comparison process. The effect of consistent practice on the comparison process may be more complex and is still debated. Behavioral studies have shown that in a novel Sternberg task the RT is linearly related to the number of items in the target set (Sternberg, 1969, 1975). This linear function is explained by assuming that targets are serially compared with a stimulus. A decrease in RT after practice could imply that the comparisons are no longer serially executed, or that speed of comparing is increased. A common assumption is that practice gradually eliminates the need for multiple comparisons, as task processing becomes more reliant on direct stimulus–response associations (Shiffrin & Schneider, 1977). In the NT, it is not possible to develop a consistent link between a stimulus and membership of the target set, so for a correct response, the stimulus has to be compared to each item of the target set. In the PT, the items that belong to the target set can acquire a new feature or meaning, namely, that of being a target. This newly acquired feature can be used to test the status of a stimulus (“is stimulus a target or non-target”) more efficiently than by using serial comparison. The WM load associated with the comparison process is consequently reduced. Furthermore, a consistent stimulus–response relation may also increase efficiency of communication between different brain regions involved in information processing. For instance, a consistent stimulus–response relation may decrease the need for rechecking the status of a stimulus, before responding.

Based on the results of this study, it is not possible to distinguish storage-related and comparison-related practice effects in prefrontal and parietal regions, since this study was primarily designed to examine the functional anatomical correlates of automatic processing. Previous studies have shown that DLPFC is involved in maintenance (Barch et al., 1997; Braver et al., 1997) and manipulation of information (d’Esposito, Postle, Ballard, & Lease, 1999). Decrease of prefrontal activation may therefore reflect both changes in the stimulus comparison and short-term storage process. In an event-related fMRI experiment, Rypma and d’Esposito (2000) report load-dependent effects in dorsal prefrontal cortex only during the encoding phase of a Sternberg task and not during the delay or response execution phase. The decrease of activity in DLPFC found in the current study cannot be assigned to differences in encoding processes, as the scans made during the encoding phase were not used. Parietal cortices have been shown to be involved in short-term storage and retrieval of verbally coded material (Henson, Burgess, & Frith, 2000; Jonides et al., 1998). Reduced activity in the right parietal cortex likely reflects a decreased need for reactivating the target set after a period of practice.

Our study, together with the studies of Garavan et al. (2000) and Buchel et al. (1999) support the hypothesis that the practice of a WM task is predominantly associated with decreased brain activity. In contrast to this finding, several imaging studies on correlates of cognitive practice report involvement of new regions after practice, indicating restructuring of activation after practice (Petersson et al., 1999a, 1999b; Petersen et al., 1998; Raichle et al., 1994). A possible explanation for this apparent discrepancy can be found in differences in the response requirements that are imposed by the NT and the PT. In the studies of Petersson et al. (1999a, 1999b), Petersen et al. (1998), and Raichle et al. (1994), a response has to be selected on the basis of an unconstrained number of alternatives. In NT, this requires controlled processing in the form of a search strategy. In the practiced version, the response selection process is different in that it can be guided by earlier responses. In the present study, as in the study by Garavan et al. (2000) and Buchel et al. (1999), practice does not limit or otherwise affect the response alternatives. Performance improvement and changes in brain activity are not likely to be secondary to differences in response selection strategies between NT and PT processing, as may be the case in the studies indicating a restructuring. Furthermore, as a Sternberg task explicitly targets the short-term storage capacity of WM, it is very sensitive to changes in the efficiency of short-term storage. In the above mentioned studies of Raichle et al. (1994), as in the studies by Wiser at el. (2000), Wildgruber et al. (1999), and Poldrack et al. (1998), the short-term storage capacity of WM is not explicitly involved in task execution.

A general problem in studying practice effects during scan sessions is that many time-related factors that may affect fMRI data are not controlled for, such as differences in mental and physiological state and MRI machine-related instabilities (Petersson et al., 1999a, 1999b). A second problem in the interpretation of functional anatomical correlates of practice is the simultaneous occurrence of general task-related practice effects and cognitive automation. The study by Garavan et al. (2000) shows that brain activity is also correlated to general task-related practice effects, which may, for instance, reflect skill learning. If a task is still sensitive to skill learning, this may confound specific effects of cognitive automation. A third problem associated with practice studies is interference of practiced performance with novel performance. This may occur if stimuli used in a novel task and a practiced task are similar or
associated. For instance, practicing a skill like backward counting involves the same stimuli as forward counting. Practice-related effects reflecting inhibition of the automated process of forward counting may confound effects of practice of backward counting.

