

Visual, Somatosensory, and Bimodal Activities in the Macaque Parietal Area PEc

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Caudal area PE (PEc) of the macaque posterior parietal cortex has been shown to be a crucial node in visuomotor coordination during reaching. The present study was aimed at studying visual and somatosensory organization of this cortical area. Visual stimulations activated 53% of PEc neurons. The overwhelming majority (89%) of these visual cells were best activated by a dark stimulus on a lighter background. Somatosensory stimulations activated 56% of PEc neurons: most were joint neurons (73%); a minority (24%) showed tactile receptive fields, most of them located on the arms. Area PEc has not a clear retinotopy or somatotopy. Among the cells tested for both somatosensory and visual sensitivity, 22% were bimodal, 25% unimodal somatosensory, 34% unimodal visual, and 19% were insensitive to either stimulation. No clear clustering of the different classes of sensory neurons was observed. Visual and somatosensory receptive fields of bimodal cells were not in register. The damage in the human brain of the likely homologous of macaque PEc produces deficits in locomotion and in whole-body interaction with the visual environment. Present data show that macaque PEc has sensory properties and a functional organization in line with the view of an involvement of this area in those processes.

Keywords: body-world interaction, dorsal visual stream, locomotion, multisensory, somatotopy

Introduction

Caudal area PE (PEc), corresponding to the caudal part of cytoarchitectural field PE, has been traditionally seen as a somatosensory association area of the posterior parietal cortex (Pandya and Seltzer 1982). Recent studies have shed light on the functional properties of PEc neurons, including the demonstration of cells with visual responses to moving light bars (Battaglia-Mayer et al. 2001; Ferraina et al. 2001; Squatrito et al. 2001) and optic flow stimuli (Battaglia-Mayer et al. 2001; Raffi et al. 2002), cells modulated by passive somatosensory inputs (mainly from the arm) (Breviglieri et al. 2006), as well as arm-reaching cells (Batista et al. 1999; Battaglia-Mayer et al. 2001; Ferraina et al. 2001) and cells modulated by oculomotor activity (Battaglia-Mayer et al. 2001; Ferraina et al. 2001). According to the results of these studies, it has been suggested that PEc is a visuomotor area involved in creating and maintaining an internal representation of one's own body (Breviglieri et al. 2006). This area is part of a mosaic of areas likely involved in early stages of motor programming, where inputs coming from eye and hand are integrated to control arm movements toward targets in the peripersonal space (Batista et al. 1999; Battaglia-Mayer et al. 2001; Ferraina et al. 2001). This hypothesis is supported by connectional studies (Johnson and Ferraina 1996; Matelli et al. 1998; Marconi et al. 2001) according

to which the caudal part of the superior parietal lobule is directly connected with dorsal premotor areas containing cells modulated by arm position and arm direction of movement (Caminiti et al. 1991), as well as by eye position signals (Boussaoud et al. 1998; Jouffrais and Boussaoud 1999).

Caudally to PEc, and bordering it, there is another visuomotor area called V6A (Galletti, Fattori, Kutz, et al. 1999). Similarly to PEc, area V6A contains visual (Galletti et al. 1996; Galletti, Fattori, Kutz, et al. 1999) and somatosensory (Breviglieri et al. 2002) cells, as well as cells modulated by eye and arm movement (Galletti et al. 1997; Fattori et al. 2001, 2005; Kutz et al. 2003). Until recently, the anatomical proximity between V6A and PEc, together with the functional similarities between the 2 areas, has made it hard to assign recording sites to either of these areas. This difficulty has been removed by a recent study (Luppino et al. 2005) that provided cytoarchitectural criteria to distinguish PEc from V6A, allowing to assign cells to either areas on the basis of an objective criterion. We therefore decided to reinvestigate visual and somatosensory properties of PEc cells by assigning recording sites on the basis of the architectural pattern of recorded brain region. We also investigated the existence in PEc of bimodal cells, sensitive to both visual and somatosensory stimulations, and we checked whether different sensory properties were spatially segregated within PEc subregions.

Materials and Methods

Three normal adult *Macaca fascicularis* weighing between 3 and 7 kg were used in this study. Data have been collected from 4 hemispheres. Experiments were carried out in accordance with National laws on care and use of laboratory animals and with the European Communities Council Directive of 24 November 1986 (86/609/EEC), and were approved by the Bioethical Committee of the University of Bologna.

A detailed description of training, surgical and recording procedures, as well as of visual and somatosensory stimulations, anatomical reconstruction of recording sites and animal care are reported elsewhere (Galletti et al. 1996; Galletti, Fattori, Kutz, et al. 1999; Breviglieri et al. 2006). Surgery to implant recording apparatus was performed in asepsis and under general anesthesia (sodium thiopental, 8 mg kg h, i.v.). Analgesics were used postoperatively (ketorolac trometazyn, 1 mg kg i.m. immediately after surgery and 1.6 mg kg i.m. on the following days).

Extracellular recordings from area PEc were daily performed using glass-coated metal microelectrodes with a tip impedance of 0.8–2 MOhms at 1 kHz. The monkeys were seated in a primate chair with the head fixed. The recording chamber was filled with saline, a hydraulic microdrive was tightly fixed on it and the electrode was advanced into the brain through the intact dura using a 1 × 1-mm surface coordinate system as a reference. Action potentials were sampled at 1 kHz. Each animal was studied over a period of 4–8 months. During the last 2 weeks of recordings, electrolytic lesions (30–40 μ A cathodal current for 30 s) were made at different depths along single penetrations carried out at different coordinates within the recording chamber.

After the last recording session, the animals were anaesthetized with ketamine hydrochloride (15 mg kg i.m.) followed by an i.v. lethal injection of sodium thiopental and perfused through the left cardiac ventricle with saline in phosphate buffer, and then with 4% paraformaldehyde in phosphate buffer, followed by 5% glycerol in phosphate buffer. Electrode tracks and location of each recording site obtained in the last 2 weeks were reconstructed on parasagittal (for 3 hemispheres) or coronal (for 1 hemisphere) sections of the brain on the basis of marking lesions. Unmarked penetrations were located on brain sections by interpolation with respect to penetrations with electrolytic lesions, taking into account the coordinates of penetrations within recording chamber. The locations of penetrations and depths of recording sites were then checked with respect to the boundaries between white and gray matter and the distance of recording site from the surface of the hemisphere (Galletti et al. 1995, 1996, 2005).

Visual Stimulation

Animals were trained to perform steady gaze fixation in a behavioral task in which they had to look for 2–6 s at a small target rear-projected on a large (80° × 80°) tangent screen placed 57 cm from the eyes, ignoring any other visual stimulus present or moving across the visual field. Fixation was monitored with an infrared oculometer (Bach et al. 1983). The fixation target could be projected in different positions on the screen in order to allow visual stimulations even in the far periphery of the visual field. A standard protocol was used for testing the visual responsiveness of cells in record. Cells were first tested with “simple” visual stimuli: single light/dark borders, spots of light, light or dark bars 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 patterns such as luminance gratings and corners of different orientations, directions, and speeds of movement, shadows with irregular contours, and shadows rapidly changing in size and/or shape.

If the cell was visually responsive, we mapped the borders of visual receptive field with the stimulus eliciting the best response. In cases where we were not able to activate the unit with the visual stimuli above described, we classified that unit as not visually responsive.

Somatosensory Stimulation

Animals got used to be manipulated and touched on the whole body by the experimenter, being rewarded with water and fruits during manipulation. Neural activity was recorded while passive somatic stimulations were applied on the whole body according to the standard protocol described in Breveglieri et al. (2002, 2006). The first somatosensory stimuli applied consisted of hair deflections by cotton flacks, touch or light pressure of the skin. If no responses were elicited, we attempted deep pressure in order to stimulate subcutaneous tissues (deep tactile stimulation), and finally slow and fast passive rotations of limb joints (proprioceptive stimulation).

