Behavioral/Systems/Cognitive

Somatosensory Cells in Area PEc of Macaque Posterior Parietal Cortex

Rossella Breveglieri, Claudio Galletti, Michela Gamberini, Lauretta Passarelli, and Patrizia Fattori

Dipartimento di Fisiologia Umana e Generale, Università di Bologna, I-40126 Bologna, Italy

PEc is an area defined on cytoarchitectural grounds, located in the posterior part of the superior parietal lobule of macaque brain (Pandya and Seltzer, 1982). The aim of this work was to assess whether passive somatosensory stimulation elicited responses in PEc neurons. Extracellular recordings were performed in three awake *Macaca fascicularis*. Passive somatosensory stimulation was performed in darkness, and eye movements were monitored continuously. Recording sites were assigned to different areas according to the cytoarchitectonic criteria described by Pandya and Seltzer (1982) and Luppino et al. (2005). Only recording sites within the limits of the cytoarchitecturally defined area PEc were taken into account in this work.

Of 147 PEc cells, 83 (56%) were modulated by passive somatosensory stimulation. The majority of them (73%) responded to joint rotations, and 24% responded to tactile skin stimulation. The majority of PEc somatosensory responses (90%) were evoked by contralateral stimulation. Joint-modulated cells were mostly activated by the upper limbs (82%). The majority of tactile receptive fields (61%) were located on the arms, and a minority was located on the legs and trunk. One-half of PEc somatosensory cells were polysensory, because they were sensitive to visual stimulation. The majority of PEc somatosensory cells were activated by active reaching movements. Somatosensory cells, somatosensory submodalities, and body part representations were not clustered in PEc subregions; in other words, PEc does not show a somatotopic organization. Although the caudal sector of the superior parietal lobule has been traditionally considered as a somatosensory area, this is the first demonstration of the presence of somatosensory cells in this cortical region.

Key words: somatotopy; superior parietal lobule; dorsal stream; cytoarchitecture; cortical maps; reaching movements

Introduction

The exposed surface of the macaque superior parietal lobule (SPL) posterior to the primary somatosensory cortex was termed area PE by Von Bonin and Bailey (1947). Many authors reported that the activity of PE neurons was modulated by somatosensory stimulation (Duffy and Burchfiel, 1971; Sakata et al., 1973; Mountcastle et al., 1975; Gardner et al., 1999). The caudal part of area PE was cytoarchitectonically identified as a distinct area, named PEc (Pandya and Seltzer, 1982). Based on somatosensory-related activity of the adjacent area PE, PEc was considered as a somatic sensory "association" area (Pandya and Seltzer, 1982). Ablation studies demonstrated that PEc is involved in tactile discrimination (Moffett et al., 1967; Murray and Mishkin, 1984), and connectional studies demonstrated that PEc is connected with the parietal areas PE, PEci, PG, and MIP (Pandya and Seltzer, 1982; Marconi et al., 2001) and with the dorsal premotor cortex (Matelli et al., 1998; Marconi et al., 2001), all regions where somatosensory cells were found (Duffy and Burchfiel, 1971; Sakata et al., 1973; Mountcastle et al., 1975; Hyvarinen, 1981;

Murray and Coulter, 1981; Colby and Duhamel, 1991; Raos et al., 2003). More recently, the caudal part of SPL (putatively area PEc) has been demonstrated to contain neurons sensitive to visual stimuli (Squatrito et al., 2001), as well as to oculomotor activity and to arm-reaching movements (Batista et al., 1999; Battaglia-Mayer et al., 2001; Ferraina et al., 2001). To our knowledge, no studies so far have taken into account passive somatosensory stimulation in PEc.

Our aim in this work was to identify area PEc on cytoarchitectural grounds and to check whether neurons located within the limits of this area were responsive to passive somatosensory stimulation. We also tested which types of somatosensory stimuli were effective in modulating PEc cells and looked for possible segregations in the distribution of somatosensory features. We found that most PEc cells were modulated by passive somatosensory stimulation, but area PEc did not show a somatotopic organization. Many PEc somatosensory cells were also modulated during active reaching movements. Modulations observed during active arm movements were generally congruent with those observed during passive movements of the arm, and we suggest that active modulations represent the actual limb posture rather than a predictive signal of the impending arm movement.

