Somatosensory Processing in the Human Inferior Prefrontal Cortex

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INTRODUCTION

Anatomical evidence indicates that several areas of the inferior prefrontal cortex receive afferents from the somatosensory system. However, the location of these regions in humans remains largely unexplored, and little information addresses the nature of their functional contribution to somatosensory processing. Three inferior prefrontal regions in monkeys possess afferents that might allow them to process or utilize somatosensory information: the orbitofrontal cortex (OFC), an area in or near the rostral extremity of the banks of the frontal operculum, and ventrolateral prefrontal cortex.

Anatomical tracing studies in nonhuman primates indicate that the OFC receives somatosensory projections from a portion of S1 (areas 1, 2), SII, and posterior insula and from area 7b in the parietal lobe (Barbas 1988; Carmichael and Price 1995; Cavada and Goldman-Rakic 1989; Morecraft et al. 1992). These projections primarily provide input to the frontal operculum, near the junction of the operculum and ventrolateral prefrontal cortex. The costs of publication of this article were defrayed in part by the payment of page charges. The authors therefore hereby state that "advertisement" in accordance with 18 U.S.C. Section 1734 solely to indicate this fact.

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1989a). Moreover, it appears to receive input from parietal area 7b (Petrides and Pandya 1984). Although uncertainty exists regarding the specific location of the homologous region in humans, it likely occupies an area near the junction of the frontal operculum and inferior frontal gyrus. Using both MEG and fMRI, Korvenoja et al. (1999) reported activation near this juncture in humans during median nerve stimulation. Activations also localized to the inferior frontal gyrus/frontal operculum region during tickling (Carlsson et al. 2000) and histamine-induced itch (Darsow et al. 2000), suggesting an affective aspect to somatosensory processing in this area. However, data on the region’s response to simple tactile stimulation remain lacking.

The third prefrontal area that may process somatosensory information falls in the ventral area of the principle sulcus (ventral area 46) in the macaque. This region receives extensive projections from SII, with additional projections arising from S1, area 7b, and the ventral frontal opercular region described above (Cipolloni and Pandya 1999; Petrides and Pandya 1984; Preuss and Goldman-Rakic 1989b). Electrophysiological study in monkeys suggests that this region participates in working memory for tactile stimuli (Romo et al. 1999). However, the role of the homologous region in tactile processing in humans is unknown. In an effort to determine the involvement of human ventral frontal regions in somatosensory processing, we analyzed data from an ongoing series of PET studies of somatosensory processing.

**STUDY 1**

**Methods**

Thirty-three individuals (18 males, 15 females) participated in Study 1. Thirty were right-handed, two were left-handed, and one was ambidextrous. The mean age of the subjects was 38 ± 15 yr. An additional 10 right-handed subjects (4 males, 6 females; mean age 35 yr) participated in a small experiment outside of the scanner to assess the subjective evaluation of the stimulus used in this study. All subjects gave written informed consent, as approved by Minneapolis VA Medical Center Institutional Review Board.

For the stimulation paradigm, subjects lay with eyes closed while tactile stimulation was administered by manually applying a repetitive (approximately 2–3 Hz) tap with a suprathreshold, 5.46 caliber von Frey hair (applying a force of 82 g/mm²) (Levin et al. 1978) at one of four stimulation sites (right index finger, right great toe, left index finger, left great toe). Subjects were instructed to count the number of pauses in the tactile stimulation; 0–3 pauses were administered prior to injection of the isotope or following scan acquisition. No pause in tactile stimulation was provided during the period of scan. Each subject participated in stimulation of one or more sites (see Table 1 for demographics by stimulation site). Under the control condition, subjects lay resting with their eyes closed (ECR) with no somatosensory stimulation.

