Foot, Hand, Face and Eye Representation in the Human Striatum

The present study aimed at determining the three-dimensional organization of striatal activation during foot, hand, face and eye movements. Seven right-handed, healthy volunteers were studied at 1.5 T using blood oxygen level dependent (BOLD) contrast. The tasks consisted of self-paced flexion/extension of the right and left fingers and right toes, contraction of the lips and saccadic eye movements. For foot, hand and face movements, striatal activation was mainly found in the putamen with a somatotopical organization, the foot area being dorsal, the face area more ventral and medial, the hand area in between. Overlap between somatotopic territories was present, more prominent for hand–face than for foot–face or foot–hand areas. In the putamen, the activated areas of the ipsi- and contralateral hand areas were not identical, suggesting a partial segregation of the ipsi- and contralateral striatal sensorimotor projections. For saccadic eye movements, bilateral activation was observed at the junction between the body and the head of the caudate nucleus and in the right putamen. These data present evidence for a somatotopic organization of the human striatum which corresponds with the topography of corticostriatal projections described in the non-human primates.

Introduction

Although the role of the basal ganglia is not precisely understood, numerous studies have demonstrated their involvement in psychomotor behavior (Brooks, 1995; Parent and Hazrati, 1995; Middleton and Strick, 2000) and basal ganglia lesions lead to various hyper- or hypokinetic movement disorders, such as tremor, dystonia or chorea (Brooks et al., 2000; Obeso et al., 2000). In non-human primates, all cortical projections upon the striatum are topographic (Selemon and Goldman-Rakic, 1985). The sensorimotor cortices mainly project toward the dorsal part of the postcommissural portion of the putamen (Künzle, 1975; Parent and Hazrati, 1995) and the sensorimotor compartment of the striatum is somatotopically organized (Künzle, 1975; Flaherty and Graybiel, 1995). In humans, previous studies have shown the potential of functional magnetic resonance imaging (fMRI) in studying basal ganglia activity during motor tasks (Bucher et al., 1995; Lehéricy et al., 1998; Maillard et al., 2000; Scholz et al., 2000).

Improved knowledge of the organization of the striatal sensorimotor compartment compared with cortical representation is critical for understanding the role of the striatum in motor behavior. The first fMRI study to address the somatotopical representation of the striatum has reported a foot and hand representation in the putamen similar to that observed in non-human primates (Lehéricy et al., 1998). Since then, other reports have further extended these findings for face movements (Maillard et al., 2000) and suggested that activation was less lateralized in the basal ganglia than in the cortex (Scholz et al., 2000).

Several questions remain to be elucidated. Studies in primates (Künzle, 1975; Hikosaka et al., 1989; Alexander and Crutcher, 1990; Parthasarathy et al., 1992; Flaherty and Graybiel, 1993) and preliminary studies in humans (Lehéricy et al., 1998; Maillard et al., 2000; Scholz et al., 2000) have suggested a dorsal to ventro-medial representation of the foot, hand and face area in the putamen, and a predominant representation of eye movements in the caudate nucleus. In humans, a comprehensive study of the three-dimensional (3-D) somatotopic representations of the foot, hand, face and eye areas in the striatum; to study the degree of overlap between these territories and between the projection zones of the ipsi- and contralateral sensorimotor cortices in primates tended to interdigitate rather than completely overlap (Flaherty and Graybiel, 1993). Basal ganglia, which are connected to bilateral cortical areas, may show more frequent bilateral activation during unilateral movements than in the primary sensorimotor cortex.

The aims of the present study were: to determine the 3-D somatotopic representation of the foot, hand, face and eye areas in the striatum; to study the degree of overlap between these territories and between the projection zones of the ipsi- and contralateral hand areas; and to study further the laterality of basal ganglia activation compared with other cortical areas.

Materials and Methods

Subjects

Seven right-handed, healthy volunteers were studied (six men, one woman; age range 24–31 years). The French National Ethics Committee approved the study. All subjects gave informed consent. Handedness was confirmed by a test of laterality (Dellatolas et al., 1988).