Materials and Methods

Functional properties of PEc neurons were studied in four hemispheres of three *Macaca fascicularis* weighing between 3 and 7 kg. Because anesthetics block cell activity in the posterior parietal cortex (Mountcastle et al., 1975), non-anesthetized, awake animals were used in this study.

Experiments were performed in accordance with national laws on the care and use of laboratory animals and with the European Communities Council Directive of November 24, 1986 (86/609/EEC), and were approved by the Bioethical Committee of the University of Bologna.

A detailed description of surgical and recording procedures, as well as anatomical reconstruction of recording sites and animal care, were reported previously (Galletti et al., 1999a). The following is a brief description of procedures not used in that report.

During the training period, animals were manipulated and touched on the entire body by the experimenter and were rewarded with water and fruits during manipulation. After the training, they were docile and cooperative with the experimenters. Recordings were made 6–7 h per day; between recording sessions, the monkeys lived in their home cage without showing any sign of pain.

After the animals were killed, a careful analysis of Nissl-stained sections of the brain allowed us to recognize the cytoarchitectural pattern of PEc and to reconstruct electrode tracks and recording sites. Recording sites were assigned to area PEc according to the cytoarchitectural criteria described by Luppino et al. (2005). As shown in Figure 1, area PEc is characterized by the presence of a clear size gradient in layer III, which is densely populated by medium-sized pyramids in its lower part, and by a dense layer V with a high number of relatively large pyramids.

Anterior to area PEc, at approximately the level of the posterior tip of the cingulate sulcus, is area PE. Figure 1 shows that in PE, the size gradient in layer III becomes more evident against a less cellular background; in layer V, large pyramids are less packed and are present in an almost continuous row.

Ventral and posterior to area PEc is area V6A. As described by Luppino et al. (2005) and shown in Figure 1, the dorsal part of area V6A is characterized by a less pronounced size gradient in layer III and by the presence of fewer and larger pyramids in layer V with respect to area PEc. The location of the border between PEc and V6A varies in different animals from ~1 mm posterior to the exposed surface of the SPL to ~1.5 mm anterior to it.

On the mesial surface of the hemisphere, PEc borders ventrally with area PGm, at ~5 mm from the dorsal cortical surface of the SPL (Pandya and Seltzer, 1982; Luppino et al., 2005). In agreement with Luppino et al. (2005), lateral and adjacent to PEc we found a different cytoarchitectural pattern that was suggested to be area MIP (Colby et al., 1988). The border between PEc and MIP is at about one-third of the depth of the intraparietal sulcus.

Somatosensory stimulation. The experimenter stood behind the animal in darkness and delivered somatosensory stimulation on both sides of the animal body. Salient events of the stimulation were signaled pushing a pedal connected to the computer for data acquisition. Somatosensory stimulation started with superficial tactile stimulation, such as hair bending, superficial touch, or light pressure of the skin. Then we performed deep tactile stimulation (deep pressures of subcutaneous tissues) as well as proprioceptive stimulations (slow and fast rotations of the joints). When a cell was found to be responsive to joint rotation, we carefully checked again whether skin stimulation around the joint was responsible for the observed neural modulation. We are aware that our operational criteria do not exclude the possible participation of other somatosensory afferences, including muscle proprioception, and that neck rotation could not be tested in our experimental conditions, because the experiments were performed with the monkey's head fixed.

When a neuron responded to a somatosensory stimulation, it was classified as follows: SKIN, when activated by light tactile stimulation of the skin; DEEP, when activated by deep pressure of subcutaneous tissues; JOINT, when activated by joint rotation.

Because it has been demonstrated recently that PEc is an area containing visual neurons (Battaglia-Mayer et al., 2001; Squatrito et al., 2001) as well as cells modulated by eye and/or arm movements (Battaglia-Mayer et al., 2001; Ferraina et al., 2001), care was taken to rule out visual, eye, and active arm influences on cell discharges during somatosensory stimulation.

To exclude visual influences, somatosensory stimulation was performed in complete darkness. In addition, between two batteries of somatosensory stimuli, light was turned on to avoid dark adaptation. Eye movements were monitored continuously using an infrared oculometer (sampling rate, 10 kHz; Dr. D. Bouis, Karlsruhe, Germany) to check whether they were responsible for neuronal discharges. On-line and off-line analyses were performed in this regard.