In order to exclude visual influences, somatosensory stimulations were performed in complete darkness. The experimenter stood behind the animal and delivered stimuli on both sides of the body. Eye position and movement were monitored to exclude the possibility that observed modulations were due to oculomotor activity.

When a neuron responded to a somatosensory stimulation, it was classified as either tactile or sensitive to joint rotation, depending on the stimulus required. Otherwise, the cells were classified as nonsomatosensory.

Bimodal Visual/Somatosensory Activity

Single PEc neurons underwent both somatosensory and visual stimulations in an order that was randomized across cells. According to the results of these tests, neurons were classified in 4 groups: bimodal, unimodal somatosensory, unimodal visual, unresponsive.

Among bimodal cells, we checked whether visual and somatosensory receptive fields were in register or not. We also compared visual properties of bimodal neurons with those of strictly unimodal visual, as well as somatosensory properties of bimodal neurons with those of unimodal somatosensory neurons.

Cytoarchitectural Assessment

Analysis of Nissl-stained sections allowed us to recognize whether recording sites were within the limits of area PEc. Recording sites were

assigned to area PEc according to the cytoarchitectural criteria described in Pandya and Seltzer (1982) and Luppino et al. (2005). Briefly, 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. On the basis of these and other more subtle cytoarchitectural criteria, area PEc is clearly distinguishable from the neighboring areas medial intraparietal area (MIP), medial area PG (PGm), V6A, and PE, as detailed in Luppino et al. (2005).

Two-dimensional and Three-dimensional Cortical Maps

Three-dimensional (3-D) and 2-dimensional (2-D) surface-based reconstructions of the studied brains were done using the software CARET (<http://brainmap.wustl.edu/caret> Van Essen et al. 2001 see Fig. 1). The reconstructions were made starting from cortical mid-thickness contours of brain sections spaced 300 μm apart. The contours were imported in CARET, together with the location of cytoarchitectonic borders of area PEc, and manually aligned to obtain a smoothed 3-D reconstruction and a flattened map of the brain (for details, see Galletti et al. 2005).

To draw the average outline of area PEc (shown in Fig. 1), we reported the borders of PEc with nearby areas V6A, MIP, PE, PGm of single cases on the atlas brain (<http://brainmap.wustl.edu/caret>). The borders with PE rostrally and V6A caudally were better defined in cases cut in sagittal plane, whereas the borders with PGm medially and MIP laterally were better defined in cases cut in coronal plane.

Electrophysiological data were reported on 2-D maps of the brains reconstructed as described in detail in (Galletti, Fattori, Kutz, et al. 1999; Breveglieri et al. 2006). We built a summary 2-D map of the 4 hemispheres we studied, mirroring the maps of the right hemispheres on those of the left hemispheres, and aligning the individual maps on the cytoarchitectonic PEc/V6A border and on the interhemispheric fissure.

Results

We recorded the activity of 198 PEc cells in 4 hemispheres of 3 animals.

Figure 1 shows the average extension of the cytoarchitectonically defined area PEc (Pandya and Seltzer 1982; Luppino et al. 2005) on 3-D (Fig. 1A) and 2-D (Fig. 1B) reconstructions on the monkey atlas brain. PEc is located in the caudalmost third of the superior parietal lobule. It extends from the caudal tip of the cingulate sulcus anteriorly, to the parieto-occipital sulcus posteriorly, and from the medial surface of the brain to the medial bank of intraparietal sulcus. The brain location of area PEc was similar across single cases.

Visual Cells

Of the 146 neurons tested for visual sensitivity, 77 cells (53%) were responsive to visual stimulation. For 64 out of 77 visual cells we were able to determine the most effective visual stimulus among the battery tested; the remaining 13 cells were lost before finishing the testing protocol, and were excluded from subsequent analyses.

A consistent finding in our experiments was that PEc visual cells tended to show stronger visual responses to dark stimuli moved against a lighter background, in comparison with stimuli of the opposite polarity. All visual stimulations were performed while the animals were fixating. Figure 2 shows examples of visual responses obtained with different types of stimuli. The unit in Figure 2A was responsive to a simple stimulus (dark bar) moving to and fro across its visual receptive field. A dark bar correctly oriented and motionless within the receptive field was also effective in activating the cell (not shown in the figure). The orientation of moving bar was a critical factor. The cell was weakly responsive to bars oriented at 45° from the preferred

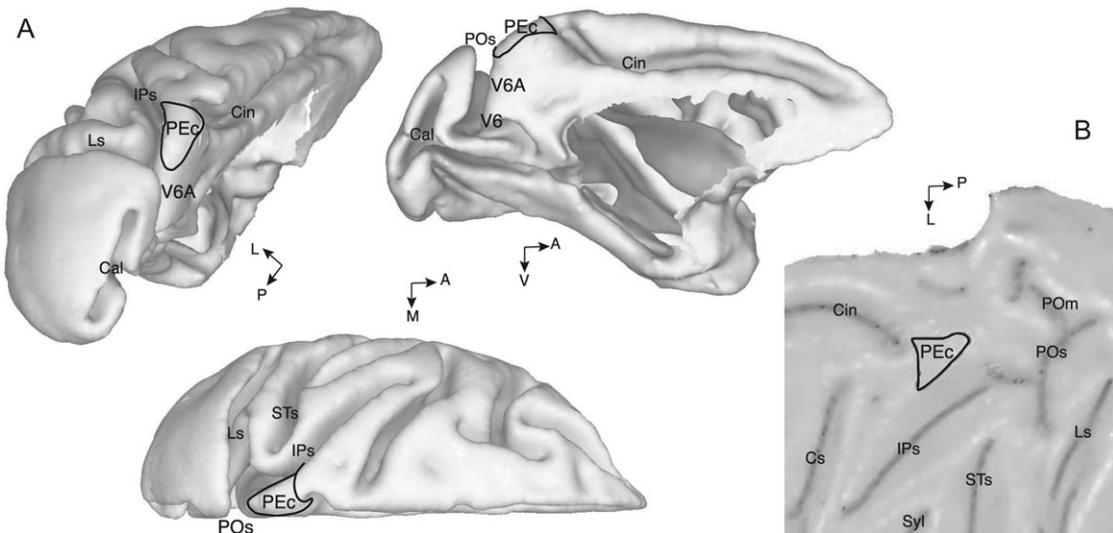


Figure 1. Brain location of area Péc. (A) Dorsomedial, medial, and dorsal 3-D views of the surface-based reconstruction of the atlas brain. (B) 2-D reconstruction of the atlas brain. The average extent and location of the cytoarchitecturally defined area Péc is outlined on each reconstruction. Location of areas V6 and V6A is also shown. Abbreviations: Cal = calcarine fissure; Cin = cingulate sulcus; Cs = central sulcus; IPs = intraparietal sulcus; Ls = lunate sulcus; POs = parieto-occipital sulcus; POm = medial parieto-occipital sulcus; STs = superior temporal sulcus; Syl = Sylvian fissure. A = anterior; V = ventral; L = lateral; P = posterior; M = medial; V6 = area V6 (Galletti, Fattori, Gamberini, et al. 1999); V6A = area V6A (Galletti, Fattori, Kutz, et al. 1999); Péc = area Péc (Pandya and Seltzer 1982).

orientation (the vertical), and was completely silent for bars oriented 90° from the preferred orientation.

