How Self-Initiated Memorized Movements Become Automatic: A Functional MRI Study

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Wu, Tao, Kenji Kansaku, and Mark Hallett. How self-initiated memorized movements become automatic: a functional MRI study. J Neurophysiol 91: 1690–1698, 2004. First published November 26, 2003; 10.1152/jn.01052.2003. We used functional magnetic resonance imaging (fMRI) and dual tasks to investigate the physiology of how movements become automatic. Normal subjects were asked to practice some self-initiated, self-paced, memorized sequential finger movements with different complexity until they could perform the tasks automatically. Automaticity was evaluated by having subjects perform a secondary task simultaneously with the sequential movements. Our secondary task was a letter-counting task where subjects were asked to identify the number of times a target letter from the letter sequences was seen. Only the performances that achieved high accuracy in both single and dual tasks were considered automatic. The fMRI results before and after automaticity was achieved were compared. Our data showed that for both conditions, sequential movements activated similar brain regions. No additional activity was observed in the automatic condition. There was less activity in bilateral cerebellum, pre supplementary motor area, cingulate cortex, left caudate nucleus, premotor cortex, parietal cortex, and prefrontal cortex during the automatic stage. These findings suggest that most of the motor network participates in executing automatic movements and that it becomes more efficient as movements become more automatic. Our results do not provide evidence for any area to become more activated for automatic movements.

INTRODUCTION

A general characteristic of the motor system is that people can perform some learned movements automatically. Automatic movements are performed without attention being clearly directed toward the details of the movement, particularly for movements that require low precision or that are commonly made (Bernstein 1967). For example, people can keep an appropriate stride length during walking without special attention. After a long period of training, even some complex tasks can be executed automatically. A skilled typist is able to type accurately while holding a conversation (Shaffer 1975). According to Fitts’s theory of motor learning, after passing through the “cognitive” and “fixation” stages, in the third stage, named “automatic” phase, the motor skill is well established and can be performed automatically in a range of contexts with limited demands on attentional resources (Fitts 1964).

Although movement automaticity has been extensively studied, its underlying physiology is still debated. It remains controversial whether there is an area specifically devoted to executing automatic movements. Some studies showed that, after practice, different regions from the prepracticed condition are activated and these regions are thought to contribute specifically to skilled performance (Jueptner et al. 1997b, 1998; Petersen et al. 1998). Other research did not find any regions activated in the overlearned condition that had not already appeared before practice (Jansma et al. 2001). Investigations on the change of activity of multiple brain areas during the learning process also have contradictory results. For example, the activity of premotor cortex was reported decreased in some studies related to learning (Jenkins et al. 1994; Jueptner et al. 1997a,b; Toni et al. 1998), whereas in others, an increase was observed (Hazeltine et al. 1997). The findings on the primary motor cortex have also been inconsistent. Karni et al. (1995) reported increased activation of motor cortex in overlearned sequences compared with the new sequence. By contrast, Toni et al. (1998) observed no increase in this region over time.

One major issue in past studies is whether the subjects achieved automaticity. In some studies, the subjects had practiced extensively and improved their performance, although no evidence proved automaticity during the investigation. In fact, even when subjects have improved a certain task after practice, their performance may not achieve the automatic state (Lang and Bastian 2002). The evidence that a task has become automatic can be proven by the fact that a secondary task can be performed with minimal interference (Passingham 1996). Therefore in the present study, we developed a dual-task paradigm to evaluate whether automaticity was achieved. The first task of our dual task was a sequence finger movement task and the secondary task was a visual cognitive task.

We used functional magnetic resonance imaging (fMRI) to investigate brain activity produced by self-initiated memorized sequential movements before and after automaticity was achieved. Whereas prior studies investigated the learning process in externally triggered movements (Grafton et al. 1995; Hazeltine et al. 1997; Jenkins et al. 1994; Jueptner et al. 1997a,b; Toni et al. 1998), how a self-initiated memorized movement becomes automatic has not been studied. Functional imaging studies have shown that, although self-initiated and externally triggered movements activate similar areas including primary motor, supplementary motor area (SMA), parietal, and insular cortices (Boecker et al. 1998; Jahanshahi et al. 1995; Jenkins et al. 2000), self-initiated movements additionally activate pre-SMA, anterior cingulate cortex, and bilateral dorsolateral prefrontal cortex (Jenkins et al. 2000). The preparation of self-initiated and externally triggered movements is
also different (Cunnington et al. 2002; Jahanshahi et al. 1995; Jenkins et al. 2000).