Whenever possible, PEc neurons responsive to passive somatosensory stimulation were also tested with visual stimulation. Standard protocols were used in this regard (see Galletti et al., 1999a,b, 2005). Briefly, cells were first tested with simple visual stimuli (light/dark borders, light or dark bars and spots of different size, orientation, direction, and speed of movement) rear-projected on the screen facing the animal. If the neuron in record was not responsive to these stimuli, testing was continued using more complex visual stimulations (light/dark gratings and corners of different orientation, direction, and speed of movement). In cases in which we were not able to activate the cell in record with the battery of simple and complex visual stimuli described above, we classified that cell as nonvisual in nature.

In some cases, PEc somatosensory cells were tested for active arm movements using the instructed-delay reaching task described by Fattori et al. (2005). Briefly, as shown in the right panels of Figure 2, reaching movements started from a home button placed outside the animal's field of view, 5 cm in front of the chest on the midsagittal line, and reached a visual target [light-emitting diode (LED)] on a fronto-parallel panel at a distance of 14 cm from the eyes. At the beginning, the monkey performed a steady fixation of the reaching target while waiting for the go signal (epoch DELAY); then it released the button and reached and pressed the LED (epoch M1); the animal then kept its hand on the LED (epoch HOLD) until it switched off. This cued the monkey to release the LED and to return to the home button (epoch M2). The task was performed in complete darkness, except for the LED, the brightness of which was reduced so that it was barely visible.

Surface-based reconstruction of studied brains. Three-dimensional surface-based reconstructions of the studied brains were performed by the software CARET [Computerized Anatomical Reconstruction and Editing Toolkit, http://brainmap.wustl.edu/caret (Van Essen et al., 2001)]. The three-dimensional reconstructions were made starting from the cortical mid-thickness contours of brain sections spaced 300 μm apart. The contours were imported in CARET, together with the location of the cytoarchitectonic borders of area PEc, and aligned manually to obtain a smoothed three-dimensional reconstruction of the brain (for details, see Galletti et al., 2005).

Electrophysiological data were reported on two-dimensional maps of the brains, as described in detail by Galletti et al. (1999a). The two-dimensional maps of each hemisphere were aligned on the cytoarchitectonic border between PEc and V6A. We also built a summary map of the four hemispheres we studied, mirroring the maps of the right hemispheres on those of the left hemispheres and aligning the individual maps on the PEc/V6A border and on the interhemispheric fissure.

Results

Figure 1, *A* and *B*, shows the extension of the cytoarchitectonically defined area PEc on three-dimensional reconstructions of the most representative hemisphere we studied. As described in detail in Materials and Methods, care was taken to distinguish the pattern of PEc from that of PE anteriorly and PGm medially according to the criteria of Pandya and Seltzer (1982), and of V6A posteriorly and MIP laterally according to the criteria of Luppino et al. (2005). Figure 1, *A* and *B*, shows that PEc occupies the caudalmost third of the SPL, from the caudal tip of the cingulate sulcus to the parieto-occipital sulcus. It extends slightly into the medial surface of the brain and into the medial bank of intraparietal sulcus.

In this study, only recording sites located in area PEc were considered.