Cell in Figure 2B showed a strong response to a dark bar, like that in Figure 2A, but, differently from it, the discharge was modulated by the direction of motion. This neuron was also responsive, although less strongly, to a light bar of the same orientation and direction of movement as the dark bar. The cell was also weakly modulated by a dark square expanding against a lighter background, whereas it did not respond to stimulus contraction.

Cell in Figure 2C was strongly responsive to complex stimulations. Simple stimuli (like light/dark borders or spots) activated only weakly the cell (not shown in the figure). Hand shadows waved across the receptive field were particularly effective, as shadows of elongated objects moving across the receptive field along their main axis of elongation. The cell showed a certain degree of orientation sensitivity, as vertical objects moved vertically evoked stronger responses than horizontal objects moved horizontally. Objects which moved perpendicularly to their main axis of elongation were not effective in modulating cell activity (not shown in the figure), contrary to what was observed in the unit illustrated in Figure 2A,B.

Cell in Figure 2D was another example of unit responsive to complex stimulation, but much less responsive, or not at all, to simple stimuli. It was activated by a dark square expanding within the receptive field, whereas a dark bar moved across the receptive field evoked a poor response, and no response at all was evoked by light bars moving with different orientations in different directions across the receptive field.

We found that the overwhelming majority ($n = 57/64$; 89%) of Péc visual cells were best activated by dark stimuli (bars, spots, or shadows of different shapes). A minority of cells was equally activated by dark and light stimuli, but none of the cells of our sample preferred light stimuli moving against a darker background. About 30% ($n = 20/64$) of the Péc visual cells gave similar responses for different visual stimuli among those we

tested, whereas the majority ($n = 44/64$) were selective for the stimulus type. Among these latter, 20% preferred simple stimuli (like neurons A and B in Fig. 2), whereas 80% preferred complex stimuli, like the neurons C and D in Figure 2. Often, cells preferred complex stimuli moved across the receptive field at a continuously varied speed, orientation, and/or direction, which avoided adaptation of cell discharge.

Receptive-field size increased with eccentricity in area Péc, and was on average larger than that of cells sampled in the nearby area V6A (see Fig. 3A; Galletti, Fattori, Kutz, et al. 1999). Regression lines from the 2 areas were significantly different one to another (1-way analysis of covariance, $P < 0.01$).

Both central and peripheral (up to about 70°) parts of the visual field are represented in Péc (gray area Fig. 3B). Although the contralateral hemifield is the most represented, a few receptive fields were also found in the ipsilateral part of the visual field, near the vertical meridian. Upper and lower contralateral quadrants are both well represented.

Cells preferring simple stimuli, complex stimuli, and non-selective cells represented more or less the same part of the visual field (Fig. 3B), though the receptive fields of cells selective for simple stimuli were all centered at eccentricities higher than 20° (Fig. 3C).

Visual Topography

We analyzed the distribution of receptive-field locations on bidimensional representations of the cortical region we studied. As evident in the Figure 4A, the contralateral hemifield was represented everywhere within Péc. Cells representing the vertical meridian, the horizontal meridian, the upper or lower quadrants, and the ipsilateral hemifield were randomly scattered throughout Péc without any evidence of spatial segregation (Fig. 4A). Similarly, receptive fields with different eccentricities were not orderly distributed within Péc (Fig. 4B), confirming the overall impression of a nontopographic representation of the visual field.

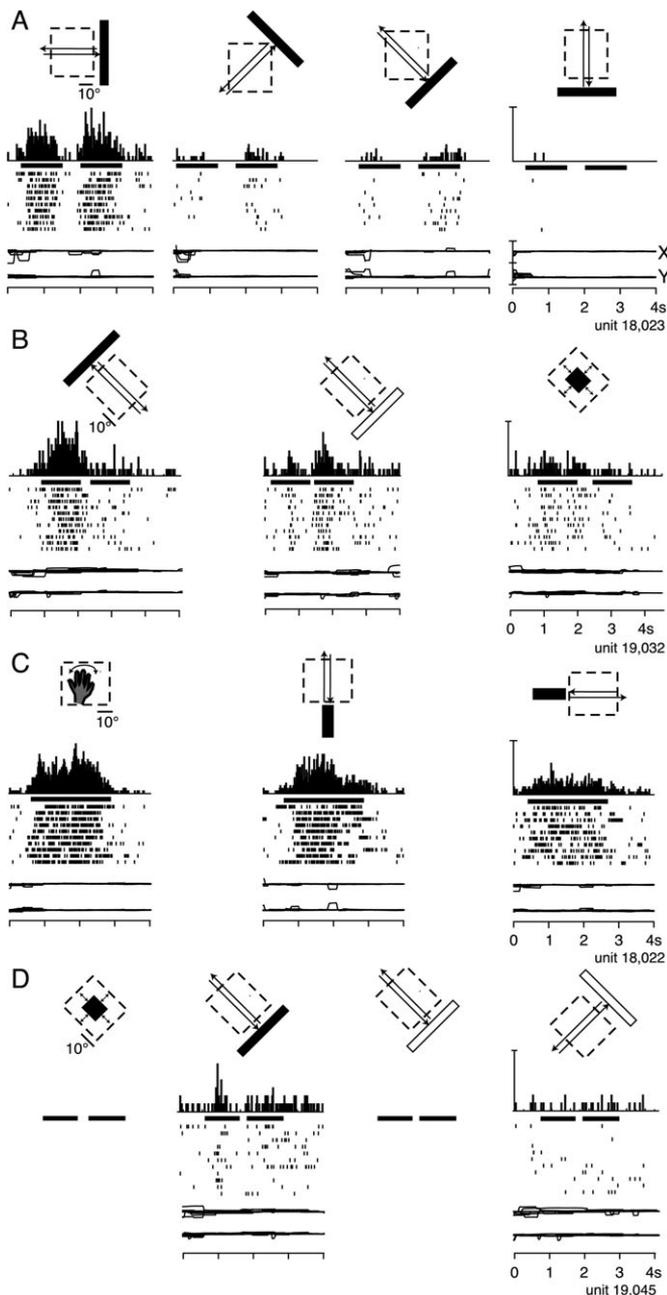


Figure 2. Responses of Péc cells to different types of visual stimuli. (A, B) neurons preferring simple stimuli; (C, D) neurons preferring complex stimuli. Each inset contains, from top to bottom, schematic representation of the stimulation of the receptive field (dashed line), peri-event time histogram, bar indicating the duration of visual stimulation, random-dot display of spikes recorded during each trial, recordings of horizontal and vertical components of eye positions. (A) Responses of a cell to moving dark bars with different orientations. (B) Responses of a cell to a moving dark bar, to moving light bars, and to expanding-contracting dark square; (C) activity of a Péc cell to hand shadows repeatedly waved across the receptive field (left), to moving dark bars with different orientations moved repeatedly on the receptive field and entering with the short side (center and right); (D) activity of a cell to expanding-contracting dark square, and to moving dark and light bars with different orientations. Bin width = 20 ms; eye traces: scalebar, 60°; vertical scales on histograms: (A) 65 spikes/s; (B) 40 spikes/s; (C) 100 spikes/s; (D) 35 spikes/s.