METHODS

Subjects

Twelve normal volunteers participated in the study (8 males, 4 females; ages 23–38 yr). All subjects were right-handed (laterality index was 0.8 to 1.0) as measured by the Edinburgh Inventory (Oldfield 1971). The protocol was approved by the Institutional Review Board, and all subjects gave their written informed consent for the study.

Tasks

Subjects were asked to perform 2 sequences of right finger tapping with different lengths of the unit sequence as an index of complexity. They were referred to as sequence-4 and sequence-12, based on the number of movements in each unit of the sequence. "Sequence-4" was 1–3–4–2, in which 1, 2, 3, and 4 refer to the index, middle, ring, and little fingers, respectively. "Sequence-12" was 1–4–3–2–2–4–1–3–4–1–2–3. Both sequences were executed at 0.5 Hz. Automaticity was evaluated by having subjects perform a visual letter-counting task simultaneously with these sequential movements. For the letter-counting task, letter sequences consisting of a random series of the letters A, G, L, and O were presented on a screen and subjects were asked to identify the number of times they saw a specific target letter (e.g., A). All sequential movements were self-initiated and self-paced. No external cue was given to help the subjects move at the specified rate. Before the first scan, all subjects practiced until they could move at the required rate. They briefly practiced each sequential movement for 10–20 min. In addition, subjects were given enough practice trials to ensure that they could perform the visual letter-counting tasks correctly with no difficulty. The number of target letters was changed for each trial. After scanning, subjects were asked to report the number of target letters.

After the first scan, subjects practiced these tasks (2 to 4 h) until they could perform sequence-4 and sequence-12 from memory 10 times in a row without error, as well as the dual tasks accurately. Only at this level were the movements considered automatic.

Functional MRI experiments

T2*-sensitive functional images were obtained using a whole-body 1.5 Tesla magnetic resonance imaging (MRI) scanner (Signa, General Electric, Milwaukee, WI) and a standard head coil. Head motion was reduced by a belt around the subject’s head. Subjects lay supine in the MRI scanner with a response device fixed to their right hand. The response device had 4 buttons, corresponding to the index, middle, ring, and little fingers of the right hand and was used to record finger movements. The subjects viewed visual signals on a screen through a mirror built into the head coil. We used an EPI gradient echo sequence (21 slices, TE = 30 ms, TR = 2,500 ms, flip angle = 90°, FOV = 22 × 22 cm, matrix = 64 × 64) to obtain functional images. A time-course series of 100 images/slice was acquired for each trial, in an off-on cycle paradigm of rest and activation. Each scanning session lasted 4 min. T1-weighted images were also acquired (128 slices, TR = 33 ms, TE = 4 ms, flip angle 25°, matrix = 25 × 192) to obtain structural three-dimensional (3-D) volume.

As mentioned above, fMRIs were acquired both before and after the subjects achieved automaticity. Two conditions were contained in each scanning session and were defined as “rest” and “active” condition, respectively. Each condition lasted 25 s and was repeated 5 times in a session. In the rest condition, subjects were asked to relax and focus on the screen in front of them without moving in the scanner. Active conditions contained sequence-4, sequence-12, or visual letter-counting task. No feedback was provided during scanning to tell subjects whether their finger movements were correct or incorrect.

Behavioral data analysis

Each subject’s performance for each task was recorded. These measurements included the errors for performing sequential movements or for counting the visual letters in each session. For sequential movements, wrong button presses were considered as errors. These data were used to evaluate whether these tasks were performed automatically after training. As mentioned above, only the performances that achieved high accuracy in both single and dual tasks were considered automatic. The performance between sequence-12 and sequence-4 was compared (2-sample t-test, P < 0.05). The difference of performance before and after automaticity was achieved and between single and dual task were calculated (repeated-measures ANOVA, P < 0.05).