None of the mentioned problems can be expected to play a role in the current study. In the present design the contribution of machine-related effects is kept to a minimum, as the NT and PT are alternated within the same scan session. In addition, this alternation precludes differential nonspecific effects of fatigue and potential loss of motivation. Secondly, the Sternberg task depends on basic skills, which can be assumed to be present and overlearned in all healthy subjects. Furthermore, a Sternberg task allows for use of a limited number of mutually exclusive stimuli for NT and PT execution, to prevent any form of interference between NT and PT processing.

The current findings are relevant for interpreting WM activity as a measure for task performance. The study shows that when a task is sensitive to practice, a decrease in activity can reflect good performance. This should be taken into account, particularly in studies where WM activity in healthy controls is compared to patients showing a WM deficit, as is the case in schizophrenia. In these patients, poor performance has been associated with increased frontal activity in schizophrenic patients (Stevens, Goldman-Rakic, Gore, Fulbright, & Wexler, 1998; Weinberger et al., 1996; Goldman Rakic, 1994). Other studies, however, failed to find a difference (Manoach et al., 1999) or found enhanced frontal activity (Curtis et al., 1998). The current finding sheds new light on this controversy. As cognitive functioning is generally based on a complex balance between automated and controlled processes, failure to coordinate these may explain some of the cognitive deficits, such as difficulty in executing complex or dual tasks, attentional deficits, and perseverance of ineffective (automated) strategies. A reduced cognitive automation capability in patients with schizophrenia may, for instance, cause increased WM activity compared to controls, if controls are in the phase of establishing automaticity while patients still are in the phase of controlled task processing. Reduced frontal activity may reflect a failure to execute a more complex task, as a consequence of reduced capability of automation of simple task-related aspects.

Conclusions

The present findings indicate that the shift from controlled to automated processing specifically reduces the demands on the capacity-limited WM system. Performance improvement is associated with a decrease of brain activity in a network of brain regions subserving WM (including bilateral but predominantly left DLPFC and right SPC), after a relatively brief period of practice. Although the different behavioral profiles of controlled and automatic processing suggest distinct processing modes, the imaging data indicate that automated processing is based on the same functional anatomical substrate but information processing is more efficient. The results also imply a complex relationship between activity and performance in the sense that good performance may be associated with increased activity reflecting higher effort, but also with decreased activity, reflecting more efficient performance.

MATERIALS AND METHODS

Subjects

Fifteen right-handed, healthy volunteers (8 males, 7 females, age 23 years, SD 2.1) participated in a single-session experiment on a Philips ACS-NT 1.5-T scanner with PT 6000 gradients. Subjects were volunteers from the environment of the University of Utrecht, the Netherlands. They were screened for major medical, neurological, and psychiatric illnesses and use of medication. Subjects signed an informed consent (approved by the Human Ethics Committee of the University of Utrecht) and were paid for their participation.

Tasks

A task based on Sternberg’s item-recognition paradigm was used to activate verbal WM (Sternberg, 1966). Similar tasks have been used previously in fMRI experiments and have been demonstrated to activate verbal WM (Rypma, Prabhakaran, Desmond, Glover, & Gabrieli, 1999; Manoach et al., 1997). The basic format of the tasks is as follows. A set of 5 consonants is shown for 5540 msec (the target set). This is then replaced by an asterisk in the center of the screen for 1000 msec, serving as a fixation point. This is replaced by one consonant that remains for 1670 msec. Ten consonants are displayed in sequence, each preceded by a 1000-msec asterisk, comprising one run. A new set of 5 consonants is then shown, followed by 10 new trials. Subjects were instructed to memorize the target set and subsequently to indicate for each presented consonant whether it belonged to the target set or not. They were instructed to respond with their right thumb, by pressing the right button for targets, and the left button for nontargets (Figure 7).

Two experimental tasks were administered, which differed only with regard to the stimuli: an NT and a PT. In the PT, the same sets were used repeatedly (target set: FGMPT, nontarget set: BJLRV). These stimuli were also used during a practice session (see Experimental Procedure for details) before the scan session. In the NT, the composition of the target set was changed after every run. The target set and the set of nontargets were chosen from the 10 remaining consonants that were not used for the PT (CDHKNQSWXZ).