Somatosensory-related activity in area PEc
Of 147 units extracellularly recorded in PEc and tested with somatosensory stimulation, 83 (56%) were clearly modulated by
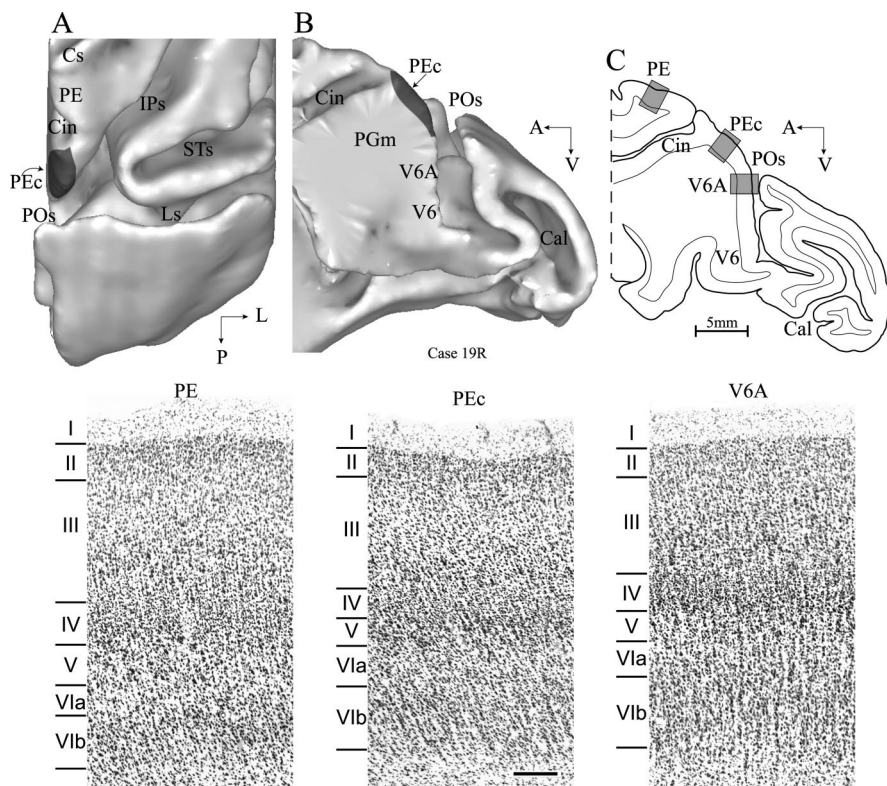
Figure 1. Brain location and cytoarchitectural pattern of area PEc. **A, B,** Dorsal and medial views of the surface-based reconstruction of the caudal half of one studied hemisphere. Dark gray areas show the extent and location of area PEc according to the cytoarchitectural pattern (see Materials and Methods). The location of areas PE, V6A, PGm, and V6 is also shown. **C,** Drawing of a parasagittal section centered on the anterior wall of the parieto-occipital sulcus. The gray boxes indicate the location of the three high-magnification views shown in the bottom panels. Dorsal is up, and caudal is right. Scale bars: **C,** 5 mm; photomicrographs, 200 μm. Cin, Cingulate sulcus; Cal, calcarine fissure; Cs, central sulcus; IPs, intraparietal sulcus; Ls, lunate sulcus; POs, parieto-occipital sulcus; STs, superior temporal sulcus; A, anterior; V, ventral; L, lateral; P, posterior; MIP, medial intraparietal area (Colby et al., 1988); PE, area PE (Pandya and Seltzer, 1982); PGm, medial area PG (Pandya and Seltzer, 1982); V6, area V6 (Galletti et al., 1999b); V6A, area V6A (Galletti et al., 1999a).

Table 1. Categories of somatosensory neurons of area PEc

	Contralateral	Ipsilateral	Bilateral	Total n (%)
JOINT	55	2	3	60 (73)
SKIN	17	3	0	20 (24)
DEEP	2	0	0	2 (2)
JOINT and SKIN	1	0	0	1 (1)
Total n (%)	75 (90)	5 (6)	3 (4)	83

JOINT, SKIN, and DEEP refer to cells activated by joint rotations, soft skin touching, and palpation, respectively (see Materials and Methods).

this type of stimulation. As shown in Table 1, PEc contains cells responsive to different somatosensory submodalities. Basically, each unit was activated by only one submodality: JOINT, DEEP, or SKIN (see Materials and Methods). In our sample, we found only one cell modulated by more than one somatosensory submodality (shoulder rotation and tactile stimulation of the skin around the elbow).

The majority of somatosensory cells (73%) were modulated by slow or fast rotation of a limb joint. Figure 2, *A1* and *B1*, shows examples of two types of these JOINT neurons. The unit in Figure 2*A1* was almost silent at rest (Fig. 2*A1*, left) but fired tonically when the arm was passively displaced upward (Fig. 2*A1*, right). The neuron in Figure 2*B1*, on the contrary, fired transiently during passive rotation of the contralateral shoulder around the vertical axis.

Less frequently (27%), neurons also responsive to tactile stim-

ulation were found. Figure 2*C* shows an example of a SKIN unit strongly modulated when the hair of the contralateral shoulder was touched.

Passive rotation of the shoulder modulated 36 of 61 PEc units, rotation of the elbow modulated 10 units, and flexion of the wrist modulated 1 unit (Fig. 2*D*). Some neurons were activated by rotation of more than one joint, but they were rare (3 of 61) in PEc. In all, 82% (50 of 61) of the PEc cells modulated by joint rotation were modulated by input coming from the arms, and 18% (11 of 61) were modulated by input coming from the lower limbs.

The majority of tactile receptive fields were located on the arm (61%; 14 of 23) (Fig. 2*E*), but some were located on the trunk (22%; 5 of 23), and some others were located on the leg (17%; 4 of 23). As shown in Table 1, the majority (90%) of PEc somatosensory responses were evoked by contralateral stimulation.