Imaging data analysis

Image analysis was performed with SPM 99 software (Wellcome Institute of Cognitive Neurology, London, UK) implemented in MATLAB. Functional images were aligned to the first image of each session for motion correction. After spatial normalization, all images were resampled into voxels that were 2 × 2 × 2 mm in size. Images were also smoothed with a Gaussian filter of 6 mm full width at half-maximum (FWHM) to minimize noise and residual differences in gyral anatomy. Both first and second level analyses were performed. In the first level, data were analyzed for each single subject separately on a voxel-by-voxel basis using the principles of the general linear model extended to allow the analysis of fMRI data as a time series (Friston et al. 1995a–c). The data were modeled using a fixed-effect boxcar design, convolved with a hemodynamic response function chosen to represent the relationship between neuronal activation and blood flow changes. The model had the same on-off frequency as the alternation frequency of the active and rest conditions, and was constructed for analysis of task-dependent activation, identical for all subjects and for all conditions. A contrast representing the effect of the active condition compared with the rest condition was defined and contrast images were calculated individually for each condition. These contrast images were used in the second level for random-effects analyses. The group result was calculated by a one-sample t-test model to identify the brain activity before and after training for each condition (P < 0.001, without correction for multiple comparisons). A paired t-test model was used to compare the pretraining results with the posttraining results for each condition (P < 0.001, uncorrected). Locations of activated areas for different conditions were displayed by superimposing them on axial sections of a Talairach–Tournoix normalized high-resolution 3-D T1-weighted MRI brain scan (Talairach and Tournoix 1988).

RESULTS

Task performance

The accuracy of sequential finger movements and visual letter counting for single sequential movements and dual tasks across all subjects are shown in Table 1. Before training, all subjects committed several errors of sequential finger movements in performing all tasks and letter counting while performing dual tasks. The wrong finger taps of the sequences were consistent across the 5 blocks during first scanning. There were more finger movement errors in performing sequence-12 than in performing sequence-4 (2-sample t-test, P < 0.05), and in performing dual tasks than in performing single tasks (ANOVA, P < 0.05). In addition, more errors were found in
performing the dual task of sequence-12/letter counting than in performing the dual task of sequence-4/letter counting (ANOVA, \( P < 0.05 \)). After training, all subjects reported that they could execute the motor sequences without paying attention to these tasks, even during performing dual tasks. Their performance was significantly improved (repeated-measures ANOVA, \( P < 0.05 \)). They made no errors in executing sequence-4. Sequence-12 and visual letter counting were about 99% correct. There were no more errors in performing sequence-12 compared with sequence-4 at the before-training stage. Our results demonstrate that after extensive training, normal subjects can achieve automaticity. A higher percentage of errors in sequence-12 compared with sequence-4 at the before-training stage was found in their performance (Sakai et al. 2003). Our results demonstrate that after extensive training, normal subjects can achieve automaticity in performing some relatively complex tasks.

Before and after training, the rate of sequential movements (both single and dual tasks) was close to the target speed of 0.55 ± 0.04 and 0.52 ± 0.03 Hz, respectively, and was not statistically different. There was less variability of between-finger movements intervals after training (1.8–2.2 s) compared with those before training (1.5–2.4 s). We found no subject who developed any particular pattern of finger movements (e.g., triplets or quadruplets). This was evaluated by examining the intervals between finger taps. We found no consistent time gaps during the performance of the sequential movements that would have suggested that the sequence was broken into segments.

**fMRI data**

A second-level one-sample \( t \)-test group analysis (\( P < 0.001 \), uncorrected) revealed that before training, both sequence-4 and sequence-12 were associated with activations at left primary sensorimotor cortex, bilateral premotor areas, bilateral parietal cortex, bilateral inferior frontal gyrus, prefrontal cortex, SMA-proper, pre-SMA, cingulate cortex, basal ganglia, bilateral insular cortex, and bilateral cerebellum (Fig. 1A). After training, the pattern of brain activity was similar to that before training. No additional activation was observed in either sequence-4 or sequence-12 (Fig. 1B). In contrast, there was less activity in bilateral cerebellum, bilateral premotor area, bilateral superior and inferior parietal lobes, left dorsal lateral prefrontal cortex, pre-SMA, anterior cingulate cortex, and left caudate nucleus compared with the before-training condition (\( P < 0.001 \), uncorrected) (Fig. 2 and Table 2).