One could argue that the process of pooling data from different cases on the same 2D map could hide visual topographies present in single cases. Although data from single cases were typically not sufficient to establish a possible visual topography in Péc, or lack thereof, they can help in visualizing

the extent of visuotopic order in small portions of this area. To this effect we analyzed sequences of receptive fields encountered during individual electrode penetrations, as illustrated in Figure 5 for 2 penetrations carried out in 2 hemispheres of one single monkey. The right hemisphere was cut sagittally (Fig. 5A) and the left hemisphere coronally (Fig. 5B). Looking at the sequence of the receptive-field locations found in penetration a (lower part of Fig. 5A), it is evident that we encountered a large scattering of receptive fields, which included scatters from ipsi to contralateral visual field (e.g., receptive fields 2-3), as well as from upper to lower visual field (receptive fields 4-5). Note that cells 2 and 3 were only 95 μm apart one from the other, and cells 4 and 5 were 210 μm apart. The total distance between cells 2 and 5 was about 500 μm : in this small region of cortex, 3 of the 4 quadrants of the visual field were represented.

The same result arises from the analysis of receptive-field sequence of penetration b, shown in the bottom part of Figure 5B. Moving the microelectrode a few tens of microns within the cortex, receptive fields “jumped” from lower to upper quadrant (receptive fields 3-4), and from periphery to central part of the visual field (receptive fields 6-7).

In summary, small regions of Péc yielded receptive fields that covered large portions of the visual field, apparently obeying no visuotopic order, and hence confirming the results obtained with the cumulative 2-D reconstructions of visual data.

Somatosensory Cells

The functional characteristics of Péc cells responding to passive somatosensory stimulation have been recently reported in a separate paper (Breveglieri et al. 2006). There, we found that 56% of cells ($n = 83/147$) were modulated by passive somatosensory stimulation. The majority of these (73%, $n = 60$) responded to joint rotations, whereas 24% responded to tactile stimulation (Fig. 6A,B). Joint-modulated cells were mostly activated by rotation of the upper limbs (82%). The majority of tactile receptive fields (61%) were located on the arms or on nearby regions of the trunk. A minority were located on the legs and on the rest of the trunk. The large majority of somatosensory responses (90%) were evoked by contralateral stimulation (Fig. 6C), but no somatotopic organization was apparent. Somatosensory cells, somatosensory submodalities, and body part representations were not clustered in Péc subregions (Fig. 6D), as better clarified by 2 exemplary groups of nearby cells reported in Figure 6E. Here we show that small areas in Péc contain somatosensory cells with receptive fields located in parts far away from each other on the body (from shoulder to hip, example 1, or from back to wrist, example 2). Here again, as also shown for Péc visual organization, a lack of topographic order is apparent.

Bimodal Visual and Somatosensory Cells

Neurons tested with both visual and somatosensory stimulations were divided in 4 categories: 34% ($n = 32$) were unimodal visual units, 25% ($n = 23$) were unimodal somatosensory units, 22% ($n = 21$) were bimodal units, and 19% were not driven by any of the sensory stimuli attempted in the present study.

No evident differences were found in the visual features of unimodal and bimodal cells, as shown in Figure 7. The represented visual field (Fig. 7A,C) and the relationship between eccentricity and the receptive-field size (Fig. 7B,D) are similar in these 2 groups of cells. The figure also shows that the visual

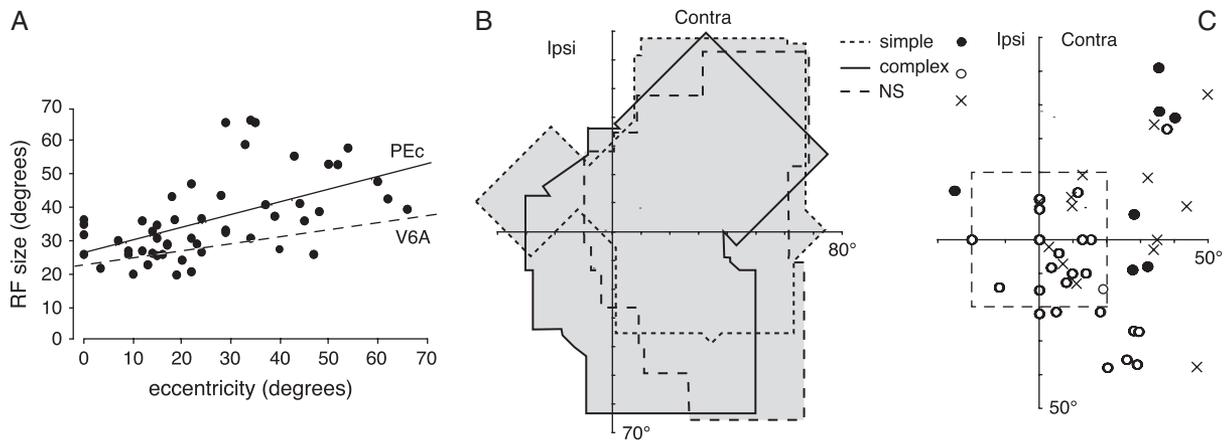


Figure 3. Visual cells of area PEc. (A) Receptive-field size versus eccentricity. Regression plot of receptive-field size (square root of area) against eccentricity for 55 PEc visual cells. The regression equation is $receptive\text{-}field\ size = 27.65^\circ + 0.3179 \times eccentricity$; regression line for V6A visual cells (dashed line) is reported for comparison ($receptive\text{-}field\ size = 21.0^\circ + 0.22 \times eccentricity$, see Galletti, Fattori, Kutz, et al. 1999). (B) Gray area indicates the total visual-field representation in area PEc, dotted line the visual-field represented by cells selective for simple stimuli, continuous line and dashed line those represented by cells selective for complex stimuli and for cells nonselective for the shape of visual stimulus respectively. Ipsi = ipsilateral visual field; contra = contralateral visual field. (C) Distribution of receptive field centers of cells preferring simple (filled circles, $N = 7$), complex (empty circles, $N = 24$) stimuli, and cells nonselective for the stimulus shape (crosses, $N = 14$). Dashed line outlines the central 20° of the visual field.

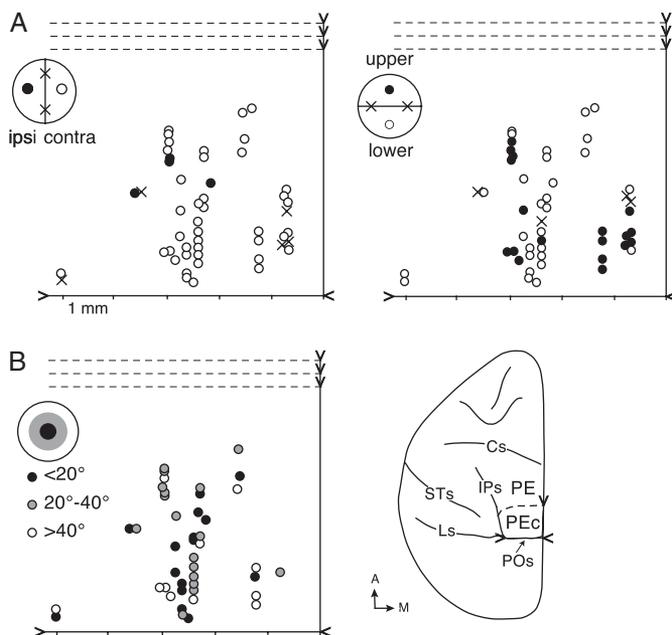


Figure 4. Visual organization of area PEc. (A) Representation of ipsilateral and contralateral hemifields (left), and of upper and lower hemifields (right), on a flat map of the caudal pole of the superior parietal lobule. Data from 4 hemispheres are summarized in each map. Different symbols indicate PEc cells whose receptive-field centers were in different parts of the visual field, as indicated at the top left part of each map. Location of each symbol in the map represents the location of each cell in area PEc. Receptive fields centered on the fovea were not considered. Maps from different cases were aligned posteriorly on the border between PEc and V6A, and medially on the interhemispheric line (see symbols $>$ $<$ on the maps and on the brain silhouette to the right; scale = 1 mm/division). Dashed lines on the maps indicate the cytoarchitectural borders between areas PEc and PE in single cases. (B) Eccentricity representation. White, gray, and black indicate PEc cells with receptive-field centers at different eccentricities, as indicated on the top left. PE=area PE (Pandya and Seltzer 1982). Other abbreviations as in Figure 1.

features were similar to those of the total population of PEc visual cells.

