NEUROSYSTEMS

Functional organization of inferior parietal lobule convexity in the macaque monkey: electrophysiological characterization of motor, sensory and mirror responses and their correlation with cytoarchitectonic areas

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Abstract

The general view on the functional role of the monkey inferior parietal lobule (IPL) convexity mainly derives from studies carried out more than two decades ago and does not account for the functional complexity suggested by more recent neuroanatomical findings. We investigated this issue by recording multi- and single units in the IPL convexity of two monkeys and characterizing their somatosensory, visual and motor responses, using a naturalistic (ethologically relevant) approach. These properties were then matched with IPL cytoarchitectonic parcellation. A further aim of this study was to describe the general properties and the localization of IPL mirror neurons, until now not investigated in detail. Results showed that each studied cytoarchitectonic subdivision of the IPL (PF, PFG, PG) is characterized by specific sensory and motor properties. A key feature of the recorded motor neurons is that of coding goal-directed motor acts. Motor responses are somatotopically organized in a rostro-caudal fashion, with mouth, hand and arm represented in PF, PFG and PG, respectively, with a certain degree of overlap between adjacent representations. In each subdivision the motor activity is associated with specific somatosensory and visual responses, suggesting that each area organizes motor acts in different space sectors. Mirror neurons have been found mainly in area PFG and their general features appear to be very similar to those of ventral premotor mirror neurons. The present data suggest that the IPL plays an important role in both action organization and action understanding and should be considered part of the motor system.

Introduction

Following the pioneering work of Mountcastle, Hyvärinen and their coworkers (Mountcastle *et al.*, 1975; Leinonen & Nyman, 1979; Leinonen *et al.*, 1979; Lynch, 1980; Hyvärinen, 1981), several studies investigated the functional organization of the inferior parietal lobule (IPL) of the monkey. Most were concerned with the functional properties of areas located inside the intraparietal sulcus (IPS), such as anterior intraparietal area (AIP) (Taira *et al.*, 1990; Murata *et al.*, 2000), ventral intraparietal area (VIP) (Colby *et al.*, 1993; Duhamel *et al.*, 1998; Avillac *et al.*, 2005, 2007) and lateral intraparietal area (LIP) (Gnadt & Andersen, 1988; Andersen *et al.*, 1990, 1997; Barash *et al.*, 1991a, b; Duhamel *et al.*, 1992; Colby *et al.*, 1996; Toth & Assad, 2002; Ipata *et al.*, 2006), while some have been devoted to the areas forming the convexity of the IPL. Of these latter studies, most have examined the neuronal properties of its caudal part (MacKay, 1992; MacKay *et al.*, 1994; Battaglia-Mayer *et al.*, 2005; Constan-

tinidis & Steinmetz, 2005; Raffi & Siegel, 2007), and just a few that of its rostral end (Gallese *et al.*, 2002; Yokochi *et al.*, 2003; Fogassi *et al.*, 2005; Gardner *et al.*, 2007).

These studies showed that the IPL contains a rich variety of neurons responsive to different sensory stimuli and that discharge in association with different types of movements. These findings led to the idea that the IPL is not only involved in associating different sensory modalities, as previously recognized, but also plays a role in motor control. Finally, these early studies also showed that the motor responses of the IPL are somatotopically organized, with the mouth field located rostrally, followed by the hand field, and by the arm and eye fields caudally (Hyvärinen, 1981).

A particularly interesting result of studies focused on the rostral IPL has been the demonstration that most of its neurons discharge in association with specific motor acts, i.e. movements with a specific goal (Gallese *et al.*, 2002; Yokochi *et al.*, 2003; Fogassi *et al.*, 2005) and that the discharge intensity of the majority of these neurons depends on the final goal of the action in which the motor act is embedded (e.g. grasping for eating or grasping for placing) (Fogassi *et al.*, 2005). A further important result concerning rostral IPL has been the description of neurons that discharge during both the

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execution and the observation of specific motor acts (parietal mirror neurons; Gallese *et al.*, 2002; Fogassi *et al.*, 2005), suggesting a role of the IPL in action understanding.

The main aim of the present study was to re-investigate the general functional organization of the convexity of the IPL originally described by Hyvärinen (1981) and to correlate its neural properties with the cytoarchitectonic of this region, as recently assessed by Gregoriou *et al.* (2006). Our second aim was to describe the properties of IPL mirror neurons and their localization in relation to neurons with other properties.