The visual letter-counting task activated SMA, bilateral premotor cortex, parietal cortex, inferior frontal cortex, superior temporal cortex, visual cortex, and left cerebellum (Fig. 3). No difference was found between the before- and after-training conditions.

At both the before- and after-training stages, the comparison between sequence-12 and sequence-4 showed more activation in the cerebellum and parietal and premotor cortices for sequence-12 (data not shown).

**DISCUSSION**

In our study, after training, all subjects performed all tasks with high accuracy. All sequential movements were performed automatically as proven by the accuracy of the sequences, stability of the intervals of movements, and most important, the performance of dual tasks. Sequences were unlikely to be performed as several chunks in that no particular pattern of time gaps was found in their performance (Sakai et al. 2003).

Our results demonstrate that after extensive training, normal subjects can achieve automaticity in performing some relatively complex tasks.

We used different sequences to investigate to what degree normal subjects can achieve automaticity. A higher percentage of errors in sequence-12 compared with sequence-4 at the pretraining stage confirmed that sequence-12 was more difficult to execute. Imaging results showed more activation in the cerebellum, parietal cortex, and premotor cortex for sequence-12 compared with sequence-4. Our finding is consistent with previous reports (Catalan et al. 1998), and suggests that more complex movement requires more brain activation.

Finger movement rate has a significant effect on brain activity. It has been shown that brain activation in several areas (i.e., primary sensorimotor cortex, cerebellum, and SMA) is related to movement frequency (Deiber et al. 1999; Sadato et al. 1997). For this reason, our subjects were required to perform the movements at certain rates. We did not use external

**TABLE 1. Performance (percentage of errors) of sequential finger movements and visual letter counting before and after training**

<table>
<thead>
<tr>
<th>Task</th>
<th>Before training</th>
<th>After training</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sequence-4</td>
<td>1.4 ± 2.6</td>
<td>0</td>
</tr>
<tr>
<td>Sequence-12</td>
<td>11.8 ± 15.5</td>
<td>0.6 ± 1.7</td>
</tr>
<tr>
<td>Letter counting</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Sequence-4/counting</td>
<td>4.9 ± 4.2/5.9±9.9</td>
<td>0.7 ± 1.9</td>
</tr>
<tr>
<td>Sequence-12/counting</td>
<td>17.1 ± 15.2/13.9±11.5</td>
<td>1.1 ± 1.9/1.2±2.2</td>
</tr>
</tbody>
</table>

Values are means ± SD for percentage of errors. The results of the dual task of sequential movements and visual letter counting are given as errors of finger movements/errors of letter counting.
activity in our study may partly be attributable to less neural network being recruited for timing control.

**Automaticity-related areas**

At the automatic stage, the brain activity pattern was similar to that before training (Fig. 1). There was less activity in bilateral cerebellum, bilateral premotor area, posterior parietal cortex, pre-SMA, anterior cingulate cortex, left caudate nucleus, and left dorsal lateral prefrontal cortex at the automatic stage (Fig. 2). Because the subjects were required to perform the same tasks before and after achieving automaticity, the rate was the same, fingers were the same, and therefore the observed differences of brain activity cannot be related to movement execution. There were more errors of the correct fingers before training, but because our movements were self-initiated and memorized and no feedback was provided to tell subjects whether their presses were correct or incorrect, a change in error detection and correction is not likely to be responsible for the activation change. This was supported by the fact that the wrong finger movements were consistent across 5 blocks during the first scan. Therefore brain activity changes must be related to automaticity.

Our observation that the cerebellum (bilateral anterior, posterior lobe, and vermis) is involved is consistent with several previous studies showing that cerebellar activity is greatest early in motor learning (Doyon et al. 1996; Jenkins et al. 1994; Jueptner et al. 1997b; Toni et al. 1998). Recently, it has been realized that the cerebellum is important not only in motor execution, but also in learning and timing control of movements (Dreher and Grafman 2002; Kawashima et al. 2000; Jueptner et al. 1997b). It projects to several areas of the prefrontal cortex by the thalamus and influences motor and cognitive operations (Middleton and Strick 2001). For our study, we propose 2 possible reasons that may explain the change of activity in the cerebellum. One is that the cerebellum is important for shifting a pretraining movement performance to a more skilled and automatic stage (Doyon et al. 1998; Jenkins et al. 1994; Lang and Bastian 2002; Thach et al. 1998). Lang and Bastian (2002) found that cerebellum-damaged patients could improve a motor task with practice, but could not learn to perform the task in a more automatic state. Skilled movements rely on the representation of the body and task and the cerebellum may play a role in storing these representations (Hore et al. 1999; Shimansky et al. 1997). The second possi-