Other functional properties of PEc somatosensory cells

Of 83 PEc somatosensory cells, we tested 45 cells with visual stimulation. One-half of them (24 of 45; 53%) turned out to be strictly unimodal, because they were driven only by somatosensory stimuli. The remaining half (21 of 45; 47%) were bimodal, because they were driven also by visual stimuli. For these latter neurons, we looked for a spatial correlation between the position of the somatosensory receptive field on the body and that of the visual receptive field on the retina. No correlation was found. We found bimodal neurons activated by shoulder rotation that showed in one case the visual receptive field on the fovea, in other cases at intermediate eccentricities in the far periphery (eccentricity higher than 40°). Even in the contralateral/ipsilateral domain, we did not find a spatial congruence between the location of somatosensory and visual receptive fields.

Twenty-nine PEc somatosensory cells sensitive to passive arm joint stimulation or having a tactile receptive field on the arm were also tested in tasks in which the animal performed active arm movements. The majority of them (22 of 29; 76%) showed a response during both passive and active arm movements, and the remaining cells (7 of 29; 24%) were not driven by active arm movements. Examples of coexistence of passive and active responses in single PEc cells are shown in Figure 2, *A* and *B*. The joint neuron in Figure 2*A1*, for instance, was also tested in an instructed-delay reaching task performed in darkness. As shown in Figure 2*A2*, it strongly discharged during the HOLD epoch of the task, when the arm was raised above the shoulder to press the visual target. Note that this active behavior was congruent with that shown by the cell in the passive somatosensory test, in which the tonic discharge evoked by the passive upward rotation of the shoulder (Fig. 2*A1*) continued as long as the arm was kept upward.

The joint neuron in Figure 2*B*, recorded 1 mm apart from the cell in Figure 2*A* in the same microelectrode penetration, fired

vigorously during an instructed-delay reaching task performed in darkness when the hand was retracted from the visual target and moved toward the animal's body (Fig. 2*B2*, M2). Also in this case, the cell behavior was congruent with that observed during passive stimulation, because the backward movement produced a rotation of the shoulder around the vertical axis similar to that produced by passive stimulation. Most PEc somatosensory cells driven by active reaching movements showed postural responses like the neurons in Figure 2, *A* and *B*.

Cortical distribution of somatosensory-related cells in PEc

To investigate whether somatosensory properties were clustered in subregions within area PEc, we reconstructed the location of units tested with passive somatosensory stimulation on flattened maps of the cortical area.

The top panels in Figure 3 show the cortical distribution of PEc somatosensory cells in one single hemisphere. It is evident that almost every type of functional properties was present in different parts of PEc, with no evident signs of functional segregation. The same held true for the other three hemispheres we studied. The bottom panels in Figure 3 show the distribution of the same type of data in a summary map obtained by the four hemispheres of this study. Again, there is no evident signs of functional segregation. In particular, Figure 3*A* suggests that somatosensory cells in PEc are not segregated, although in the summary map, cells modulated by somatosensory input seem to be less present in the posteromedial part of the area. Figure 3*B* shows that somatosensory submodalities are also not clustered in PEc. Figure 3*C*, finally, shows that although the upper limb is over-represented, it is not segregated in any particular region of the recorded area. Similarly, leg representation, although less present than the arm representation, was found in all parts of PEc. In other words, our data indicate a lack of somatotopy in area PEc.

To investigate whether somatosensory properties were clustered in different cortical layers, we analyzed the distribution of somatosensory cells through the PEc cortical thickness. We found that along single PEc penetrations, somatosensory cells were present in both superficial and deep layers. To quantify the distribution through the cortical depth, we divided the cortical width we recorded from into two parts. Taking into account that the average position of the fourth layer in PEc is at 3/5 of the cortical width (Luppino et al., 2005), we divided the recording sites into supragranular and infragranular ones. The results of this study showed that the incidence of somatosensory cells is not