Figure 8 summarizes the somatosensory properties of unimodal and bimodal cells of area PEc. Unimodal somatosensory cells have receptive fields that cover a similar range of body

parts as the total population of PEc somatosensory cells (compare Fig. 8A with Fig. 6A). Also the preference of joint versus tactile stimulation (Fig. 8B) and the bias toward the contralateral part of the body (Fig. 8C) are very similar in unimodal and total cell population (see Fig. 6B,C).

Similarly to unimodal somatosensory, in bimodal neurons, somatosensory tactile receptive fields and joints modulating cell's activity were mostly located on upper limbs (Fig. 8D). We did not find any bimodal cell modulated by somatosensory stimuli with a receptive field on distal parts of the limbs, contrary to what observed in the unimodal somatosensory cells (see Fig. 8A). Bimodal cells could be modulated by passive joint rotation or by tactile stimulations in almost the same percentage (Fig. 8E), again in contrast with unimodal somatosensory cells that clearly preferred joint rotations (see Fig. 8B). Similarly to unimodal somatosensory cells, instead, the majority (90%) of somatosensory receptive fields of bimodal cells was located on the contralateral side of the body (compare Fig. 8F with Fig. 8C).

No systematic relationship was found in bimodal cells between the location of visual and somatosensory receptive fields, contrary to what observed in another visuo-somatosensory area containing bimodal cells (ventral intraparietal area [VIP], Duhamel et al. 1998). For instance, PEc cells with somatosensory receptive fields located on the shoulder, could have visual receptive fields located in either central, peripheral, contralateral, or ipsilateral part of the visual field (see Fig. 9A). In turn, cells with the visual receptive field in the same part of the visual field could have the somatosensory receptive field in different parts of the body (see Fig. 9B-D).

Figure 10 shows the distribution of unimodal and bimodal cells within area PEc. Visual and somatosensory cells are mixed together, but it is quite evident that they are distributed along a medio/lateral visuo-somatic trend, with the visual cells more concentrated in the postero-medial part of the area and the somatosensory cells in the antero-lateral part of PEc; bimodal visual/somatic cells are distributed in between. Apart from this trend, no clear clustering of sensory properties was observed, and in several recording sites we found cells with different functional properties one near to another.

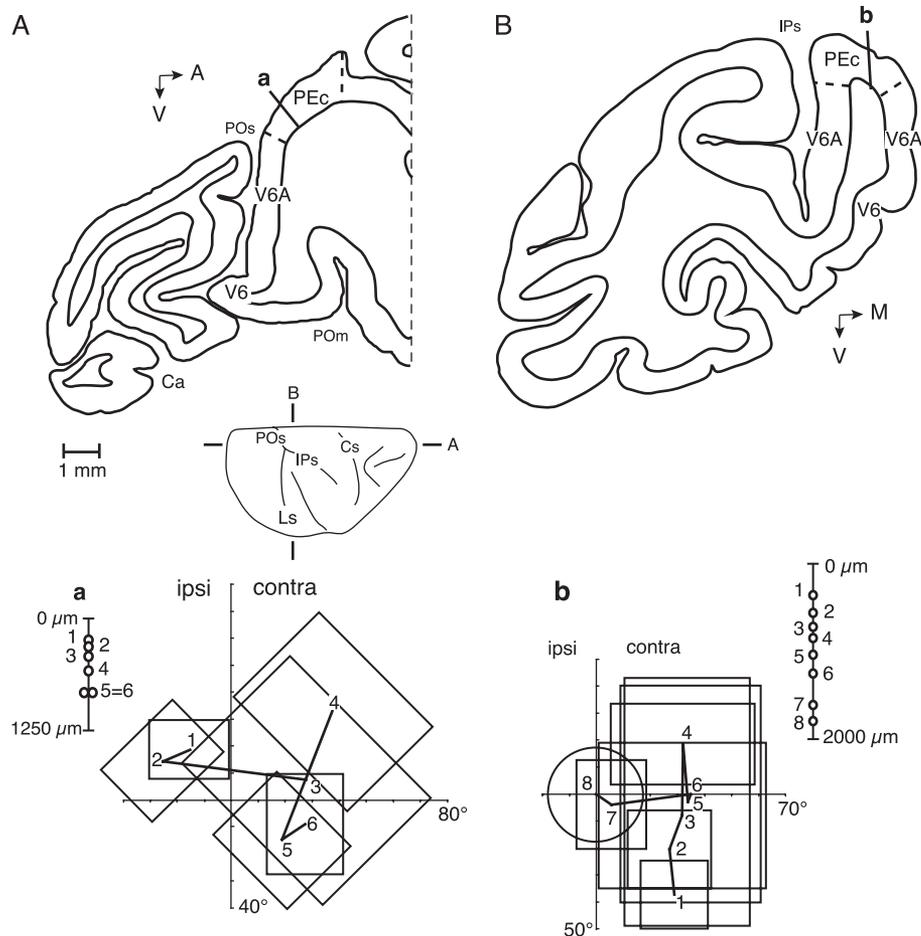


Figure 5. Visual representation in single penetrations carried out in area PEc. (A, B) Top: Parasagittal (A) and coronal (B) sections of 2 hemispheres of one case, taken at the levels shown on brain silhouette below. **a** and **b** show the reconstruction of 2 microelectrode penetrations carried out in PEc. Bottom: Visual receptive-field sequence of neurons encountered in each penetration. Cells are numbered progressively along the penetration track (shown aside each receptive-field sequence). Abbreviations as in Figures 1, 3, and 4.

Discussion

In the present study we characterized visual, somatosensory, and bimodal cells in area PEc, taking advantage of recently established cytoarchitectonic criteria to assign recording sites to this area (Luppino et al. 2005). Over half of the PEc cells were sensitive to visual stimulation, these being maximally activated by dark stimuli moving in a light background, as it is typically the case in natural scenes (Bex and Makous 2002). Moreover, the majority of cells required relatively complex, and dynamic visual stimuli for strong responses. Although analysis of the receptive fields of visual cells suggested that these were not retinotopically organized, receptive fields of adjacent neurons typically overlapped at least partially, showing no evidence of map discontinuities, as typically observed in occipital visual areas (Rosa 2002). Thus, the overall lack of visual topography may be the result of a large amount of receptive-field scatter, proportional to the large size of single cell receptive fields (Hubel and Wiesel 1974).

The lack of visual topography, together with the large receptive-field size, certifies the position invariance of the visual representation in PEc. It remains that in area PEc, even a broad, large-scale visuotopic order, showing at least different areal locations mirroring different visual-field quadrant representations, is apparently absent. The absence of a visuotopic order, together with the continuity of visual map in nearby neurons,

suggests that PEc elaborates visual information for a functional purpose which nothing has to do with the representation of the visual field as it is.

PEc has a high proportion of visual cells and also of somatosensory cells. The majority of somatosensory neurons responded to joint rotations, and a minority to tactile stimulations. There was no evidence of somatotopic organization. We found a polymodal convergence (visual and somatosensory) in 22% of PEc cells. We found a puzzling lack of systematic relationship between visual and somatosensory input onto single PEc cells. These bimodal cells were mixed with unimodal visual and unimodal somatosensory neurons without any evident sign of a spatial pattern of segregation. However, we observed a gradient of sensory inputs across PEc with more somatic input rostrally and laterally and more visual input caudally and medially.