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**TABLE 2. Brain areas more activated during performing sequence-12 task at the before-training condition than after-training stage**

<table>
<thead>
<tr>
<th>Cluster Size</th>
<th>Activated Areas</th>
<th>x</th>
<th>y</th>
<th>z</th>
<th>Z Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>480</td>
<td>L Parietal Cortex</td>
<td>-46</td>
<td>-40</td>
<td>50</td>
<td>6.10</td>
</tr>
<tr>
<td>148</td>
<td>L Pre-SMA</td>
<td>-4</td>
<td>6</td>
<td>53</td>
<td>5.83</td>
</tr>
<tr>
<td>87</td>
<td>L Premotor Area</td>
<td>-26</td>
<td>-12</td>
<td>63</td>
<td>5.80</td>
</tr>
<tr>
<td>154</td>
<td>L Cerebellum, Posterior Lobe</td>
<td>-26</td>
<td>-48</td>
<td>-28</td>
<td>5.48</td>
</tr>
<tr>
<td>38</td>
<td>L Cerebellum, Anterior Lobe</td>
<td>-31</td>
<td>-40</td>
<td>-22</td>
<td>4.93</td>
</tr>
<tr>
<td>31</td>
<td>R Parietal Cortex</td>
<td>24</td>
<td>-53</td>
<td>60</td>
<td>5.34</td>
</tr>
<tr>
<td>73</td>
<td>R Parietal Cortex</td>
<td>42</td>
<td>-36</td>
<td>63</td>
<td>5.17</td>
</tr>
<tr>
<td>109</td>
<td>R Cerebellum, Anterior Lobe</td>
<td>24</td>
<td>-49</td>
<td>-20</td>
<td>5.14</td>
</tr>
<tr>
<td>53</td>
<td>R Cerebellum, Posterior Lobe</td>
<td>26</td>
<td>-36</td>
<td>-32</td>
<td>4.88</td>
</tr>
<tr>
<td>15</td>
<td>R Premotor Area</td>
<td>36</td>
<td>-2</td>
<td>56</td>
<td>4.89</td>
</tr>
<tr>
<td>15</td>
<td>L Prefrontal Cortex</td>
<td>-34</td>
<td>42</td>
<td>20</td>
<td>4.83</td>
</tr>
</tbody>
</table>

The coordinates are given as stereotaxic coordinates referring to the atlas of Talairach and Tournoux. Cluster size is the number of voxels. All areas were significant at $P < 0.001$ (uncorrected). Abbreviations: L, left; R, right; SMA, supplementary motor area.
bility is that the cerebellum is important in timing control. Ivry and Keele (1989) suggested that the neocerebellum has a timing function, whereas Kawashima and colleagues (2000) found that the bilateral anterior lobe is involved in the generation of accurate timing. Sakai and colleagues (1999, 2000) showed that the memory of simple rhythms involves the anterior cerebellum, whereas the memory of complex rhythms and the adjustment of movement timing in response to irregular external triggers involve the posterior cerebellum. Our study required that the subjects learn to generate and keep the timing of movements by themselves. At the pretraining stage, subjects had to pay more attention while performing the tasks rhythmically. After training, they performed the movements automatically and the central timing-control mechanism was less activated. Our data did not allow us to distinguish between these 2 possibilities. However, we speculate that both these functions were involved.

The bilateral premotor cortex was significantly less activated at the automatic stage. Our finding of the role of the premotor cortex parallels many previous studies. Jenkins et al. (1994) and Jueptner et al. (1997a,b, 1998) reported that the premotor cortex is more activated during learning than during performing overlearned sequences. Toni et al. (1998) showed that the left dorsal premotor cortex had an initial large and sustained activation, followed by a decrease during the learning process. Each premotor area is a nodal point for a discrete set of afferent inputs from subcortical nuclei and cortical areas constituting different systems of movement control (Dum and Strick 1991; He et al. 1993). The premotor cortex is important in the temporal organization of sequential movements (Halsband et al. 1990, 1993), selection of movements (Deiber et al. 1991), and in the generation of motor sequences from memory that fit into a precise plan (Grafton et al. 1992; Shibasaki et al. 1993). All these mechanisms must be included during the early learning process of a complex movement.