PASSIVE SOMATOSENSORY STIMULATIONS
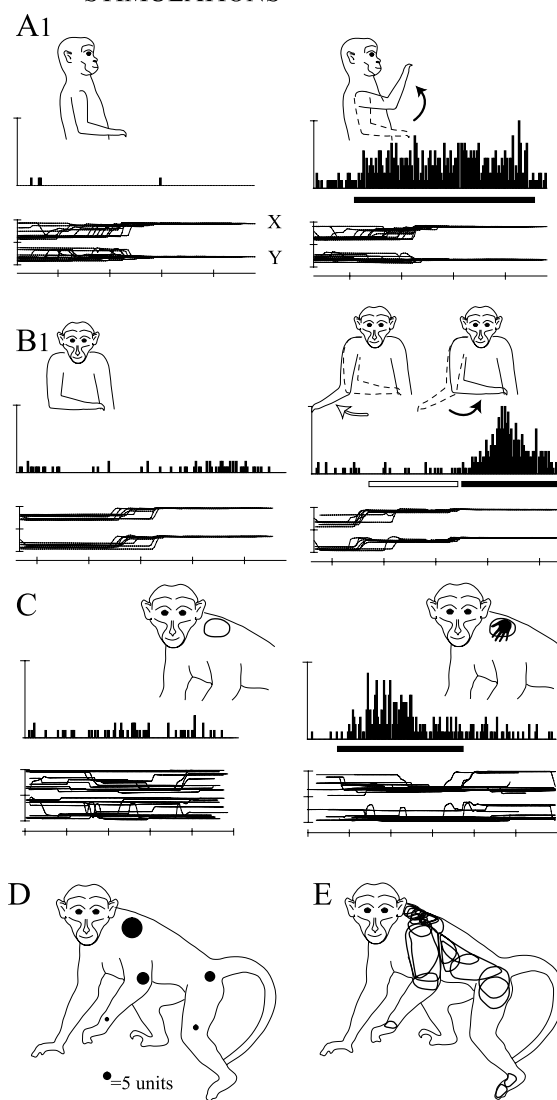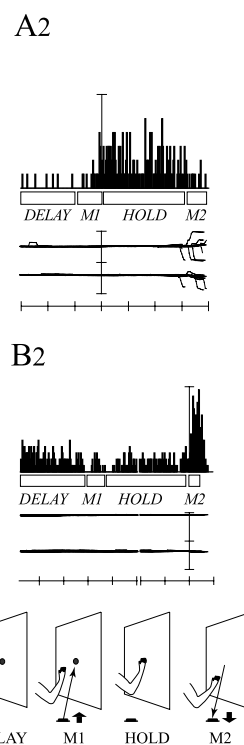
ACTIVE ARM MOVEMENTS

Figure 2. PEc somatosensory cells. *A*, *B*, Examples of JOINT neurons studied with passive stimulations and active movements. *A1*, Tonic response of a PEc cell to passive joint stimulation (see diagram above the panel). Left, Ongoing neural activity of the cell. Right, Activity of the same cell during passive joint rotation. *A2*, Activity of the same unit during execution of active arm movements in a reaching task (see diagram below panel *B2*). Activity has been aligned with the onset of the HOLD epoch. Data in each panel (from top to bottom) are as follows: peri-event time histogram of single-unit activity; bar indicating the duration of passive stimulation, or the duration of the different behavioral epochs in the reaching tasks; recordings of X and Y components of eye positions. *B1*, Phasic response of a PEc cell to passive joint stimulation (see diagram above the panel). All other details are as in *A*. *B2*, Activity of the same unit during execution of active reaching movements. Activity has been aligned with the onset of the return arm movement (M2). *C*, Response of a PEc cell to tactile stimulation of the shoulder skin (see diagram above the panel). All other details are as in *A*. *D*, Locations (black dots) of the joints modulating PEc cells. The size of each dot is proportional to the number of modulated units. *E*, Locations of PEc tactile receptive fields (thick lines drawn on the animal body). All somatosensory receptive fields have been reported on the left side of the body. Scale bars on histograms: horizontal: *A–C*, 500 ms per division; vertical: 40 spikes/s (*A1*), 30 spikes/s (*A2*), 100 spikes/s (*B1*), 60 spikes/s (*B2*), and 70 spikes/s (*C*); bin size, 15 ms; eye traces, 60° per division.

significantly different in supragranular and infragranular parts of the PEc cortex (χ^2 test; NS). A similar behavior was also observed for somatosensory submodalities and for body parts representation (χ^2 test; NS).