Jansma et al. 739
As an additional control task, a choice RT task was used, which did not require memorization of a target set. Instead of a target set, two arrows were shown for 5340 msec, one pointing left and the other pointing right. Subjects were then presented with a series of 10 single arrows, pointing either to the left or to the right. For each arrow, subjects were instructed to press with the right thumb on the left or right button as quickly and accurately as possible, depending on the direction that the presented arrow pointed in.

In all tasks used during the practice session and the scan session, half of the stimuli were targets. All consonants were presented in capitals. Subjects were not informed whether the target set was practiced or novel.

**Experimental Procedure**

The experiment was divided into two parts: a practice session and a scan session. After detailed explanation of all procedures, subjects first underwent the practice session in a table and chair setting. Total training time was approximately 45 min and was divided into four periods of equal length, with short breaks in between. Each period started with a 10-trial practice block, in which subjects were given feedback about their performance (i.e., nature of the response and their RT). This was followed by a block of 200 trials without feedback. In total, each subject practiced 840 trials. Each trial began with an asterisk presented in the center of the screen for 1670 msec, serving as a fixation point. Stimuli were then displayed for 1500 msec. During the whole practice session, the target set and non-target set did not change.

During the scan session, tasks were presented in four blocks of 4.16 min each. Within these blocks, the 3 tasks alternated every 32 sec in a semirandomized order, each task appearing twice. Each block always began and ended with an additional rest period of 32 s denoted as resting state (RS). This period started with a presentation of the word “REST” during 5340 msec, followed by a blank screen. Subjects were instructed to relax with their eyes open without moving.

In the first and third block, task order was as follows: RS–CT–PT–NT–NT–PT–CT–RS. In the second and fourth block, the PT and NT changed places, and the four tasks appeared in the following order: RS–CT–NT–PT–PT–NT–CT–RS. Thus, subjects performed each task 8 times.

**fMRI**

Subjects were positioned supinely in the scanner. Head movement was reduced by using a strap around the forehead, foam padding, and a bed on rollers. A mirror fixed to the headcoil enabled subjects to see a throughput-projection screen positioned near the feet. A video projector, located outside the scanner room, projected the computerized tasks on this screen. A pneumatic push-button box with air pressure cables was used to record responses. Scan sessions lasted approximately 40 min. Training and scanning took place on the same day.

For the BOLD-sensitive image acquisition, the navigated echo 3-D PRESTO pulse-sequence was used (Ramsey et al., 1998; Gelderen et al., 1995; Liu, Sobering, Duyn, & Moonen, 1993). The particular advantage of 3-D PRESTO over other available techniques such as FLASH or EPI is the ability to scan a relatively large 3-D volume in a short period (105 mm slab in 2670 msec in the present experiment). This allows for direct registration of functional and structural volumes (Thiran, Ruttimann, & Unser, 1998) and minimal contribution of inflow effects (Duyn, Moonen, van Yperen, de Boer, & Luyten, 1994).

Functional images were obtained with the following parameter settings: TE, 35.6 msec; TR, 25 msec; flip angle, 10.5°; FOV, 182 × 225 × 105 mm; data matrix, 52 × 64 × 30 mm; voxel size, 3.51 mm isotropic; scan time, 2670 msec (transaxial scan orientation). Four functional series of 96 3-D scans each were run (total time per series 4.16 min). Twelve scans (i.e., 3-D volumes) were acquired during each task epoch (lasting 32 s). Each scan series started approximately 6 sec after task presentation had begun to compensate for the delay in vascular response to neuronal activity (Ogawa et al., 1992). One volume was acquired with a flip angle of 30°, for registration purposes, followed by an anatomical scan for spatial localization of observed activity during later analysis (anatomical scan: 3-D FFE; TE, 4.6; TR, 30 msec; flip angle, 30°; FOV, 256 × 256 mm; matrix, 128 × 128 × 130 mm; slice thickness, 1.2 mm; scan time, 7 min).
Analyses: Behavioral Data

During the practice session, RT of correct responses was averaged per 10 trials per subject, and subsequently over all subjects, yielding a series of 80 group-mean RT values. During the scan session, a mean RT was determined for each subject per task over all correct responses. In addition, for each subject, the mean standard deviation of responses was determined over all correct responses. Group-mean RT and standard deviation were separately tested for a difference between the NT and PT, and for a difference between the PT and CT.