Both pre-SMA and cingulate motor cortex activity decreased with automaticity. Area 6 on the medial wall of the brain contains 2 separate areas: the SMA-proper in the caudal portion and the pre-SMA in the rostral portion (Picard and Strick 1996). In the present study, we found activation in both SMA-proper and pre-SMA for the pretraining condition, whereas the activity significantly decreased in the pre-SMA but not in the SMA during the automatic stage. The pre-SMA is important in motor control. First, the pre-SMA is known to be critical in planning and decision components of more complex movements, and might especially play a primary role in the early preparation of self-initiated movements (Cunnington et al. 2002; Deiber et al. 1991; Jenkins et al. 2000). It contains a higher proportion of neurons with activity changes during preparation for movement than does the SMA-proper (Matsuzaka et al. 1992). Second, the pre-SMA is important in acquiring of new motor sequences. In monkeys, it was shown that cells in the pre-SMA were activated more for new movements than learned tasks (Hikosaka et al. 1999; Nakamura et al. 1998). Local inactivation of the pre-SMA led to deficits in acquiring new sequences (Nakamura et al. 1999). A neuroimaging study in human subjects also showed that pre-SMA activity decreased when subjects had learned to perform a sequential movement (Sakai et al. 1998). Third, the pre-SMA plays a role in controlling time, especially for self-paced movements (Kawashima et al. 1999, 2000; Larson et al. 1996). All these roles might be involved in the process of automaticity in the current study.

The cingulate motor cortex includes the rostral cingulate zone (RCZ) and the caudal cingulate zone (CCZ) (Picard et al. 1996). In our study, the RCZ was less activated during the automatic stage, whereas the CCZ was constantly activated. Previous studies also reported that the anterior cingulate cortex was strongly activated only in the pretraining condition (Jenkins et al. 1994; Jueptner et al. 1997a,b; Toni et al. 1998). There have been relatively few studies on the RCZ; its role is not fully defined, but may include both motor and cognitive functions (Picard and Strick 2001). Two theories predominate about the overall function of the RCZ: the “conflict monitoring” theory emphasizes its evaluative function (Botvinick et al. 1999), whereas the “attention/selection of action” theory emphasizes its motor function (Petersen et al. 1988). In monkeys, Shima et al. (1991) found that the anterior cingulate (corresponding to the RCZ in humans) had a greater role in self-paced movements than the CCZ. Similar to the pre-SMA, the RCZ shows greater activation during internally generated movements (Deiber et al. 1999; Wessel et al. 1997) and is more involved in early processes of movement preparation (Ball et al. 1999) and in the internal representation or imagination of movement (Stephan et al. 1995). It is also reported to be active when subjects generate a new movement, decide what to do (Deiber et al. 1991; Frith et al. 1991; Jueptner et al. 1997; Playford et al. 1992), or when to do it (Jahanshahi et al. 1995). Therefore during pretraining process, the RCZ appears to be more activated as more internal preparation, mental rehearsal, and monitoring mechanisms are recruited to execute self-initiated complex sequential movements.

In the basal ganglia, we found a change of activity in the left caudate nucleus. Toni et al. (1998) also reported that the left caudate was activated early in the learning process and decreased rapidly thereafter. The basal ganglia are involved in movement executing, programming, and controlling (Alexander and Crutcher 1990). They project to motor cortical areas including primary motor cortex, premotor area, SMA-prepro, pre-SMA, and cingulate motor area through the thalamus. These connections are thought to be involved in acquiring and coordinating motor sequences (Nakano 2000). The caudate nucleus receives a heavy projection from the dorsal lateral prefrontal cortex, pre-SMA, and other frontal association areas (Selemon and Goldman-Rakic 1985), and it is known that the prefrontal cortex is activated when subjects learn a new motor sequence (Jenkins et al. 1994; Jueptner et al. 1997a). In monkeys, it was shown that caudate nucleus neurons are preferentially activated for learning a new motor sequence (Hikosaka et al. 1999; Inase et al. 2001; Miyachi et al. 2002). The greater activation of the caudate nucleus in the pretraining condition may reflect the robust need of mental rehearsal of the sequence or preparation for the next move during pretraining (Jueptner et al. 1997b). More evidence for the role of the basal ganglia in the learning process is derived from studies of Parkinson’s disease (PD). PD patients cannot make automatic movements. For example, they have to direct their attention to the task and think about each step if they are to make adequately long steps; otherwise the steps become small. Another deficiency is difficulty in performing 2 separate motor tasks simultaneously (Benecke et al. 1986). It is suggested that the reason for these phenomena is that their ability in making automatic move-
ments is defective or they have difficulty in switching a learned task to the automatic phase. These results suggest that the basal ganglia may have a possible role in shifting a learned performance to the automatic stage.