Visual and Somatosensory Sensitivities in Area PEc

Recent studies (Battaglia-Mayer et al. 2001; Squatrito et al. 2001) have reported the presence of visual neurons in area PEc in percentages (65% and 45%, respectively) not dissimilar from the one we found in the present work. Results are remarkably similar, in particular if we take into account the different stimuli used (light bars in previous studies vs. light and dark stimuli in present report), the different extents of visual field tested

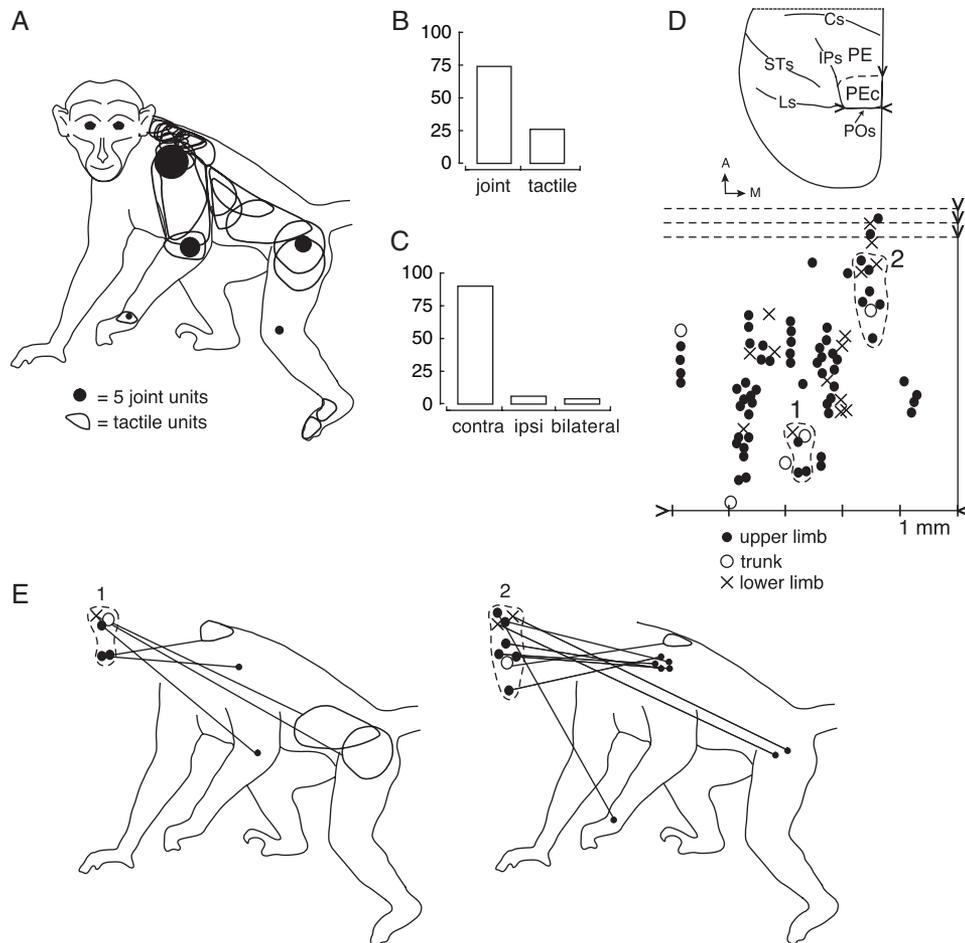


Figure 6. Somatosensory representation in area PEc. (A) Locations of somatosensory receptive fields in PEc: joints (black dots) and tactile receptive fields (thick lines drawn on the animal body). The size of each dot is proportional to the number of modulated units. All somatosensory receptive fields have been reported on the left side of the body. (B) Incidence of joint and tactile cells. (C) Incidence of contralateral (contra), ipsilateral (ipsi), and bilateral modulations. (D) Cortical distribution of PEc somatosensory cells. Bottom: Flattened summary map of the dorsal exposed surface of PEc showing the cortical distribution of somatosensory representation. Dashed lines labeled with numbers 1 and 2 encircle 2 groups of cells whose somatosensory receptive fields are located where illustrated in the monkey silhouettes in (E). It is evident that cells in nearby parts of the cortex had somatosensory receptive fields in different parts of the body. Abbreviations as in Figures 1 and 4.

(central 30° in previous studies vs. virtually the entire visual field here), and the location and extent of recording sites (the medialmost part of PEc in previous studies vs. the full extent of PEc here). Also in agreement with previous reports is the absence of a retinotopic map (Battaglia-Mayer et al. 2001; Squatrito et al. 2001).

Present data suggest that visual cells are not uniformly distributed across the area, showing an increasing gradient toward the postero-medial part of PEc. Such a gradient-like organization is relatively common in high-order sensory association areas, including for example the inferior temporal cortex (Rosa and Tweedale 2005).

Thanks to the sensitivity of several PEc visual cells to contracting/expanding optic flow stimuli, with a strong directional tuning (Raffi et al. 2002), it was suggested that PEc can code heading movements during locomotion. Present data on PEc visual responsiveness to complex visual stimuli (continuously moving and changing in size) support this hypothesis. This plausible role in controlling body stance during locomotion was suggested also for dorsomedial area (DM) of the marmoset (Lui et al. 2006), an area likely homologous to macaque area V6 (Rosa and Tweedale 2001, 2005). We suggest that area V6, rich in direction selective cells (Galletti, Fattori, Gamberini, et al.

1999), sends directional visual inputs for motor control to PEc through area V6A (Galletti et al. 2001) and thus enables PEc to perform visual analyses during locomotion.

Even the complete representation of inferior and superior contralateral quadrants up to the far periphery seen in PEc (present results) supports the view of a role for this area in locomotion, as in locomotion the entire visual environment sweeps across the retina, and PEc visual cells seem to be well equipped to evaluate visual information in that situation. Visually induced self-motion (vection) requires wide stimuli that are perceived as emanating from a distance (Dichgans and Brandt 1978; Delorme and Martin 1986; Howard and Heckmann 1989; Previc and Neel 1995). Thus, only those visual areas whose neurons have extremely large receptive fields and with a complete representation of the visual field up to the far periphery (like PEc, see Fig. 3) can qualify as the site of vection and other ambient visual processes.

In humans, there is a stronger parieto-occipital activation for expanding than for receding optical flow (Tootell et al. 1996). This same preference has been found in monkey area PEc (Raffi et al. 2002) and anecdotally confirmed here (see the examples of Fig. 2B–D with stronger responses to enlarging than to contracting visual stimuli). These data together suggest that it is