Materials and methods

The experiments were carried out on two awake (M1 and M2), partially restrained macaque monkeys (*Macaca nemestrina*). All experimental protocols complied with the European law on the humane care and use of laboratory animals and were approved by the Veterinarian Animal Care and Use Committee of the University of Parma as well as by the Italian Minister of Health.

Before recordings, the monkeys were habituated to seat on a primate chair, to be touched by the experimenters and to have their limbs mobilized. They were also trained to interact with the experimenters (see below). After the habituation period, the monkeys were operated under general anesthesia (ketamine hydrochloride, 15 mg/kg i.m.) and a system for keeping the monkey head fixed to the head-holder of the primate chair and a titanium recording chamber were implanted. The surgical procedures were the same as previously used in our laboratory (Fogassi *et al.*, 1996a, 2005).

Recording procedures

During the experiments monkeys were seated on a primate chair with their head fixed. Neuronal recording was performed using a multi-electrode device (Alpha Omega Eng., Nazareth, Israel) that was attached to the head holder. This device consisted of a head-stage, holding eight glass-coated microelectrodes (impedance 0.5–1 MΩ) spaced 2 mm from each another, in a single row. This inter-electrode distance was chosen in order to collect data simultaneously on neurons located several millimeters apart and to compare their properties. Each microelectrode could be lowered independently by an electric engine, controlled by a dedicated software package (EPS; Alpha Omega), with an angle of 35° in order to penetrate the dura perpendicularly. The definition of the recording and microstimulation parameters, visualization of the depth values of electrode penetrations, and acquisition of multiunit activity were performed by means of dedicated software (ALPHA MAP and MCPPLUS; Alpha Omega). The output signal from each electrode was pre-amplified and sent to a PC for acquisition and subsequent analysis. Individual action potentials were also isolated, by using a dual voltage–time window discriminator (Bak Electronics, Germantown, MD, USA). The output signal from the voltage–time discriminator was monitored on an oscilloscope and fed to a PC for acquisition (Lab-View-based software) and subsequent statistical analysis.

A contact-detecting circuit was used to align neural activity with external events. The signal produced by the closure of this circuit was sent to a PC whenever the monkey touched a metal surface. Signals from this circuit were also used to align neural activity during visual and somatosensory stimulation. In these cases the signal was triggered either by the experimenter by manually closing the circuit whenever a stimulus was presented to the monkey, or automatically when it touched the monkey's skin. Histograms of the neuronal activity were constructed by averaging ten individual trials.

The recording microelectrodes were also used for electrical microstimulation (train duration, 50 ms; pulse duration, 0.2 ms; frequency, 330 Hz; current intensity, 3–40 µA). The current strength was controlled on an oscilloscope by measuring the voltage drop across a 10-kΩ resistor in series with the stimulating electrode.

A recording chamber was stereotaxically implanted, in a position such as to record from a cortical region extending, in the rostro-caudal axis, from the hand and mouth fields of area F1 (primary motor cortex) to the posterior part of the IPL, and, in the medio-lateral axis, from the lateral part of the superior parietal lobule (SPL) to the superior temporal gyrus.

The eight-electrode row was oriented along a medio-lateral axis. The first recording sessions started in the anterior part of the chamber, in order to identify the hand and mouth fields of area F1 and of primary somatosensory cortex (SI). Functional identification was based on the properties emerging from clinical testing of neurons responding to active movements and passive stimulation, and on types of movements evoked by electrical microstimulation. Once these regions were identified, the subsequent recording sessions were carried out moving the electrode row caudally in steps of 1 mm.

During each experimental session each electrode was inserted one after the other inside the dura until the first neuronal activity was detected for each of them. Each electrode was then deepened into the cortex independently one from the other, in steps of 500 µm until the border between the gray and the white matter was reached. At each site, multiunit and single-unit activities were recorded and their correlation with any type of sensory stimulation and motor activity was noted on a protocol and subsequently inserted into a database.

In a subsequent experimental phase we further recorded the region in which mirror neurons were found in order to extend the database of this class of neurons to evaluate their properties better. These data were not included in the general mapping study in order to avoid sampling bias.