**Table 1. Subject demographics by stimulation site (Study 1)**

<table>
<thead>
<tr>
<th>Stimulation Site</th>
<th>N</th>
<th>Male</th>
<th>Female</th>
<th>Right-Handed</th>
<th>Left-Handed</th>
<th>Ambidextrous</th>
<th>Age (yr)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Right finger</td>
<td>18</td>
<td>11</td>
<td>7</td>
<td>2</td>
<td>1</td>
<td>37 ± 12</td>
<td></td>
</tr>
<tr>
<td>Right toe</td>
<td>13</td>
<td>9</td>
<td>4</td>
<td>1</td>
<td>1</td>
<td>34 ± 14</td>
<td></td>
</tr>
<tr>
<td>Left finger</td>
<td>12</td>
<td>6</td>
<td>6</td>
<td>1</td>
<td>1</td>
<td>39 ± 13</td>
<td></td>
</tr>
<tr>
<td>Left toe</td>
<td>23</td>
<td>14</td>
<td>9</td>
<td>22</td>
<td>1</td>
<td>39 ± 16</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>33</td>
<td>18</td>
<td>15</td>
<td>30</td>
<td>2</td>
<td>38 ± 15</td>
<td></td>
</tr>
</tbody>
</table>

Ages are means ± SD.

To assess the subjective evaluation of the stimulus, 10 subjects were given the same stimulation and instructions as were delivered during the scanning sessions. All subjects were first stimulated on the toe, since the likelihood of rating the stimulus negatively appeared greatest at this site. Following the session of toe stimulation, subjects were asked to rate the pleasantness/unpleasantness of the stimulus using a Likert scale: 1 (very unpleasant), 2 (moderately unpleasant), 3 (mildly unpleasant), 4 (neutral), 5 (mildly pleasant), 6 (moderately pleasant), and 7 (very pleasant). Subjects were asked to use the same scale to rate the stimulus when it was applied to the finger.

**PET imaging and analysis**

Regional cerebral blood flow (rCBF) was estimated from normalized tissue activity (with measured attenuation correction) using an ECAT 953B camera (Siemens, Knoxville, TN) in 2D mode. Each subject was administered an intravenous bolus infusion of 40 mCi H215O. Activity was integrated for 1 min after H215O reached the brain. Automatic software (Minoshima et al. 1994) aligned images to the AC-PC line and applied nonlinear warping to Talairach space (Talairach and Tournoux 1988). The resultant images were smoothed to a final image resolution of 10-mm full-width at half-maximum. We omitted scan pairs that demonstrated movement of more than 2 mm or rotation of greater than 2 deg, relative to the first emission scan. A Z-score of 3.3, roughly corresponding to a P value of <0.0005, served as the threshold for statistical significance. The rationale for this value stems from a bootstrap analysis of 50 ECR scans in which on average less than one focus emerged due to chance when applying this threshold (Zald et al. 1998).

Additionally, we performed a reproducibility analysis to determine the convergence of the results across conditions. This analysis employed a simple logistic recoding of the data such that the Z-score map for each contrast was converted to a binary map of pixels with Z-score >2.5 set to 1 and <2.5 set to 0. The four binary maps were then summed, to produce a map containing values of 0–4 indicating the number of contrasts showing a significant increase at each pixel.

Functional images were overlaid on a model T1-weighted anatomical MRI that was spatially warped to the Talairach template. The three-dimensional surface projections were obtained using mri3dX [K. Singh, Aston University, UK (http://www-users.Aston.ac.uk/~singhkd/mri3dX/)]. Cross-sectional figures were produced using iiV [CNU, Minneapolis VAMC (http://james.psych.umn.edu/iiV.html); Lee and Pardo 2000].

**Results**

Table 2 displays the Talairach coordinates for ventral frontal activations arising during somatosensory stimulation. In each of the four stimulation conditions (vs. ECR) significant rCBF increases localized to the ventral frontal lobe (Fig. 1). Two sectors of the ventral frontal lobe accounted for most of these foci. A large area that encompassed the posterior-most portions of the inferior frontal gyrus (IFG) (pars orbitalis and triangularis) and the underlying frontal operculum (including both the superior and the ventral rims of the frontal operculum) appears as the more lateral focus in Fig. 1 and in the coronal and axial slices in Fig. 2. This area showed consistent activity in the right hemisphere, as can be seen in the reproducibility map pre-
sented in Fig. 3. In contrast, the left hemisphere equivalent only reached statistical significance in one comparison.