Imaging

The MR protocol was carried out using at 1.5 T whole-body system using blood oxygen level dependent (BOLD) fMRI. The head of the subject was immobilized using foam cushions and tape. The protocol included: (i) one sagittal TI-weighted image to localize functional and anatomical axial slices; (ii) 20 axial gradient echo echo-planar (EPI) images (5 mm no gap, TR = 3000 ms, TE = 60 ms, bandwidth = 125 kHz, α = 90°, FOV = 240 × 240 mm², matrix size: 64 × 64, in-plane resolution = 3.75 × 3.75 mm²); and (iii) 110 axial contiguous inversion recovery 3-D fast SPGR images (1.5 mm thick, TR = 400 ms, FOV = 240 × 240 mm², matrix size = 256 × 256) for anatomical localization. Images were acquired over 60–90 min.

Tasks

The subjects performed five different tasks: (i) flexion/extension of the fingers of the right hand; (ii) flexion/extension of the fingers of the left hand; (iii) flexion/extension of the toes of the right foot; (iv) contraction of the lips; and (v) saccadic eye movements. Saccadic eye movements consisted in horizontal ocular movements of −20° in the leftward and rightward directions performed in the dark with eyes closed. All movements were self-paced. Specific instructions concerning the movements to be made were given to the subjects immediately before the experiment. Movements were shown to the subjects by the experimenter at a rate of ∼1 Hz, without any explicit instruction given concerning the movement frequency. Before the scan, subjects performed each...
The resulting set of voxel values for each contrast constituted an SPM compared using linear contrasts comparing motor tasks and rest. The hypotheses about regionally specific condition effects, the estimates were applied to filter subject-specific low frequency drift related mostly to differences between runs were also modeled. A temporal cut-off of 120 s was applied to reflect signal equilibrium.

### Coordinates of significant cluster maxima in the group analysis for left and right hands, right foot, lip and eye movements

<table>
<thead>
<tr>
<th>Anatomic area (Brodmann area)</th>
<th>Hemisphere</th>
<th>Right hand movement</th>
<th>Left hand movement</th>
<th>Right foot movement</th>
<th>Lip movement</th>
<th>Saccadic eye movement</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>x</td>
<td>y</td>
<td>z</td>
<td>T-score</td>
<td>x</td>
</tr>
<tr>
<td>Cortical areas</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Inferior frontal area (BA 44/45)</td>
<td>R</td>
<td>54</td>
<td>12</td>
<td>0</td>
<td>6.8</td>
<td>60</td>
</tr>
<tr>
<td>L</td>
<td></td>
<td>-54</td>
<td>9</td>
<td>3</td>
<td>5.6</td>
<td>-51</td>
</tr>
<tr>
<td>Primary sensorimotor area (BA 4)</td>
<td>R</td>
<td>39</td>
<td>-21</td>
<td>69</td>
<td>18.8</td>
<td>60</td>
</tr>
<tr>
<td>L</td>
<td></td>
<td>-38</td>
<td>-18</td>
<td>66</td>
<td>13.7</td>
<td>-3</td>
</tr>
<tr>
<td>Lateral premotor area (BA 6)</td>
<td>R</td>
<td>39</td>
<td>-6</td>
<td>66</td>
<td>14.8</td>
<td>63</td>
</tr>
<tr>
<td>L</td>
<td></td>
<td>-39</td>
<td>-6</td>
<td>57</td>
<td>9.0</td>
<td>-57</td>
</tr>
<tr>
<td>Medial premotor area pre-SMA</td>
<td>R</td>
<td>0</td>
<td>3</td>
<td>51</td>
<td>8.1</td>
<td>6</td>
</tr>
<tr>
<td>L</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Medial premotor area post-SMA</td>
<td>R</td>
<td>3</td>
<td>0</td>
<td>66</td>
<td>9.2</td>
<td>3</td>
</tr>
<tr>
<td>L</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Inferior parietal/SII area (BA 40/43)</td>
<td>R</td>
<td>66</td>
<td>-21</td>
<td>30</td>
<td>5.0</td>
<td>63</td>
</tr>
<tr>
<td>L</td>
<td></td>
<td>-54</td>
<td>-24</td>
<td>21</td>
<td>7.7</td>
<td>-51</td>
</tr>
<tr>
<td>Striatum</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Caudate nucleus</td>
<td>R</td>
<td>18</td>
<td>-3</td>
<td>21</td>
<td>5.3</td>
<td>15</td>
</tr>
<tr>
<td>L</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Anterior part of the putamen</td>
<td>R</td>
<td>30</td>
<td>3</td>
<td>3</td>
<td>3.8</td>
<td>30</td>
</tr>
<tr>
<td>L</td>
<td></td>
<td>-27</td>
<td>9</td>
<td>0</td>
<td>4.6</td>
<td>-24</td>
</tr>
<tr>
<td>Posterior part of the putamen</td>
<td>R</td>
<td>33</td>
<td>0</td>
<td>3</td>
<td>4.4</td>
<td>-3 -3</td>
</tr>
<tr>
<td>L</td>
<td></td>
<td>-30</td>
<td>0</td>
<td>3</td>
<td>5.4</td>
<td></td>
</tr>
<tr>
<td>Ventral striatum</td>
<td>R</td>
<td>30</td>
<td>6</td>
<td>-9</td>
<td>4.6</td>
<td>27</td>
</tr>
<tr>
<td>Thalamus</td>
<td>R</td>
<td>15</td>
<td>-12</td>
<td>6</td>
<td>5.4</td>
<td>12</td>
</tr>
<tr>
<td>L</td>
<td></td>
<td>-12</td>
<td>-15</td>
<td>6</td>
<td>6.0</td>
<td>-6</td>
</tr>
<tr>
<td>Cerebellum</td>
<td>R</td>
<td>18</td>
<td>-45</td>
<td>-18</td>
<td>15.9</td>
<td>12</td>
</tr>
<tr>
<td>L</td>
<td></td>
<td>-15</td>
<td>-45</td>
<td>-18</td>
<td>13.0</td>
<td></td>
</tr>
</tbody>
</table>