Clinical testing of multiunit and single-unit activity

In order to characterize neuronal properties the following testing procedures were applied.

'Light touch' was assessed by lightly touching the skin or bending the hairs with cotton wad or small brushes, or by blowing air puffs on small body-parts. 'Deep touch' was assessed by applying pressure to restricted cutaneous territories by touching with a stick, by tapping with fingers or by squeezing muscle bellies. Directional selectivity of neurons responding to tactile stimuli was assessed by moving them in different directions. 'Joint' responses were tested by means of slow and fast mobilization of joints. All testing was performed on different body-parts with the monkey's eyes open and closed.

Visual properties were studied by presenting three-dimensional (3D) objects (e.g. food items and solids) of different shape, size and orientation at different space locations and distances from the monkey. The objects were presented to the free-gazing monkeys by removing a screen occluding their vision, or by abruptly introducing them in the visual field by hand or by means of a stick (in this latter case the experimenter's hand was not visible). The same stimuli were also moved along tangential planes following linear or circular trajectories at different distances from the monkey or along trajectories directed toward or away from the different body-parts. These stimuli were presented by hand. Spots of light generated by a laser pointer were also projected and moved on a screen, located in front of the monkey.

Neural responses to the observation of motor acts were also tested. To this end, an experimenter performed various hand or mouth motor

acts in front of the monkey. Hand motor acts were the following: grasping, manipulating, tearing, breaking, holding, placing, releasing and taking away objects. Some of these acts were performed with two hands (e.g. bimanual holding or manipulation). Mimed hand motor acts were also performed in front of the monkey (for details see Gallese *et al.*, 1996). Mouth motor acts were as follows: biting, holding with the teeth, breaking, chewing, sucking, licking (for details see Ferrari *et al.*, 2003a). All hand motor acts were performed at different distances from the monkey with the right, the left or both hands. Hand and mouth motor acts were performed in different space sectors with respect to monkey body position and with different directions.

In addition to object-related movements, non-object-related movements, done by the experimenters, were also presented. They consisted of orienting the head or the trunk in different directions, displacing arms or legs (e.g. flexion, extension, abduction, etc.) and walking.

All recorded neurons were also tested for their motor properties. Hand- and arm-related activity was assessed as follows. Monkeys were presented with pieces of food or objects of different size, shape and orientation, located in different space quadrants, with respect to the monkey's body. The monkeys were allowed to reach for and grasp them, and, in the case of food, to bring it to the mouth and eat it. Hand movements were tested using objects that elicit different types of grips. The following types of grips were evoked: 'precision grip', 'finger prehension' and 'whole hand prehension'. Precision grip requires the opposition of the pulpar surface of the last phalanx of the index finger and of the thumb, or of the thumb and the radial surface of the last phalanx of the index finger ('side grip'). Precision grip is used to grasp small objects. Finger prehension is performed by using all fingers, but not the palm. It is used for grasping middle-sized objects. There are two types of whole hand prehension. In both, the fingers are wrapped around the object with the palm in contact with it, but in one the thumb is opposed to the other fingers (as in grasping a sphere), while in the other the thumb is not used (as in grasping a syringe filled with juice). The whole hand is performed to grasp large objects. Other types of hand-related movements (manipulation, tearing, breaking, placing) were also studied.

In order to dissociate neural responses related to grasping from those related to reaching, food or objects were introduced near the monkey's body, so that they could be grasped without extending the arm. Neural responses were attributed to reaching when they required arm projection in space and were not present during grasping with the arm restrained. In addition, food or objects were presented in different positions of the reaching space in order to identify reaching neurons also on the basis of their possible spatial selectivity. Simple arm extension was distinguished from reaching by putting a large panel close to the monkey so that it extended the arm to push it away, without performing any reaching or grasping act.

Mouth movements were studied by giving the monkey pieces of food of different size and hardness or a syringe filled with juice. Different types of stimuli elicited different types of mouth movements such as biting, breaking, chewing, sucking and licking.

Arm-, hand- and mouth-related motor properties were studied both in light and in dark conditions so as to evaluate neural properties with or without visual guidance.

Eye-related motor activity was studied by presenting objects of interest, such as pieces of food, in different parts of the visual space and moving them in different directions. Spots of light, generated by a laser pointer, were projected on a screen located in front of the monkey and moved with different speed and direction. This testing enabled us to elicit fixation, saccades and pursuit eye movements.