The above reported data indicate a lack of any type of functional segregation in the somatosensory domain. We looked for the existence of other types of functional segregation, but without success. For instance, PEc bimodal neurons combining visual and somatosensory inputs were mixed with those that were strictly
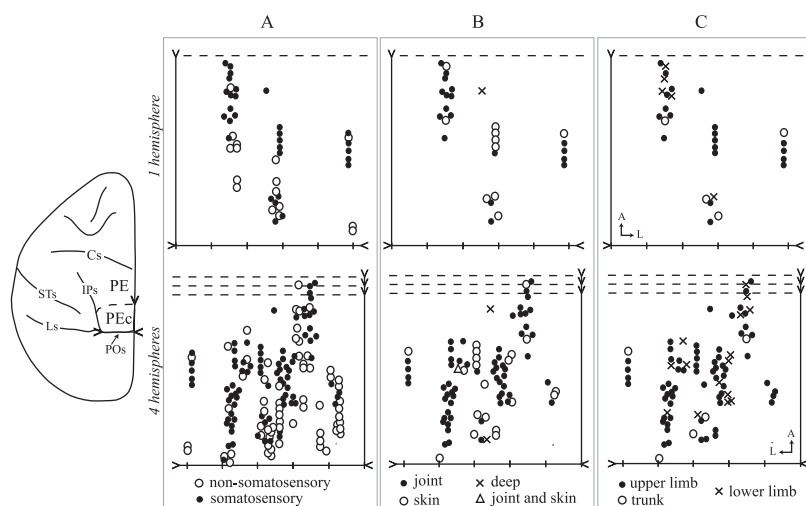
Figure 3. Cortical distribution of PEc somatosensory cells. Flattened maps of the dorsal-exposed surface of PEc showing the cortical distribution of cells sensitive to somatosensory stimulation (**A**), to different submodalities of somatosensory stimulation (**B**), and to somatosensory input coming from different body parts (**C**) are shown. Top, Maps from a single hemisphere. Bottom, Summary maps from the four hemispheres of this study. Maps from different cases are aligned posteriorly on the border between PEc and V6A (scale, 1 mm per division) and medially on the interhemispheric line (see symbols >< on the maps and on the brain silhouette on the left). The dashed lines on the maps indicate the cytoarchitectural borders between areas PEc and PE (antero-posterior extent of PEc was slightly different from case to case). Cs, Central sulcus; IPs, intraparietal sulcus; Ls, lunate sulcus; POs, parieto-occipital sulcus; STs, superior temporal sulcus; A, anterior; L, lateral; PE, area PE (Pandya and Seltzer, 1982).

somatosensory. We also looked for a topographical order in the distribution of somatosensory cells with and without active arm-movement activity, but again we did not find an order or a trend. Finally, limb postures, as well as preferred direction of movement, did not reveal a topographical organization (e.g., cells in Fig. 2, *A* and *B*, recorded 1 mm apart in the same penetration). More detailed studies are needed to definitively assess this point.

Discussion

In the present work, we describe the functional properties of cells recorded from area PEc in awake animals. Among the cells recorded in the caudal part of the SPL, we analyzed here only the properties of those cells that were found to be located within the limits of area PEc defined according to the cytoarchitectonic criteria described by Pandya and Seltzer (1982) and Luppino et al. (2005).

This is the first study that analyzes the somatosensory properties of single cells in area PEc. We found that many neurons in area PEc could be driven by somatosensory stimulation. We did not find any clustering of somatosensory properties, both in single cases and at population level. Even adjacent cells in the same penetration were modulated by somatosensory stimuli applied on different parts of the body or by different somatosensory submodalities. Although we are aware that we did not record from the entire extent of PEc, these data strongly suggest a lack of somatotopy in this cortical area. Despite this lack of somatotopy, the body representation is quite complete in PEc. The fact that we did not find head representation could be attributable to a recording bias or could be an actual feature of PEc. More data are needed to verify this point.

Somatosensory cells represent the 56% of our PEc population, a value that is inferior to that reported for more anterior parts of the SPL [area PE or Brodmann's area 5 (Duffy and Burchfiel, 1971; Sakata et al., 1973; Mountcastle et al., 1975; Gardner et al., 1999)]. The lower percentage of somatosensory cells in PEc with respect to area PE could be attributable to the fact that PEc also

contains visual cells (Battaglia-Mayer et al., 2001; Ferraina et al., 2001; Squatrito et al., 2001), rarely found in area PE (Sakata et al., 1973; Mountcastle et al., 1975).