Coordinates are in millimeters relative to the anterior commissure, corresponding to the Talairach and Tournoux atlas (Talairach and Tournoux, 1988). Activation differences were considered significant at $P < 0.05$ corrected for multiple comparison inside the volume of the whole brain. For basal ganglia, activation differences were considered significant at $P < 0.001$ and if their spatial extent was $>4$ voxels ($P < 0.05$ corrected for multiple comparison inside the volume of the striatum). L = left; R = right; SMA = supplementary motor area.

Data were corrected for multiple comparisons inside the volume of the whole brain. For basal ganglia, data were first thresholded at $T > 3.09$ ($P < 0.001$). In these thresholded maps, activated clusters were corrected for multiple comparisons inside the volume of the striatum [small volume correction (Worsley et al., 1996)] and considered significant if their spatial extent was $>4$ voxels, corresponding to a $P < 0.05$ corrected. In this case, the small volume correction is valid because the statistical analysis is guided by a very strong anatomical hypothesis, with well-defined and invariant anatomical landmarks across subjects (Worsley et al., 1996). To study the degree of overlap between areas activated during the different movements in the striatum, data were analyzed as a function of the statistical thresholds (from $P = 10^{-6}$ to $P = 10^{-2}$) uncorrected for multiple comparison, as the degree of overlap depends on the statistical threshold used to detect activation. For individual analysis, parametric maps were constructed using the same contrasts and thresholds as for the group analysis.

### Three-dimensional Anatomical Localization in the Basal Ganglia

The 3-D reconstruction of the basal ganglia was obtained using semi-automatic segmentation software based on region growing. Activation maps in the basal ganglia were superimposed on 3-D reconstructions of the normalized images. Overlap between clusters activated in the striatum during the various motor tasks was calculated using dedicated automatic software.

### Results

#### Striatum

**Somatotopic Representation of the Foot, Hand and Face Areas in the Putamen**

In the group analysis ($P < 0.05$, corrected for multiple comparison), activation was contralateral to right finger movements and bilateral for foot and left hand movements (Table 1). Bilateral lip movements were associated with bilateral activation in...
the putamen. Saccadic eye movements were associated with activation in the anterior part of the right putamen. Within the left putamen, pixels activated during movements of the foot were located in the dorsal part of the structure, pixels activated during lips movements were located more ventrally and medially, and pixels activated during hand movements were located in between (Figs 1 and 2). No significant pixel was activated in the left putamen during eye movements. Activation largely predominated at the level of the anterior commissure and in the post-commissural putamen (Figs 1 and 2). Some activated pixels were also found in the pre-commissural putamen.