Data analysis and map construction

The functional properties of neural activity (single neurons and multiunit activity) identified at each recoding site was noted for each penetration and used to reconstruct the functional organization of the IPL. Only sites located between the cortical surface and a depth of 3000 μm were included in the database. This depth was chosen in order to include the cortex lying inside the dimples present in the IPL convexity (mainly in PF and PFG, see Fig. 1A). Thus, seven was the maximum number of recording sites (steps of 500 μm) in each penetration. Only those penetrations in which three or more sites showed reliable neural activity were included in the analysis. Cortical sites deeper than 3000 μm were used for establishing the location of intraparietal, lateral and superior temporal sulci and to identify the cortical areas located inside the bank of the various sulci. The properties of neurons recorded from these sites will not be described in the present study.

For each penetration site, we identified the properties of single and multiunit activity. Responses to somatosensory and visual stimuli and their characteristics were marked. The same was done for the somatomotor- (hence called 'motor') and eye movement-related activity. The presence of these properties was reported on penetration maps in terms of percentage of sites per penetration in which each property was found.

Single neuron analysis

In the case of mirror neurons, and occasionally in the case of other neuron categories, the activity was acquired in response to sensory stimuli and during movement execution (ten trials for each condition). In order to assess whether the neuron activity significantly differed in the different experimental conditions, the activity of neurons, expressed as mean firing rate (spikes/s, bin width 20 ms), was measured in two different time epochs. The first corresponded to the background activity before stimulus application/presentation, in the case of sensory stimulation, or movement initiation (2000–1000 ms before alignment). The second corresponded to a 500-ms time interval related to the passive or active tested event. The neuron activity was then analysed by using a two-way ANOVA (factors: Condition, Epoch), followed by Newman–Keuls *post-hoc* comparisons, in order to assess the difference in activity between experimental conditions. All analyses were performed with a significance criterion of $P < 0.05$.