A second strong area of activation localized to the OFC. In all cases the activation included the right anterior orbital gyrus and the neighboring lateral orbital gyrus (Figs. 1 and 3). Additional activations arose in other sectors of the right and left OFC, but without as much consistency. The data did not provide consistent evidence for the involvement of an area equivalent to the ventral principal sulcus in monkeys. Specifically, a prominent focus emerged in the middle frontal gyrus

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**TABLE 2. Ventral frontal activations with tactile stimulation vs. ECR (Study 1)**

<table>
<thead>
<tr>
<th>Stimulation Site</th>
<th>n</th>
<th>Topographical Location</th>
<th>Hemi- Brodmann Area</th>
<th>x</th>
<th>y</th>
<th>z</th>
<th>Z</th>
</tr>
</thead>
<tbody>
<tr>
<td>Right finger</td>
<td>18</td>
<td>IFG (triangularis)/frontal operculum</td>
<td>R</td>
<td>45</td>
<td>35</td>
<td>26</td>
<td>-4</td>
</tr>
<tr>
<td></td>
<td></td>
<td>IFG (triangularis)</td>
<td>R</td>
<td>45</td>
<td>39</td>
<td>39</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Middle frontal gyrus</td>
<td>R</td>
<td>46</td>
<td>44</td>
<td>44</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Anterior/lateral orbital gyrus</td>
<td>R</td>
<td>11, 47/12</td>
<td>33</td>
<td>41</td>
<td>-14</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Anterior orbital gyrus</td>
<td>L</td>
<td>10, 47/12</td>
<td>-33</td>
<td>53</td>
<td>-11</td>
</tr>
<tr>
<td>Right toe</td>
<td>13</td>
<td>IFG (triangularis) frontal operculum</td>
<td>R</td>
<td>45</td>
<td>42</td>
<td>21</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Basal operculum/IFG (orbitalis)</td>
<td>R</td>
<td>47/12</td>
<td>30</td>
<td>23</td>
<td>-4</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Posterior/medial orbital gyrus</td>
<td>R</td>
<td>13, 47/12</td>
<td>21</td>
<td>21</td>
<td>-20</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Anterior orbital gyrus</td>
<td>L</td>
<td>10, 47/12</td>
<td>-30</td>
<td>53</td>
<td>-11</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Posterior/medial orbital gyrus</td>
<td>R</td>
<td>13</td>
<td>21</td>
<td>30</td>
<td>-18</td>
</tr>
<tr>
<td>Left finger</td>
<td>12</td>
<td>IFG (orbitalis/triangularis)</td>
<td>R</td>
<td>45, 47/12</td>
<td>42</td>
<td>23</td>
<td>-2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Anterior/lateral orbital gyrus</td>
<td>R</td>
<td>11, 47/12</td>
<td>37</td>
<td>44</td>
<td>-9</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Anterior orbital gyrus/frontal pole</td>
<td>L</td>
<td>10, 47/12</td>
<td>-39</td>
<td>50</td>
<td>-7</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Frontal pole</td>
<td>R</td>
<td>10</td>
<td>30</td>
<td>53</td>
<td>0</td>
</tr>
<tr>
<td>Left toe</td>
<td>23</td>
<td>Medial orbital gyrus</td>
<td>R</td>
<td>11m</td>
<td>17</td>
<td>39</td>
<td>-18</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Medial orbital gyrus</td>
<td>R</td>
<td>11m</td>
<td>15</td>
<td>37</td>
<td>-22</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Anterior orbital gyrus</td>
<td>R</td>
<td>11</td>
<td>28</td>
<td>46</td>
<td>-14</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Basal operculum/IFG</td>
<td>R</td>
<td>45, 47/12</td>
<td>33</td>
<td>19</td>
<td>2</td>
</tr>
</tbody>
</table>

The labeling of orbital frontal gyri follows the nomenclature and probability maps of Chiavaras et al. (2001). Brodmann labeling follows the conventions of Petrides and Pandya (1994), except the boundary between 47/12 and 11 is treated with a degree of uncertainty, because recent work by Ongur and Price (2000) suggests that the boundary between this area lies far more medial than indicated by Petrides and Pandya. We also adopted the term 11m to indicate the portion of area 11 lying in the medial orbital gyrus.