We found that the bilateral superior and inferior parietal lobes were more activated during the pretraining condition. Toni et al. (1998) also reported an increase in the parietal cortex early in learning and related the phenomenon to the increase in preparation for the movements when learning. The parietal cortex is related to motor selection with external information, such as auditory and visual cues, based on integration of spatial information (Deiber et al. 1991; Grafton et al. 1992). Jenkins et al. (1994) found greater activation of bilateral posterior parietal cortex during learning of auditory-cued sequential finger movement and speculated that this activation might be related to more spatial attention required during learning than during the well-learned task. Parietal areas also play a role in the temporal aspects of the sequence to ensure that each movement occurs after successfully completing the preceding move. Patients with parietal cortex damage have difficulty in predicting the time required to perform differentiated finger movements (Sirigu et al. 1996). Posterior parietal areas could be recruited to store information about the motor sequence (Sadato et al. 1996) and may have a role in selecting and monitoring a sequence. Deiber et al. (1996) reported activation in this region when subjects prepare to make finger movements. It is possible that the greater activation in this region in the pretraining condition relates to more spatial, temporal attention and preparation in selecting the correct program and finger for each movement.

Extensive studies have investigated the role of the dorsal lateral prefrontal cortex in the learning process (Deiber et al. 1997; Jansma et al. 2001; Jenkins et al. 1994; Jueptner et al. 1997a,b). It has been shown that the lateral prefrontal cortex is important in generating a new movement (Deiber et al. 1991; Jueptner et al. 1997a,b), in task rehearsal (Perides et al. 1993), and in performance monitoring (Owen et al. 1996). It is heavily involved in the early performance of a novel movement (Grafton et al. 1995; Honda et al. 1998; Jueptner et al. 1997a,b). In addition, it has been suggested that one of the important functional role of the dorsal lateral prefrontal cortex is the timing control of a self-paced movement task (Kawashima et al. 2000; Larsen et al. 1996; Wessel et al. 1995). Thus the reduced activity in this region in our study might also be attributed to less requirement of time control at the automatic stage.

Given our results, we found that multiple brain regions, including the cerebellum, premotor area, posterior parietal cortex, pre-SMA, anterior cingulate cortex, basal ganglia, and dorsal lateral prefrontal cortex, appear to contribute to the acquisition of new self-initiated sequences in parallel, whereas some regions also play an important role in shifting the pretraining sequence to the automatic stage. It was not the purpose of the present study to dissociate the various functions that are included in learning processes.

**Automatic execution–related areas**

The pattern of activation at the automatic stage was similar to that at the pretraining condition. Most of the motor-related areas were activated at the automatic stage, suggesting that most of the motor network participates in automatic movement execution. We found no additional areas activated specifically for automaticity. In contrast, some studies of humans and monkeys reported that the posterior putamen was more activated during the overlearned condition (Hirosaka et al. 1999; Jueptner et al. 1997b, 1998; Miyachi et al. 2002). One possible reason for this difference might be ascribed to the use of different paradigms. In the present study, we used self-initiated memorized complex sequential movements, whereas Jueptner and colleagues used externally triggered relatively easy movements. Our paradigm engaged almost the entire motor network, including the posterior putamen in both before- and aftertraining stages (Fig. 1). Menon et al. (2000) also found that the posterior putamen is activated in a memory-guided sequential movement and, in their study, the task was not automatically executed. A monkey study revealed that there are heterogeneous groups of neurons in the putamen, and that each group participates in retrieving a different type of information required for movement based on either external sensory events or on internally stored information (Kimura et al. 1992). All these results suggest that the posterior putamen is not specifically related to the automaticity in a self-initiated memorized movement.