Overlap was observed between the hand, foot and face areas (Table 2, Fig. 2). Table 2 indicates the variation of the degree of overlap between toe, finger and lip areas as a function of the statistical threshold. As expected, the mean volume of activation varied as a function of the statistical threshold, but was larger for the finger and lip than for toe movements (Table 2). Overlap was limited between the foot and both the hand and face areas, observed at the lowest statistical thresholds, whereas the foot area was completely separated from both the hand and face areas at the highest thresholds. Overlap was more pronounced between the hand and face areas, including about half the activated volume and was still present at the highest statistical thresholds. Distances between centers of mass of the three territories tended to increase slightly with increasing levels of statistical stringency. Except at the lowest statistical threshold of $P < 0.01$, this somatotopic organization tended more to form oblique rather than horizontal bands on coronal sections.

Individual analysis confirmed that activation was mainly contralateral to the moving fingers or toes (Table 3, Fig. 3), whereas activation in the putamen ipsilateral to the moving limb was weaker and smaller. Overall, foot, hand and face activation

![Figure 1](http://cercor.oxfordjournals.org/) Somatotopic body representation in the left striatum during toe (red), finger (light green), lip (dark blue) and eye (yellow) movements (group analysis). Cluster-level activation differences were considered significant at $P < 0.05$ corrected for multiple comparison inside the volume of the striatum. Overlap between territories is represented in light blue. Within the putamen, pixels activated during movements of the foot were located in the dorsal part of the structure, pixels activated during lip movements were located more ventrally and medially, and pixels activated during hand movements were located in between. Abbreviations: Ant, anterior; CN, caudate nucleus; Post, posterior; Pu, putamen.

![Figure 2](http://cercor.oxfordjournals.org/) Variation of the overlap between toe (red), finger (light green) and lip (dark blue) areas in the left putamen as a function of the level of statistical stringency (from $P < 0.01$ to $P < 0.000001$, group analysis). Limited overlap was observed between the foot and both the hand and face areas. Overlap (in light blue) was more pronounced between the hand and face areas and still present at the highest statistical thresholds. Except at the lowest statistical threshold of $P < 0.01$, this somatotopic organization tended to form vertico-oblique bands on coronal sections. Abbreviations: Ant, anterior; L, left; Post, posterior; R, right.

164 Body Representation in Human Striatum • Gerardin et al.
was reproducible across subjects with variability in extent and center of mass. Statistical comparison (signed rank test) of the centers of mass of foot–hand–face activation in the putamen confirmed that the foot area (mean Talairach coordinates ± SD: 27.7 ± 1.0; –1.8 ± 4.9; 8.6 ± 2.3) was located dorsal to the hand (mean Talairach coordinates ± SD: 28.8 ± 1.2; –5.1 ± 9.1; 6.8 ± 1.9) and the face areas (mean Talairach coordinates ± SD: 26.9 ± 1.7; –0.4 ± 4.8; 3.8 ± 2.6) and that the face area was medial and ventral to the hand area (all P-values <0.02). No difference was found in the rostro-caudal axis. Three-dimensional reconstruction in individual subjects of foot, hand and face areas showed that activated areas tended to form discrete zones rather than to be distributed in uniform clusters (Fig. 3).

Ipsi- and Contralateral Representation of Hand Areas in the Putamen
For hand movement, activation was larger in the contralateral than the ipsilateral putamen. Ipsilateral activation was more prominent for the non-dominant than the dominant hand movements (Table 4). In the left putamen, ipsilateral activation tended to be anterior to contralateral activation (Fig. 4). The activated zones of the ipsi- and contralateral hand areas were largely separated with only moderate overlap (11% of the right hand area in the left putamen at P < 0.001). In the right putamen, activation during right hand movement was weak and largely overlapped with activation during left hand movement.

Caudate Nucleus
In the group analysis, the caudate nucleus was not activated
during right hand and foot movements (Table 1). Bilateral activation was observed during saccadic eye movements extending from the head of the caudate into the body of the nucleus (Table 1, Fig. 5). Right caudate activation was also observed during left hand and lip movements (Table 1).