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**FIG. 1.** Surface renderings of the ventral surface of the brain displaying the contrasts between attending to somatosensory stimulation vs. resting with eyes closed. In all conditions activity localizes to the anterior orbitofrontal cortex (OFC) (green arrow) and the posterior ventrolateral surface (blue arrow).

**FIG. 2.** Coronal and axial slices displaying the location of the focus in the inferior frontal gyrus (triangularis/orbitalis) and underlying operculum. Note, in the axial slice for the right finger condition, an area of activity can also be seen in the right middle frontal gyrus (an area that may be equivalent to the ventral principal sulcus region in monkeys). These slices make evident the relatively medial (opercular) nature of the inferior frontal gyrus (IFG) opercular foci. This cannot be seen as clearly in the surface renderings, which only show areas of activation close to the surface of the brain.
during stimulation of the right finger, but not during other conditions. rCBF increases also emerged in nonfrontal brain regions, but this will be the subject of another article.

In the subjective evaluation of the stimulus, 9 of the 10 subjects rated the tactile stimulation of the toe as neutral. One subject found it mildly unpleasant. Eight of the nine subjects rating the stimulus as neutral for the toe also found it similarly neutral for the finger. One subject found the finger stimulation mildly unpleasant, although they rated the toe stimulation as neutral. The individual that found it mildly unpleasant on the toe rated the stimulation of the finger as neutral.

**STUDY 2**

While Study 1 indicates that rCBF increases in areas of the ventral frontal lobe during somatosensory stimulation, it remains unclear what cognitive or perceptual processes are associated with these increases. These activations could, for instance, reflect a passive sensory representation, a general attentional process (unrelated to a specific sensory modality), or a more modality-specific sensory process. To at least partially clarify these issues, we analyzed data from a second study, which employed an intermodal attention task. In both conditions subjects viewed a fixation point and received somatosensory stimulation. In one condition subjects were instructed to attend to the somatosensory dimension while in the other condition they attended to the visual dimension. Because the actual sensory stimulation was identical across conditions, differences in activation between conditions likely reflect modality-specific processing. In contrast, passive sensory representations or more general attentional factors (unrelated to a specific sensory modality) should largely cancel out in this experiment.

**Methods**

Thirteen healthy, right-handed individuals (8 males, 5 females) participated in Study 2. All subjects gave written informed consent, as approved by Minneapolis VA Medical Center Institutional Review Board. Subjects were instructed to fixate continuously on a 1 × 1 cm crosshair against a black background that was displayed on a 38-cm computer monitor placed 43 cm in front of their eyes. Concomitantly, tactile stimulation was administered by manually applying a repetitive von Frey hair (3–5 Hz) at one of two stimulation sites (right index finger and right great toe). During each stimulation event, the subject performed under one of two attentional conditions. In the first condition (attend somatosensory/passive fixation), the subject was instructed to count the number of pauses in the tactile stimulation and to passively fixate on the central fixation point. In the second condition (attend visual/ignore somatosensory), the subject was instructed to count the number of times the luminance of the central fixation point dimmed and to ignore the somatosensory stimulus. No pause in tactile stimulation or change in the luminance of the fixation point occurred under either condition during scan acquisition. Thus subjects received the same absolute amount of sensory stimulation under both conditions; the difference lay in the sensory modality to which the subject attended. Each subject performed one attend somatosensory/passive fixation and one attend visual/ignore somatosensory condition at each of the two stimulation sites. The conditions were administered in a pseudo-random counter-balanced order.

**PET imaging and analysis**

Imaging parameters and image processing were identical to Study 1. Since the primary aim of this second study was to elucidate the features of areas showing activation in the first study, we utilized a region of interest (ROI) analysis on two locations: right IFG pars triangularis/operculum (x = 39, y = 19, z = 4) and the right OFC (x = 33, y = 44, z = −12). Spherical ROIs (12 mm diameter) were placed at the center of the area of overlap across stimulation conditions, as seen in the reproducibility map in Study 1. A paired, two-tailed, t-test was performed on the mean normalized rCBF within each ROI to assess differences in these regions while attention is directed to the tactile or the visual stimulus.