The incidence of somatosensory modulations in PEc is similar to that observed in area 7 of the macaque inferior parietal lobule (Leinonen et al., 1979), in agreement with the fact that the cortical region named PEc was originally indicated as area 7 by Brodmann (1909). However, contrary to area 7 (Leinonen et al., 1979; Gardner et al., 1999), our study finds a predominance of joint modulations in PEc (73%) (Table 1). Because proprioceptive input could be more useful than tactile ones in monitoring the state of body parts during movement, we suggest that PEc somatosensory neurons could be useful for monitoring body part movement as well as posture holding in space. This hypothesis is strengthened by the fact that the majority of PEc somatosensory cells were also activated by active arm movements in a congruent way with respect to what was observed during passive movements or posture holding (Fig. 2*A*,*B*). The active responses rather than a predictive signal of the impending arm movement could represent the actual posture of the arm, and PEc neurons could encode a map of the body in space.

Area PEc is more somatosensory related than the adjacent area V6A (Galletti et al., 1999a), where only ~30% of cells are sensitive to somatosensory stimulation (Breveglieri et al., 2002). Although more represented than in V6A, PEc somatosensory cells are less representative of the distal parts of the arm. This suggests that PEc is less involved than V6A in the control of grasping movements (Fattori et al., 2004). In addition, only the upper limbs are represented in V6A, leading us to suggest that V6A is involved in the control of visually guided arm reaching (Fattori et al., 2005). Because both upper and lower limbs and trunk are represented in PEc, we suggest that this area is involved in a more complete control of movements and posture holding, like that required when the animal moves around and interacts with the external world.

Similarly to what was observed in V6A (Breveglieri et al., 2002), in PEc there is a relative low incidence of multijoint neurons and/or neurons modulated by more than one somatosensory submodality. Areas PEc and V6A seem to have simpler somatic properties with respect to areas PE and 7, where multijoint or multimodality cells were often observed (Duffy and Burchfiel, 1971; Sakata et al., 1973; Mountcastle et al., 1975; Leinonen et al., 1979). Both PEc and V6A neurons show tactile receptive fields quite small and restricted on a single part of the body, whereas single neurons in areas 5 and 7 are generally larger and could even be split in two parts spatially separated on different body segments (Sakata et al., 1973; Leinonen et al., 1979).

More difficult is the comparison of PEc properties with the properties of cells of the adjoining areas MIP (Colby et al., 1988), PGm, and PEci (Pandya and Seltzer, 1982). Area MIP was reported to contain somatosensory neurons (Colby and Duhamel, 1991), but an extensive study of the passive somatosensory properties of MIP cells is still lacking. The role of PGm in elaborating

somatosensory information was not attributable to a direct analysis of the somatosensory properties of the cells but was inferred from the anatomical connections of this area (Pandya and Seltzer, 1982). Area PEci, located on the mesial surface of the parietal lobe around the cingulate sulcus and also known as the supplementary sensory area (Murray and Coulter, 1981), contains cells sensitive to passive somatosensory stimulations (Murray and Coulter, 1981) and shows a complete representation of the body, similarly to what we find here in area PEc. Contrary to what we see in PEc, however, PEci shows a quite clear somatotopic organization.

Present data, together with those from literature, suggest that the caudal part of the SPL is a region that integrates hand and arm postures with visual information about extrapersonal space, with different areas playing distinct roles in guiding different goal-directed behaviors.

Conclusions

Area PEc seems to be more closely related to area V6A than to area PE. In fact, both PEc and V6A contain visual neurons and somatosensory cells guided by basic somatosensory stimuli, whereas PE is poor, if any, of visual neurons and shows complex somatosensory properties. This is in line with the functional trend within the SPL regarding visual and somatosensory domains. Moving anteriorly from V6A to PEc, and from this latter to PE, visual sensitivity progressively decreases and somatosensory sensitivity progressively increases, in good agreement with the fact that we are moving from visual to somatic regions of the brain.

Our data show that PEc mainly represents the contralateral half of the body and lacks of multijoint neurons as well as of tactile receptive fields located in two or more different parts of the body. These features contrast with the established idea that cells in the most caudal aspects of the SPL have more complex properties than cells located more anterior (Moffett et al., 1967; Lynch, 1980). On the other hand, our finding that PEc contains a mixture of somatosensory submodalities and body-part representations suggests for PEc a rather complex function, such as that of comparing different types of somatosensory input from different parts of the body and of visual inputs from different parts of the visual field. We suggest that this matching could be useful for the purpose of creating and maintaining an internal representation of one's own body and of its parts in the surrounding space.

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