Individual analysis showed that caudate activation was more frequent during saccadic eye movements (five out of seven subjects) than during the other tasks (Table 3).

Activation was also observed in the ventral striatum during left hand and lip movements.

**Signal Intensity Variation**

Signal changes, expressed as the average percent, were slightly lower in the putamen (1.54, 1.89 and 1.67% during finger, lip and toe movements in the left putamen, respectively) than in the primary sensorimotor cortex (1.84, 1.88 and 1.90%...
These findings provide functional evidence for a somatotopic organization of the human striatum similar to that observed in non-human primates, with a foot–hand–face disposition along a dorsolateral to ventromedial gradient and a predominant representation of saccadic eye movements in the caudate nucleus. Overlap between somatotopic territories was present, which may allow interaction between information about different body parts. In the putamen, the activated areas of the ipsi- and contralateral hand areas were not identical, suggesting a partial segregation of the ipsi- and contralateral striatal sensorimotor projections.

**Somatotopic Representation of Foot, Hand and Face in the Putamen**

The ‘foot’ area was located in the dorsal part of the structure, the ‘face’ area was located more ventrally and medially, and the ‘hand’ area was located in between (Figs 1 and 2). Studies in rats (Brown and Sharp, 1995) and primates (Künzle, 1975; Alexander and DeLong, 1985; Liles and Updyke, 1985; Kimura, 1990; Flaherty and Graybiel, 1993; Parent and Hazrati, 1995) have shown a pronounced degree of somatotopic coding in cortico-striatal projections. Anatomical studies of the somatotopic body representation in the striatum using anterograde tracers (Künzle, 1975; Flaherty and Graybiel, 1993) have reported a similar foot–dorsal, face–ventromedial organization, and the arm area between the foot and the face areas. Electrophysiological studies using microstimulation and microelectrode recordings in the putamen have provided similar results (Alexander and DeLong, 1985; Liles and Updyke, 1985; Kimura, 1990, 1992). A more rostral situation of the ‘foot’ area has also been described, but was not found in the present study. However, unlike the somatotopic maps of the sensorimotor cortex, striatal projections from different body parts of the primary sensorimotor cortex seem to be distributed in patches in the matrix, with a confluent dense ‘main field’ and fainter satellite zones (Flaherty and Graybiel, 1993). This pattern has been compared with the fractured somatotopy described in the cerebellum with multiple patchy representation of body parts. This raises the question of whether such an organization is specific to the squirrel monkey and related to its different locomotor behavior (Flaherty and Graybiel, 1993), or whether it is common across species and represents a characteristic of striatal somatotopy.

In humans, the present results confirm our preliminary study at 3 T for foot and hand representation (Lehéry et al., 1998). More recently, a triangular pattern has been reported in the putamen, with the face medial to foot and hand representation (Maillard et al., 2000). The present study is more in favor of somatotopic pattern in vertico-oblique bands on coronal sections, with the ‘face’ area more ventral and medial and the foot more dorsal and lateral (Fig. 2), in agreement with animal studies (Alexander and Crutcher, 1990; Brown and Sharp, 1995). Centers of mass distances between territories tended to be higher in the present study than previously reported (Maillard et al., 2000). The currently limited spatial resolution of fMRI studies may account for these differences between studies. Individual analysis suggested that activated areas were not distributed uniformly, but rather tended to appear as discrete zones reminiscent of the patchy distribution observed in primates. It remains to be determined whether this organization reflects the presence of a single discontinuous body map or of separate functionally differentiated body maps in the putamen (Flaherty and Graybiel, 1993). Given the limited spatial resolution of conventional magnets compared to histological studies, this patchy distribution needs to be confirmed at higher spatial resolution. Studies at very high field strength may help elucidate during finger, lip and toe movements in the left hemisphere, respectively).

Signal changes were 1.80% in the caudate nucleus and 1.85% in the frontal eye field (FEF) during eye movements.

**Thalamus**

Activation was observed in the ventrolateral–ventral posterolateral areas of the thalamus (comprising the somatosensory, cerebellar and pallidal afferent territories of the thalamus), contralateral to the moving hand or foot and bilaterally during lip and eye movements (Table 1).