In addition to the primary sensorimotor cortex, other motor areas such as cerebellum, premotor area, parietal cortex, SMA-proper, and CCZ were also involved in automatic movement execution. The bilateral cerebellum was activated during pretraining and automatic execution of the sequential movements. The activity in the ipsilateral side was stronger than that in the contralateral side (Fig. 1). A previous study showed that when the movement was simple, activation was only in the ipsilateral cerebellum (Catalan et al. 1998). This suggests that for executing a simple task only the ipsilateral cerebellum is involved; however, during pretraining and automatically executing a complex sequence, the entire cerebellum is engaged.

The premotor cortex is considered to be the center of complex skilled movements and can be separated into discrete areas (Dum and Strick 1991). It is thought to be more involved in executing externally triggered movements (Mushiake et al. 1991). However, other studies revealed that the premotor cortex participates in both internally generated and externally triggered tasks (Kura and Wise 1988; Okano and Tanji 1987). Jenkins and colleagues (2000) found greater activation of this region during self-initiated movements than during externally triggered movements. Activity of the premotor cortex is also modulated by task complexity. It has been reported that activating the premotor cortex increases with performing longer sequences (Catalan et al. 1998; Sadato et al. 1996).

During the automatic stage, the main activity in the SMA was caudal, the SMA-proper. It has been shown that the SMA-proper has a role in storing learned motor sequences in monkeys as well as in human subjects (Grafton et al. 1994; Jenkins et al. 1994; Tanji and Shima 1994, 1995; van Mier et al. 1998). Cells in the SMA-proper usually did not differentiate between new and learned sequences (Nakamura et al. 1999). Activation of the SMA-proper, unlike the pre-SMA, was related to sensorimotor processes, not learning processes (Hirosaka et al. 1996). Neurons in the SMA-proper were more active when the sequence was remembered and self-determined. It has been suggested that there is some functional specialization of the SMA-proper for controlling internally referenced motor
output. It may be mainly involved in executing a self-initiated movement, whereas the pre-SMA is important in its preparation (Jenkins et al. 2000).

Similar to the SMA, the main activation of the cingulate motor cortex was also located in the caudal portion, the CCZ. In a monkey study, it was demonstrated that the dorsal cingulate motor area (CMAd), corresponding to CCZ in humans (Picard and Strick 1996, 2001), is involved more than any other medial area in preparing and executing highly practiced, remembered movement sequences. In a human study, it has also been shown that the CCZ is activated primarily in relation to movement execution (Fink et al. 1997). In the CCZ, both sequential and faster movements were associated with greater activation (Deiber et al. 1999). It was suggested that the motor functions of the medial wall that were traditionally attributed to the SMA in human subjects, such as generating programming internally and executing sequential movements, actually may involve the CCZ alone or in combination with the SMA (Picard and Strick 1997).

Mechanism of dual-task interference

The poor performance of the dual tasks compared with each single task at the pretraining stage indicated that interference occurred between the 2 component tasks. The underlying mechanism of dual-task interference remains controversial. The dual-task interference has been described as a competition referring to the focus of mental activity on a task. It is based on the assumption that attention resources are limited. Therefore when people perform 2 tasks simultaneously, attention must be divided between the tasks. How attention is divided between the 2 tasks relies on several factors, including task complexity, familiarity, and importance. According to the capacity-sharing model, dual-task interference occurs only if the available resource capacity is exceeded, resulting in a decline in performance for one or both of the tasks (Pashler 1994). Our imaging results showed that the brain areas activated by the visual letter-counting task overlapped with that of the sequential movement task in the bilateral premotor areas, parietal cortex, SMA, anterior cingulate area, basal ganglia, and cerebellum (Figs. 1 and 3). The behavioral data of our investigation support this model. During the pretraining stage, subjects appeared to attend to both sequential movements and letter-counting task, leading to reduced performance for both tasks. Sequence-12 led to greater deterioration of letter-counting performance than did sequence-4. After training, the sequential movements were automatically performed; therefore capacity was no longer exceeded and subjects needed to focus only on the letter-counting task to perform the dual tasks accurately. This issue will be explored in a subsequent report.

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REFERENCES