To examine the frontal cortex for other changes in activity, a pixel-wise subtraction was performed. For ease of reporting, we performed a combined analysis in which the two stimulation sites were paired together (i.e., a single analysis is reported which included both the attend finger and the attend toe conditions and their corresponding attend visual/ignore somatosensory conditions).

**Results**

The ROI located in the right IFG pars triangularis/operculum showed a significant increase in rCBF [$t(12) = 3.21, P = 0.0075$] with attention to the somatosensory stimulus when compared with attending to the visual stimulus. The ROI in the OFC showed a slight, though nonsignificant [$t(12) = 0.98, P = 0.35$] increase in rCBF with attention to the visual stimulus.

In the pixel-wise analysis, the contrast of attending to somatosensory stimulation/passive fixation versus attend vision/ignore somatosensory produced a significant activation of the right IFG pars triangularis near its border with the opercularis portion of the IFG (x = 42, y = 17, z = 7; Z-score = 3.2). These coordinates overlap with the IFG area identified in the contrast between somatosensory stimulation and ECR in Study 1. As displayed in Fig. 4, this represents a smaller area of activation than was seen in Study 1. Nevertheless, the results indicate that attention significantly influences the response to somatosensory stimulation in this region. A similar activation...
emerged in the homologous area in the left hemisphere \((x = 37, y = 17, z = 4, Z\text{-score} = 3.0)\). In contrast, rCBF increases in the right OFC, and middle frontal gyrus regions identified in Study 1 did not demonstrate significantly different activations across conditions.

**DISCUSSION**

These data provide evidence for at least two discrete ventral frontal brain regions that respond to somatosensory stimulation: posterior IFG/frontal operculum and anterior OFC. Contrasts between somatosensory stimulation and resting with eyes closed produced consistent activations in these regions regardless of the site and side of stimulation. Although there are some differences in the specific locations of peak significance, the overall pattern of activity shows strong convergence across stimulation conditions (Fig. 3).

It would be difficult to attribute any functional significance to slight differences in the coordinates of an activation peak between stimulation conditions. Several factors could contribute to the specific pattern of rCBF change. Most likely, since the individuals used in the first study only partially overlapped across conditions, individual differences could have influenced the specific pattern of activity resulting from tactile stimulation. Another potential factor is differences in the statistical power of each comparison. The number of subjects differed for each of the contrasts in the first study (Table 1), leading to a greater statistical power for some conditions. However, reducing the group size in these conditions (right finger and left toe) only affected the absolute statistical significance, having little effect on the localization and number of significant foci for these contrasts. A third potential factor is a difference in receptor densities in the finger and toe, which could influence changes in rCBF with stimulation. However, the stimulus strength was at a level easily detected at both the finger and the toe and the level of activity in the frontal cortex was similar between stimulation sites. Sensitivity of the skin at these locations does not appear to impact these results in the ventral frontal cortex.

In the first study, the largest ventral frontal area of activation involves the posterior IFG and underlying anterior frontal opercular region. The involvement of this area in somatosensory processing is consistent with the existing, albeit limited, data on the neural connections of the anatomically similar area in monkeys. Although the nature of the processing in this region cannot be fully determined from this study, this area of the posterior IFG appears to have a role in selective attention to touch. In the second study, subjects showed significantly greater activation under the “attend somatosensory” condition than under the “attend visual” condition. Since stimulation was identical between conditions, the modulation in activity cannot simply reflect a passive representation of touch.

It may be argued that attending to one modality or the other required greater vigilance, which could lead to the greater activation in posterior IFG. This region might then represent a more generalized attention area. Regions of the IFG have shown increased activity with selective attention to several sensory modalities (Hopfinger et al. 2000; Pardo et al. 1991; Pugh et al. 1996). Although the study design did not include performance measures to stringently assess task difficulty, activity in other cortical areas support the similarity in attentive demands between tasks. Specifically, attention to either modality showed comparable levels of rCBF in the supramarginal gyrus of the parietal lobe and dorsolateral frontal cortex, which are commonly associated with directed attention (Hopfinger et al. 2000; Kim et al. 1999; Pardo et al. 1991; Pugh et al. 1996). Assuming a comparable level of vigilance in the two conditions, the second study supports a role for the posterior IFG/frontal operculum in some aspect of selectively attending to touch.