**Cortex**

For hand, foot and lip movements, activation was observed in the primary sensorimotor cortex, premotor cortex, supplementary motor area, inferior frontal area (BA44/45), secondary somatosensory area (SII) and cerebellum (Table 1). In the primary sensorimotor cortex, activation was always contralateral to the moving fingers or toes (Table 3). Bilateral activation was observed in the inferior frontal area and SII (Tables 1 and 3). For saccadic eye movements, activation was observed in the FEF and supplementary eye field (SEF; Tables 1 and 3).

**Discussion**

These findings provide functional evidence for a somatotopic organization of the human striatum similar to that observed in non-human primates, with a foot–hand–face disposition along a dorsolateral to ventromedial gradient and a predominant representation of saccadic eye movements in the caudate nucleus. Overlap between somatotopic territories was present, which may allow interaction between information about different body parts. In the putamen, the activated areas of the ipsi- and contralateral hand areas were not identical, suggesting a partial segregation of the ipsi- and contralateral striatal sensorimotor projections.

**Somatotopic Representation of Foot, Hand and Face in the Putamen**

The ‘foot’ area was located in the dorsal part of the structure, the ‘face’ area was located more ventrally and medially, and the ‘hand’ area was located in between (Figs 1 and 2). Studies in rats (Brown and Sharp, 1995) and primates (Künzle, 1975; Alexander and DeLong, 1985; Liles and Updyke, 1985; Kimura, 1990; Flaherty and Graybiel, 1993; Parent and Hazrati, 1995) have shown a pronounced degree of somatotopic coding in cortico-striatal projections. Anatomical studies of the somatotopic body representation in the striatum using anterograde tracers (Künzle, 1975; Flaherty and Graybiel, 1993) have reported a similar foot–dorsal, face–ventromedial organization, and the arm area between the foot and the face areas. Electrophysiological studies using microstimulation and microelectrode recordings in the putamen have provided similar results (Alexander and DeLong, 1985; Liles and Updyke, 1985; Kimura, 1990, 1992). A more rostral situation of the ‘foot’ area has also been described, but was not found in the present study. However, unlike the somatotopic maps of the sensorimotor cortex, striatal projections from different body parts of the primary sensorimotor cortex seem to be distributed in patches in the matrix, with a confluent dense ‘main field’ and fainter satellite zones (Flaherty and Graybiel, 1993). This pattern has been compared with the fractured somatotopy described in the cerebellum with multiple patchy representation of body parts. This raises the question of whether such an organization is specific to the squirrel monkey and related to its different locomotor behavior (Flaherty and Graybiel, 1993), or whether it is common across species and represents a characteristic of striatal somatotopy.

In humans, the present results confirm our preliminary study at 3 T for foot and hand representation (Lehéry et al., 1998). More recently, a triangular pattern has been reported in the putamen, with the face medial to foot and hand representation (Maillard et al., 2000). The present study is more in favor of somatotopic pattern in vertico-oblique bands on coronal sections, with the ‘face’ area more ventral and medial and the foot more dorsal and lateral (Fig. 2), in agreement with animal studies (Alexander and Crutcher, 1990; Brown and Sharp, 1995). Centers of mass distances between territories tended to be higher in the present study than previously reported (Maillard et al., 2000). The currently limited spatial resolution of fMRI studies may account for these differences between studies. Individual analysis suggested that activated areas were not distributed uniformly, but rather tended to appear as discrete zones reminiscent of the patchy distribution observed in primates. It remains to be determined whether this organization reflects the presence of a single discontinuous body map or of separate functionally differentiated body maps in the putamen (Flaherty and Graybiel, 1993). Given the limited spatial resolution of conventional magnets compared to histological studies, this patchy distribution needs to be confirmed at higher spatial resolution. Studies at very high field strength may help elucidate during finger, lip and toe movements in the left hemisphere, respectively).

Signal changes were 1.80% in the caudate nucleus and 1.85% in the frontal eye field (FEF) during eye movements.

**Thalamus**

Activation was observed in the ventrolateral–ventral posterolateral areas of the thalamus (comprising the somatosensory, cerebellar and pallidal afferent territories of the thalamus), contralateral to the moving hand or foot and bilaterally during lip and eye movements (Table 1).