Incorrect responses were divided into incorrect responses and misses. The number of incorrect responses was separately analyzed for each type of error, using a paired means t test. The RT for incorrect responses were not analyzed.

Analyses: Scan Data

After reconstruction, functional and anatomical data were processed off-line on an HP workstation using PV-wave® processing software. Prior to analysis, all functional images were registered to one high contrast functional scan to correct for small translations and rotations between scans (Thevenaz et al., 1998). Scans were normalized for mean volume signal intensity and were then smoothed using a Gaussian filter (FWHM: three voxels ~ 10.5 mm). The outermost four slices (two on each end of the slab) were not analyzed. The first two images of each task condition, during which task instructions were presented, were excluded from further analysis.

Signal analysis involved two steps. First, fMRI signals were analyzed voxelwise, using a multiple regression algorithm (Worsley & Friston, 1995) to assess individual activation maps for each condition, and to remove linear machine-related trends in the signal. This resulted in individual activation maps for the three tasks: NT versus RS (“NT–RS contrast”), PT versus RS (“PT–RS contrast”), and CT versus RS (“CT–RS contrast”). A fourth contrast was created showing the signal differences between the NT (NT–RS contrast) and the CT (CT–RS), denoted as “NT–CT contrast.” Subsequently, in order to create group-average activity maps, all individual activity maps were spatially normalized onto a standard average brain using a linear transformation (Collins, Neelin, Peters, & Evans, 1994). Only voxels that contained signal from all subjects were included in the group analysis. All individual anatomical background scans were also spatially normalized and averaged using the same method, to provide an anatomical background for the group activation patterns.

Next, groupwise t maps were calculated over all spatially normalized individual activity maps by testing the values in each voxel against zero. A t value of 3.88 was used as an activity threshold. This value corresponds to an uncorrected p < .0001, or an expected number of false-positive isolated regions of approximately one, based on a search in approximately 1000 resolution elements (i.e., units of size FWHM(x) by FWHM(y) by FWHM(z), where FWHM is the full width at half maximum of the smoothed images) in the scanned volume (Worsley, Evans, Marrett, & Neelin, 1992). Group activation maps were generated for the NT–RS, PT–RS, CT–RS, and NT–CT contrasts. Subsequent data analysis consisted of two stages, that is, selection of brain regions and comparison of activity in these regions across task conditions. This strategy allows for direct testing of hypotheses concerning practice-related changes of activity in regions that are selectively involved in the task.

The analysis of primary interest was one involving effects of practice on brain regions that were selectively involved in WM. To that purpose the NT–CT contrast was used to identify WM regions.

Of secondary importance was the question whether other regions than those involved in WM, were affected by practice. For that purpose, region selection was also conducted on the NT–RS and PT–RS contrast. The NT–RS contrast was used to test if additional regions, not involved or not fully overlapping the regions selected by the NT–CT contrast, were also affected by practice. The PT–RS contrast was used to select regions involved in PT processing. This analysis was specifically aimed at finding regions with increased activity after practice, as these regions may reach significance in the PT–RS contrast. Clusters reaching significance (t > 3.88) in the CT–RS contrast were identified, but not further analyzed for effects of practice.

Analysis of Activity in Selected Regions

To test for effects of practice, activity in each selected region was averaged across the voxels within that region, for the NT–RS, the PT–RS, and the NT–CT contrasts separately. This yielded a measure of activity for each task, in each region. Next, a multivariate analysis (GLM with repeated measurements) was used to test the set of regions for effects of practice. This was done for each selection set separately (NT–RS, PT–RS, NT–CT). Practice effects were examined further with paired t tests, using one-sided p values.

Acknowledgments

The authors thank the anonymous reviewers for their comments. This research was supported in part by Solvay Duphar and by the University Medical Center Utrecht.

Reprint requests should be sent to: Johan Martijn Jansma, MS, Department of Psychiatry, University Medical Center Utrecht, HP A01.126, Heidelberglaan 100 3584 CX, Utrecht, The Netherlands, or via e-mail: j.m.jansma@azu.nl.

Jansma et al. 741
The data reported in this experiment have been deposited in the National fMRI Data Center (http://www.fmridc.org). The accession number is 2-2001-IIIRM.

REFERENCES