The strongest and most consistent OFC focus localized to the anterior orbital gyrus, with additional activations falling in the medial orbital gyrus. The anterior orbital gyrus region is homologous to area 12m in monkeys, which is known to possess somatosensory input. Interestingly, this area responded substantially to both finger and toe stimulations (Study 1), whereas previous discussions of possible somatosensory projections have primarily focused on possible representations of the digits of the hand and orofacial regions (Carmichael and Price 1995; Preuss and Goldman-Rakic 1989a). Such discussions reflect the strong digital and orofacial representations in the areas projecting to the OFC. However, given the multiple routes through which the OFC receives somatosensory information, it is conceivable that this input includes representations that extend beyond the hand and face.

Previous neuroimaging studies have not typically observed OFC activity during somatosensory tasks except when the stimuli possessed strong hedonic properties. In some cases this may reflect a limited field of view or the problems associated with magnetic inhomogeneity in this region (Ojemann et al. 1997). Nevertheless, the absence of OFC responses in many other neuroimaging studies remains unclear. Studies observing...
OFC responses include hedonically valenced tactile stimuli (Francis et al. 1999), thermosensation (Coghill et al. 2001; Craig et al. 2000), and pain perception (Coghill et al. 2001; Petrovic et al. 2000; Peyron et al. 1999). In each of these works an argument may be made that hedonic (pleasantness-unpleasantness) features of the stimuli contributed to the engagement of the OFC. Although no measure of potential hedonic properties of the stimulus was made during the time of scanning, an investigation of the subjective responses was performed in a separate group of subjects. This study revealed that nearly every subject (9 of 10 for each location) rated the stimulus as neutral, neither pleasant nor unpleasant. The exceptions, one case for each the finger and toe, rated the stimulus as mildly unpleasant. This supports the finding that the stimuli in the present study lacked a strong hedonic meaning, suggesting that the OFC’s participation in somatosensory processing may extend beyond an isolated role in hedonic coding. Of note, OFC lesions in both monkeys and humans produce deficits in somatosensory tasks (Passingham and Ettlinger 1972; Roland 1987). Such deficits have typically been attributed to attentional or other nonspecific factors. However, in the present study, we found no evidence that the OFC activations were specifically dependent on directing attention to the somatosensory modality. It also appears unlikely that the activation is related to a general nonspecific attentional factor, since the OFC does not routinely activate in other attention demanding tasks or in tasks subtracting resting states from active states (Raichle et al. 2001). Future studies will hopefully better characterize the nature of somatosensory processing in this region.

We found only partial support for the engagement of the ventrolateral cortex corresponding to the inferior principal sulcus region in the monkey. This area (middle frontal gyrus) showed activation in the right hemisphere during stimulation of the right finger, but not other conditions. The lack of a response to toe stimulation may be interpreted in light of anatomical data emphasizing digits and orofacial representations in the afferent projection to this region. However, the absence of responses to left finger stimulation remains puzzling (see next paragraph). More robust engagement of this area may be restricted to tasks involving specific cognitive components, such as working memory (Romot et al. 1999). Thus investigation of its participation in somatosensory processing in humans may require utilization of more cognitively demanding tasks.

The greater right-sided activation of inferior frontal regions in the present studies warrants mention. This pattern of lateralization occurred regardless of the side of stimulation. The asymmetric nature of this response provides additional evidence that the activations do not represent a passive representation of touch (for which one would expect activations contralateral to the side of stimulation). These results parallel recent observations of strong right OFC and anterior frontal operculum responses during thermal stimulation (Coghill et al. 2001; Craig et al. 2000). This pattern also appears consistent with the well-established right hemisphere dominance in spatial attention (Mesulam 2000) and previous findings regarding somatosensory attention (Pardo et al. 1991).

In summary, the present studies clearly demonstrate the presence of inferior frontal brain regions responsive to somatosensory stimulation. The areas identified show reasonable correspondence to areas previously observed to possess somatosensory input in monkeys and thus appear to indicate a conservation of these pathways in humans. Future studies will hopefully clarify the specific task conditions that engage these areas.

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