**Cortex**

For hand, foot and lip movements, activation was observed in the primary sensorimotor cortex, premotor cortex, supplementary motor area, inferior frontal area (BA44/45), secondary somatosensory area (SII) and cerebellum (Table 1). In the primary sensorimotor cortex, activation was always contralateral to the moving fingers or toes (Table 3). Bilateral activation was observed in the inferior frontal area and SII (Tables 1 and 3). For saccadic eye movements, activation was observed in the FEF and supplementary eye field (SEF; Tables 1 and 3).

**Discussion**

These findings provide functional evidence for a somatotopic
this point (Yacoub et al., 2001). Furthermore, very high field
MRI may also provide information on other smaller basal ganglia
nuclei, such as the pallidum, the subthalamic nucleus and the
substantia nigra, which are not yet accessible to conventional
magnets.

Segregation or Convergence of Sensorimotor Areas

Overlap between somatotopic territories is a matter of debate: it
may be limited (Lehéricy et al., 1998) or more prominent
(Maillard et al., 2000). Overlap between distant cortical terri-
tories in the putamen may have functional significance in
allowing interaction between information about different body
parts. Using fMRI, the degree of overlap depends on several
factors, such as the spatial resolution of functional images, data
processing, which often includes image spatial filtering, field
strength and the statistical threshold used to detect activation.

Results in the present studies show that overlap between foot,
hand and lip territories was only partial, mainly observed at the
periphery of each territory. Overlap was limited between the
‘foot’ and the other two territories and larger between the ‘hand’
and ‘face’ territories. This fits well with animal data. In monkeys,
although overlap was uncommon for the dense ‘main field’ of
distant somatotopic zones, it was the rule for the fainter satellite
zones surrounding these dense zones, even for body parts as
distant as foot and hand (Flaherty and Graybiel, 1993).

Ipsi- versus Contralateral Representation of Hand Areas
in the Putamen

In contrast to the primary sensorimotor cortex, in which
activation was always contralateral to the moving fingers or toes,
activation in the putamen was bilateral for unilateral hand and
foot movement, confirming previous reports (Scholz et al.,
2000). For hand movement, activation was larger in the
contralateral than the ipsilateral putamen. Although motor
cortical areas project mainly to ipsilateral subcortical structures,
a substantial fraction of these connections also project contra-
laterally via the corpus callosum (Wiesendanger et al., 1996).

In monkeys, the primary sensorimotor cortex sends a modest con-
tralateral projection (Flaherty and Graybiel, 1993; Wiesendanger
et al., 1996), whereas the SMA sends nearly symmetric bilateral
projections (McGuire et al., 1991; Wiesendanger et al., 1996).
Similarly, pallido-thalamic projections are known to be bilateral
(Hazrati and Parent, 1991). These bilateral projections probably
represent the anatomical substrate of bilateral striatal activation.

In monkeys, contra- and ipsilateral hand projections formed
distinguishable input system in the putamen, largely avoiding
each other (Flaherty and Graybiel, 1993). This organization
suggests that the putamen segregate motor information about the
ipsilateral and contralateral distal part of the body (Flaherty
and Graybiel, 1993). The present results are consistent with
animal data (Flaherty and Graybiel, 1993), as the projection
zones of the ipsi- and contralateral hand areas in the left putamen
were largely separated, with only moderate overlap. However,
ipsilateral activation tended to be anterior to contralateral acti-
vation, in contrast to non-human primates in which projections
were at approximately the same antero-posterior levels (Flaherty
and Graybiel, 1993). This may be due to the concomitant
activation of the SMA territory in the putamen, which has been
located more rostrally than the primary sensorimotor territory in
monkeys (Selemon and Goldman-Rakic, 1985).

Thalamic activation was only observed in the hemisphere
contralateral to the moving hand and foot. Thus, information
related to unilateral limb movement may be conveyed through the
basal ganglia in both hemispheres and converge to the
contralateral thalamus. This point needs to be confirmed,
however.