VISUAL PROPERTIES

UNIMODAL CELLS

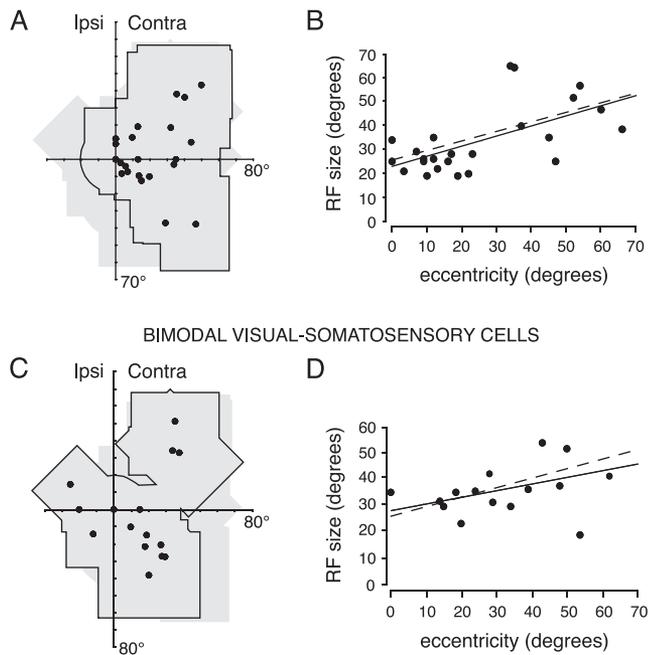


Figure 7. Visual properties of unimodal and bimodal Péc cells. (A, C) Continuous line: Visual-field representation of unimodal visual (A) and bimodal (C) cells; gray area: visual-field representation of all Péc visual cells (see Fig. 3). (B, D) Receptive-field (square root of area) size versus eccentricity for unimodal (B) and bimodal (D) cells (continuous lines). The regression equation is $\text{receptive-field size} = 23.03^\circ + 0.4051 \times \text{eccentricity}$ for unimodal cells ($N = 24$); $\text{receptive-field size} = 28.50^\circ + 0.2529 \times \text{eccentricity}$ for bimodal cells ($N = 15$). For comparison, regression line of Péc visual cells (dashed line) is also reported (see Fig. 3). Other conventions as in Figure 3.

plausible that Péc is involved in perception and/or in visually guided motor control of forward locomotion, which is of course more common with respect to backward locomotion in humans and monkeys.

The mixture of visual and somatosensory neurons observed in Péc, and the presence of bimodal visual/somatosensory cells as well, suggest a complementary regional integration within the area between the 2 sensory modalities. As the somatosensory activity is mainly referred to the limbs, this integration between visual and somatosensory information appears useful to coordinate motor activity during locomotion, particularly when one moves in a complex visual environment which requires a continuous interaction between body parts (upper limbs, trunk, lower limbs) and objects in the visual world. The particular sensitivity of these visual cells to stimuli continuously changing in form, size, and speed (present results), together with the presence in this same area of somatosensory cells sensitive to joint rotations or tactile stimulations (present results and Breveglieri et al. 2006) and of reach-related neural activity (Batista et al. 1999; Fattori et al. 2000; Battaglia-Mayer et al. 2001; Ferraina et al. 2001), fully agree with this view.

During locomotion, the brain has to relate body movements with the flow of visual information coming from the entire visual environment. The analysis of visual scene during locomotion is different from that required during prehension of small objects. In grasping an object, we need specific information about features and spatial location of that object, and the fact that visual and somatosensory receptive fields are in register

could be useful in that process. In visually guided locomotion this need is less compelling, given the more global interaction between body and visual environment. Thus, the nontopographic and nonregistered organization of visual and somatic information, as well as the interaction between these 2 inputs upon single cells observed in Péc seem to be in line with the suggested functional role of this area.

Another support for the role here suggested for Péc is provided by a case study (Kase et al. 1977) reporting topographical disorientation and abnormalities of body movement after damage of the posterior part of the superior parietal lobule, a region of the brain likely containing the homolog of monkey area Péc. The patient in the long period was not particularly impaired in reaching and grasping objects under visual guidance, but she was impaired in the whole-body interaction with a goal object in the surrounding visual world, like in lying in the appropriate way on a bed, or in modifying her body posture in an appropriate way in order to sit on a chair. Kases's patient showed long lasting behavioral abnormalities in whole-body movements for interacting with the visual environment. These functions, lost in Kase's patient due to the lesion in a region likely homolog to monkey area Péc, seem to be supported by the results reported here and in other studies about Péc, and strongly support the role of Péc in controlling locomotion and whole-body interactions with the visual environment.

More recent studies of human brain imaging reported activations in dorsomedial parietal regions of the brain likely including the human homologous of area Péc, in experiments where the subjects had to use vision in order to judge self-motion or to guide locomotion, to control postural balance, to guide vehicles (De Jong et al. 1994; Tootell et al. 1996; Brandt et al. 1998; Kleinschmidt et al. 2002). It remains unclear whether this brain region could be considered as the human homolog of area Péc, or the homolog of the neighboring area V6A, or even whether it includes both areas or even other neighboring areas with similar functional characteristics. Further experiments are needed to verify this point.

Is Péc an Independent Functional Area?

Area Péc contains both visual and somatosensory cells. The same kinds of cells are also contained in areas V6A (Galletti et al. 1996; Galletti, Fattori, Kutz, et al. 1999; Breveglieri et al. 2002) and MIP (Colby and Duhamel 1991; Klam and Graf 2003), with which Péc shares borders in the caudal part of the superior parietal lobule. Thus, the question might arise of whether Péc is an independent cortical area or is part of the nearby areas V6A and MIP. Another possibility is that these subdivisions have relatively indistinct borders, merging gradually into each other. The main arguments in favor of Péc as an independent area are centered on its distinctive architecture (Luppino et al. 2005) and a different set of anatomical connections (Johnson and Ferraina 1996; Matelli et al. 1998; Marconi et al. 2001). Moreover, despite some similarities in functional properties, there are also functional differences. For instance, visual receptive fields of Péc cells are on average larger than those of V6A cells for a same given eccentricity (see Fig. 3A), and a lower percentage of Péc cells shows strong responses to simple visual stimuli such as bars and spots, in comparison with V6A (see Galletti et al. 1996; Galletti, Fattori, Kutz, et al. 1999). Visual cells of area MIP are insensitive to the direction of movement of visual stimuli (Colby and Duhamel 1991), whereas almost all Péc