Histology, reconstruction of the recorded area and anatomo-functional comparison

Before the animals were killed, electrolytic lesions (10-μA cathodic pulses per 10 s) were performed at known coordinates at the external borders of the recorded region. After 1 week, each animal was anesthetized with ketamine hydrochloride (15 mg/kg i.m.) followed by an i.v. lethal injection of pentobarbital sodium and perfused through the left cardiac ventricle with buffered saline, followed by fixative. The brain was then removed from the skull, photographed, and then frozen and cut coronally. Each second and fifth section (60 μm thick) of a series of five were stained using the Nissl method. The locations of penetrations were then reconstructed on the basis of electrolytic lesions, stereotaxic coordinates, depths of penetrations and functional properties. More specifically, penetrations deeper than 3000 μm located inside the IPS with properties typical of AIP and LIP (see Andersen *et al.*, 1997; Rizzolatti *et al.*, 1997; Colby, 1998) were used to localize the medial border of IPL convexity and to identify different rostro-caudal levels. Briefly, AIP is characterized by the
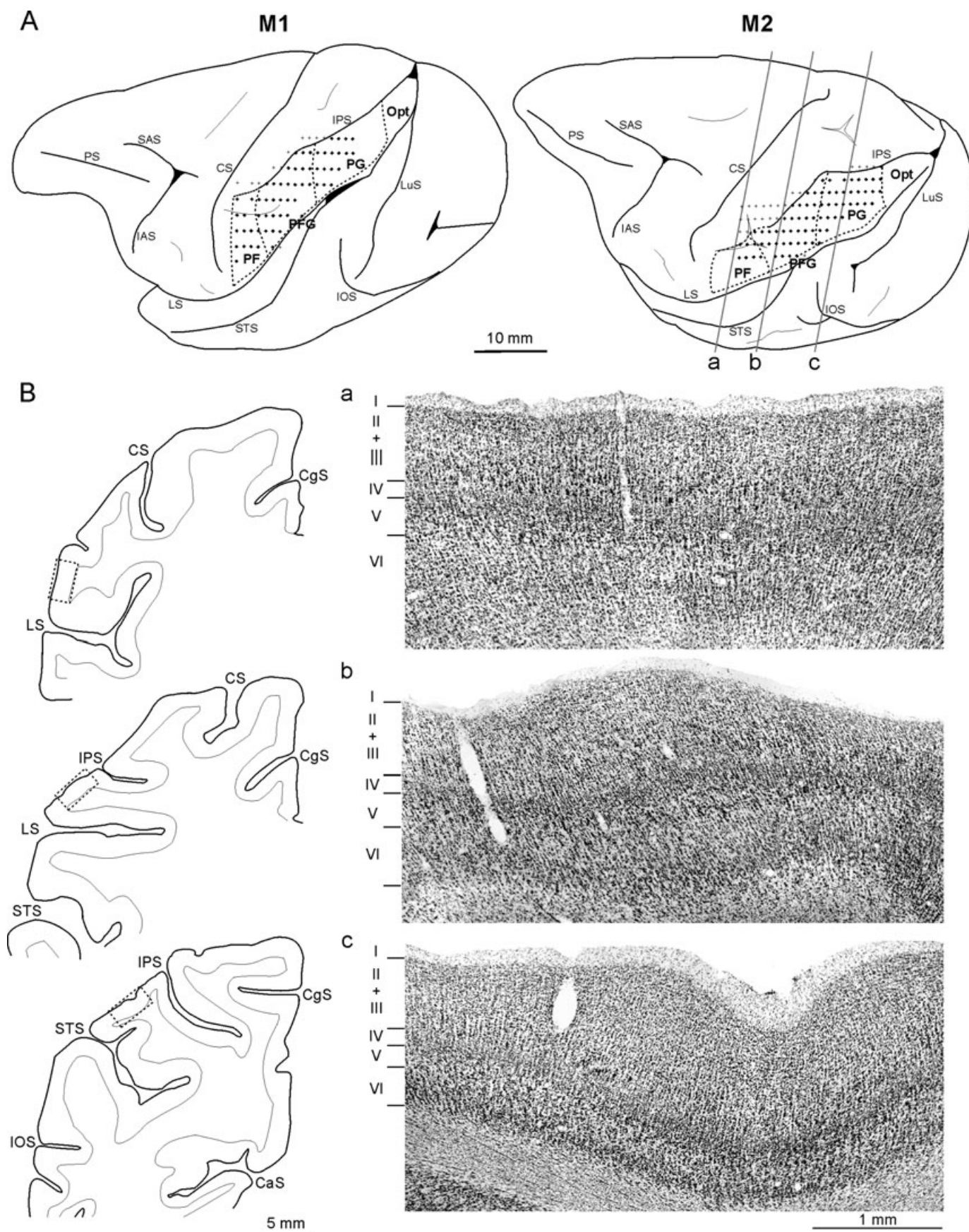
systematic presence of motor and visuomotor neurons, the discharge of which is related to grasping and manipulation and to observation of graspable objects of specific size and shape. In addition, somatosensory responses are virtually absent. LIP is characterized by strong responses during saccades and fixation. Very often the response precedes the saccade movement. The lateral borders of IPL were identified by the penetration depth (more than 3000 μm) and by the appearance of acoustic properties. The rostral border of the recorded region was defined based on the disappearance of the properties typical of SI.

Subsequently, the cytoarchitectonic features of IPL convexity areas were identified, based on the criteria defined by Gregoriou *et al.* (2006). As cytoarchitectonic features often change gradually from one region to another, the borders between adjacent areas were drawn in the middle of transitional zones (about 0.5 mm wide). The reconstructed grid was then related to this cytoarchitectonic parcellation. This allowed us to attribute the functional properties of each penetration to a specific cytoarchitectonic area. The number of sites in which each property was present in each area was then calculated and expressed as percentage of the total number of sites of that area. The frequency of each functional property in each area was then compared with that of the same property in the other two areas, by using a Fisher exact probability test.

Results

General organization of IPL convexity

Anatomical localization and cytoarchitectonic properties of the recorded region

A lateral view of the left hemispheres of the two monkeys (M1 and M2) is presented in Fig. 1A. The figure illustrates the investigated region (penetration grid) and the cytoarchitectonic parcellation of IPL (areas PF, PFG and PG), properties of which are described below.