Saccadic Eye Movement and Caudate Nucleus Activation

Saccadic eye movements were associated with bilateral acti-
vation in the caudate nucleus. Caudate nucleus activation was
more specifically observed during saccadic eye movements,
wheresas caudate activation was rarely observed during the other
tasks. Caudate nucleus activation extended from the head of
the caudate well into the body of the nucleus, predominat-
ing at the same coronal level of the anterior pole of the thal-
amus. Activation in the right putamen, also observed during
saccadic eye movements, was located nearby right caudate
activation (Fig. 4). These data are in agreement with non-human
primate studies (Künzle and Akert, 1977; Shook et al., 1991;
Parthasarathy et al., 1992). Anatomical studies showed that the
FEF and SEF projected principally to the caudate nucleus and
adjoining parts of the putamen. Within the caudate nucleus, the
projection field of these two regions was located at the coronal
level of the rostral pole of the thalamus (Künzle and Akert, 1977);
or extended from the level of the anterior pole of the putamen
to the posterior body of the caudate nucleus (Shook et al.,
1991; Parthasarathy et al., 1992). In contrast to these studies, the
anterior part of the caudate nucleus, which also receives SEF and
FEF projections, was not activated. Electrophysiological studies
in primates have suggested that neurons in more rostral parts of
the caudate nucleus were activated during tasks which require
higher-order processes than simple saccadic eye movements
(likosaka et al., 1989). In humans, a previous fMRI study has
reported a predominance of caudate activation during saccadic
eye movements, without further precision on the localization
(Scholz et al., 2000).

Cortico-subcortical Loop

Motor-related activation occurred mainly in the putamen at the
level of the anterior commissure and in the post-commissural
putamen. This area corresponds to the sensorimotor territory of
the striatum in primates, the major target of cortical efferents
from the primary motor and somatosensory cortices (Künzle,
1975; Alexander and DeLong, 1985; Liles and Updyke, 1985;
Alexander and Crutcher, 1990; Kimura, 1990; Flaherty and
Graybiel, 1993; Brown and Sharp, 1995; Parent and Hazrati,
1995). In positron emission tomography (PET) and fMRI studies,
Talairach coordinates of peak activation in the putamen during
simple finger movements, such as a highly practiced sequence
(Jenkins et al., 1994), a repetitive movement of the middle finger
(Jueptner et al., 1997), or flexion/extension of all fingers
(Lehéricy et al., 1998), were similar to those observed in the
present study. The same applies for foot movement: –27, –6, 11
(Lehéricy et al., 1998) compared with –30, 0, 9 in the present
study. Small interstudy variation may be due the limited spatial
resolution of functional images and to differences in data
analysis. In these tasks and in the present tasks, cortical acti-
vation was mainly restricted to the motor cortex, the posterior
SMA and the cerebellum. However, when subjects learned a new
sequence of finger movements with additional cognitive demand
(Jenkins et al., 1994; Jueptner et al., 1997), generated a random
sequence of finger movements making a new decision on each trial as to which finger to move (Jueptner et al., 1997), or
imagined hand movements (Gerardin et al., 2000), more anterior
parts of the striatum were activated (caudate nucleus and
putamen rostral to the anterior commissure), as well as pre-
frontal cortex and the anterior cingulate area. Thus, the differ-
ent territories of the basal ganglia may be activated during
movements in relation to specific cortical areas corresponding to the cortico-basal ganglia-thalamo-cortical loops described in monkeys (Alexander and Crutcher, 1990; Parent and Hazrati, 1995).

In summary, these results show the 3-D somatotopic organization of the human striatum, confirming the foot–hand–face disposition along a dorsal to ventromedial gradient in the putamen. Overlap between somatotopic territories was present, although variable, depending on the level of statistical stringency. This overlap may allow interaction between information about different body parts. Comparison between the projection zones of the ipsi- and contralateral hand areas in the left putamen suggested that they were not identical, as described in primates. Saccadic eye movements were more specifically associated with caudate nucleus activation, in line with animal studies.

Notes
This research was supported by grants from the Délégation à la Recherche Clinique (DRC) and the Assistance Publique-Hôpitaux de Paris (CRC 96067).

Address correspondence to Dr Stéphane Lehéricy, Service de Neuroradiologie, Bâtiment Babinski, Hôpital de la Salpêtrière, 47 Bd de l’Hôpital, 75651 Paris Cedex, France. Email: stephane.lehericy@psl.ap-hop-paris.fr.

References