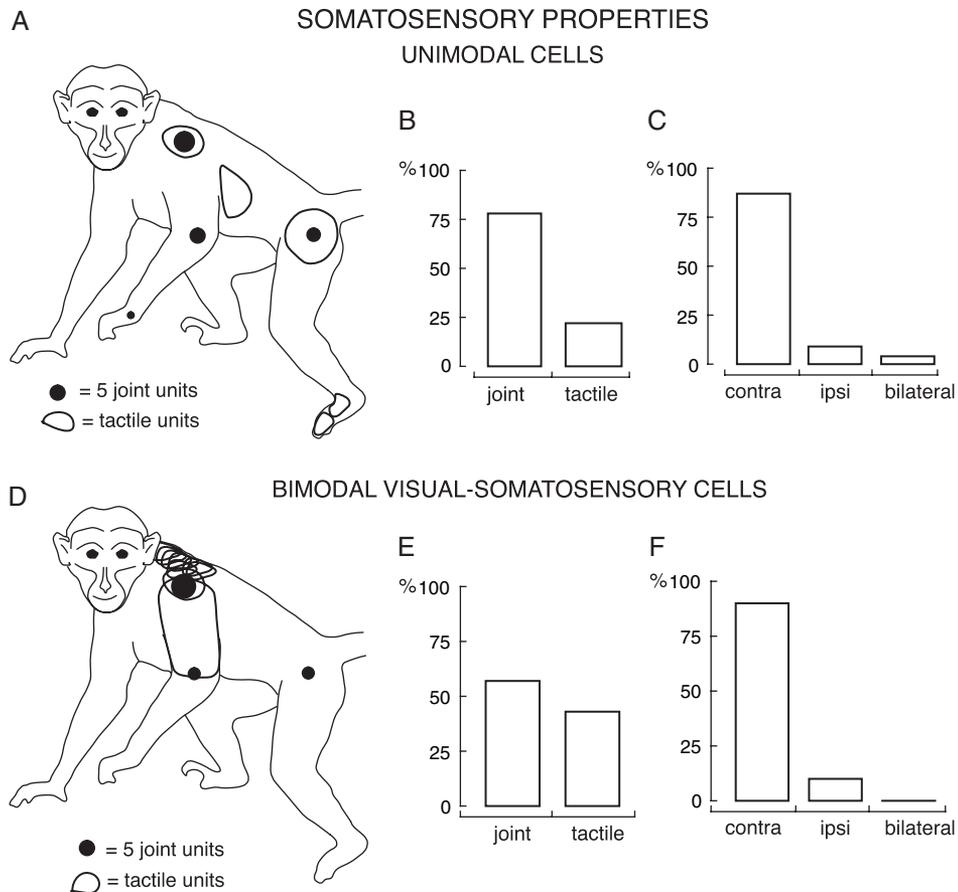


Figure 8. Somatosensory properties of unimodal and bimodal PEC cells. (A, D) Locations of joints (black dots) and of tactile receptive fields (thick lines drawn on the animal body) of unimodal (A) and bimodal (D) cells. All somatosensory receptive fields have been reported on the left side of the body. (B, E) Incidence of proprioceptive and tactile modulations for unimodal (B) and bimodal (E) cells; (C, F) incidence of contralateral, ipsilateral, and bilateral somatosensory modulations for unimodal (C) and bimodal (F) neurons. Conventions as in Figure 6.

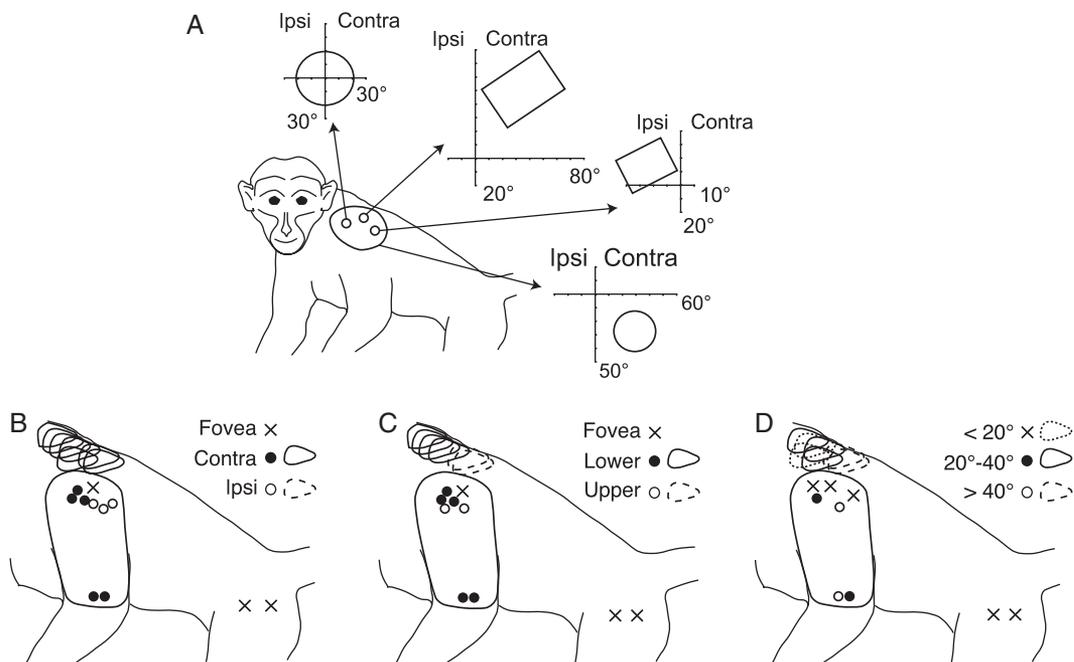


Figure 9. Relationships between body and visual-field representations in bimodal PEC cells. (A) Visual receptive-field locations of 4 bimodal cells activated by somatosensory stimuli applied on the shoulder. (B-D) Locations of tactile receptive fields (thick lines drawn on the animal body) and joints (filled and open circles and crosses) modulating bimodal cells. Somatosensory receptive fields are represented with crosses, continuous and dashed lines according to the location of the visual receptive field, as indicated in the right upper part of each inset. Cells having visual receptive field on the meridians were not considered. Other conventions as in Figures 3 and 6.

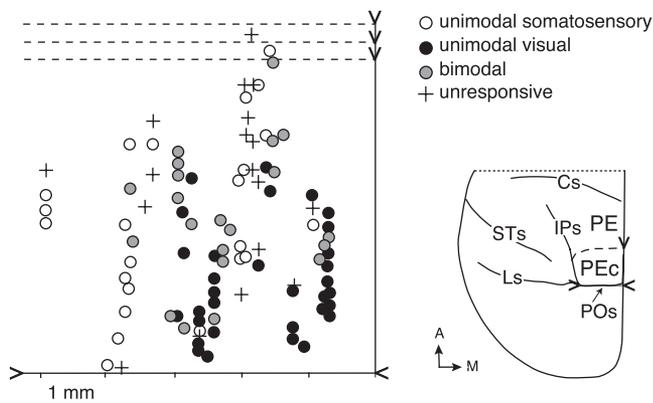


Figure 10. Cortical distribution in PEc of unimodal visual, unimodal somatosensory, bimodal, and unresponsive cells. The flat map of the caudal pole of superior parietal lobule summarized data from 4 hemispheres. Details as in Figures 1 and 4.

cells were direction selective (Squatrito et al. 2001). Finally, the present data show that visual cells in PEc are more concentrated in the postero-medial region of the area (see Fig. 10), at the border with V6A, whereas visual cells in V6A are more concentrated in the ventral part of the area (Fattori et al. 1999; Galletti, Fattori, Kutz, et al. 1999), at the opposite side with respect to the border with PEc. The same is also true for area MIP, which is known to contain a higher percentage of visual cells in its ventral part (Colby and Duhamel 1991), far from the border with PEc. In other words, the regions with the highest number of visual cells in the 3 nearby areas PEc, V6A, and MIP are not in continuity, as it would be perhaps expected if these were parts of the same functional area.

The incidence of somatosensory cells in PEc (56%, present results and Breveglieri et al. 2006) is higher than that in V6A (32%, Breveglieri et al. 2002); the incidence of somatosensory cells in area MIP has not yet been reported. PEc somatosensory receptive fields are mostly located on the proximal parts of the limbs (present results and Breveglieri et al. 2006), whereas in V6A they encompass both proximal and distal parts of the arms (Breveglieri et al. 2002), and in area MIP they are mostly located on distal part of the arms (Colby and Duhamel 1991).

In summary, on balance, the evidence argues against PEc, V6A, and MIP being part of a same cortical area. Recently, it was proposed that the various primate posterior parietal areas emerged as differentiations of a single somatotopic map (Manger et al. 2002). Our data do not contradict this hypothesis, given that the somatosensory receptive fields in PEc are more proximal than those in area MIP (Colby and Duhamel 1991) and in VIP (Duhamel et al. 1998), which become gradually more located in distal limb (in MIP) or face (in VIP) as more lateral parietal areas become involved. Also the different cytoarchitectural patterns of these areas do not contradict this view, as in the parietal areas of the ferret different cytoarchitectures in the face versus body representations were found (Manger et al. 2002). In summary, the differences between PEc and more lateral parietal areas could reflect functions related to different body parts, without necessarily implying that these areas perform very different neural operations. We believe that PEc and the adjoining areas in superior parietal lobule mentioned so far are different functional areas, some of them (like VIP) likely mainly involved in the representation of the movements of external objects toward some body parts, and others (like PEc,

V6A, and MIP) likely mainly involved in guiding body interaction with the visual world.

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