In both monkeys, the studied region extended rostro-caudally from the posterior part of the primary somatosensory cortex to the posterior half of the IPL, with the exception of its caudalmost part. It comprised the cortex between the IPS, medially, and the lateral sulcus (LS) and the superior temporal sulcus (STS), laterally. Some penetrations were also made in the most lateral sector of the SPL, the lateral part of the primary sensory cortex, and the areas located in the bank of IPS (AIP,

VIP and LIP). A few penetrations were performed in the superior temporal cortex. The functional properties of the areas located around IPL provided important landmarks to delimit the region of focus of the present study, but their description is outwith the current aim and will be not presented here.

The cytoarchitectonic parcellation was based on the criteria described by Gregoriou *et al.* (2006). Photomicrographs showing sections representative of the cytoarchitectonic organization of three areas (PF, PFG, and PG), taken from M2 are presented in Fig. 1B. Area PF (Fig. 1Ba) is characterized by the presence of a cell size gradient in layer III with medium-sized pyramids spread in its lower half, a homogeneous layer IV and a layer V characterized by rather small pyramids. Area PFG (Fig. 1Bb) shows a less distinct cell size gradient in layer III, with medium-sized pyramids concentrated mainly in its lowest part. The most distinctive feature of PFG as compared with PF and PG is its prominent layer V, characterized by the presence of medium-sized as well as by scattered large pyramids. Area PG (Fig. 1Bc) is more homogeneous than PF and PFG in layer III, where density is also increased. The border with layer IV is sharply defined and layer V is prominent and populated by small densely packed pyramids.

Active and passive somatotopic maps

The data of the present study are based on 132 penetrations, 60 made in IPL of M1 and 72 in that of M2. In total we studied 245 sites in M1 (mean site per penetration = 4.08) and 352 in M2 (mean site per penetration = 4.89).

Table 1 shows the numbers of penetrations and sites in which we observed responses to somatosensory and visual stimuli, or activity related to body-parts (motor activity) and eye movements. There were many more sites showing body-parts-related motor activity than sites with eye-movement-related activity. Note, however, that no records were made in the caudalmost part of IPL, where eye-movement-related activity is typically found (Mountcastle *et al.*, 1975; Hyvärinen, 1981; Andersen *et al.*, 1990; Battaglia-Mayer *et al.*, 2005; Raffi & Siegel, 2007).

Figure 2A illustrates the localization, in IPL, of responses to somatosensory and visual stimuli and of motor activity associated with body-parts and eye movements. It is evident that body-parts motor activity (green) is distributed along the whole recorded region.

TABLE 1. Types of responses recorded in the two monkeys

Responses observed	M1		M2	
	Penetrations (total *n* = 60)	Sites (total *n* = 245)	Penetrations (total *n* = 72)	Sites (total *n* = 352)
Motor	52/60 (86.6%)	177/245 (72.2%)	62/72 (86.1%)	220/352 (62.5%)
Eye-related	11/60 (18.3%)	35/245 (14.2%)	23/72 (31.9%)	74/352 (21%)
Somatosensory	40/60 (66.6%)	99/245 (40.4%)	40/72 (55.5%)	159/352 (45.1%)
Visual	46/60 (76.6%)	117/245 (47.7%)	59/72 (81.9%)	212/352 (60.2%)

FIG. 1. Reconstruction of the penetrations and cytoarchitectonic subdivision of the recorded region. (A) Dorsolateral view of the two studied hemispheres, in which the penetration grids are superimposed on the cytoarchitectonic parcellation of IPL convexity. Individual penetrations are indicated by filled diamonds (IPL) and crosses (non-IPL). Dashed lines indicate the borders between adjacent cytoarchitectonic areas. In M2, lines a, b and c indicate the levels at which the coronal sections, shown in B, were taken. (B, left) Outlines of three sections passing through three different IPL cytoarchitectonic areas (a, PF; b, PFG; c, PG). The small dotted rectangles indicate the sector of the coronal section corresponding to the low-power photomicrographs of the Nissl-stained sections shown on the right. (B, right) Roman numbers correspond to the different cortical layers. Cytoarchitectonic areas are identified according to Gregoriou *et al.* (2006). CaS, calcarine scissure; CgS, cingulate sulcus; CS, central sulcus; IAS, inferior arcuate sulcus; IOS, inferior occipital sulcus; IPS, intraparietal sulcus; LS, lateral sulcus; LuS, lunate sulcus; PS, principal sulcus; SAS, superior arcuate sulcus; STS, superior temporal sulcus.
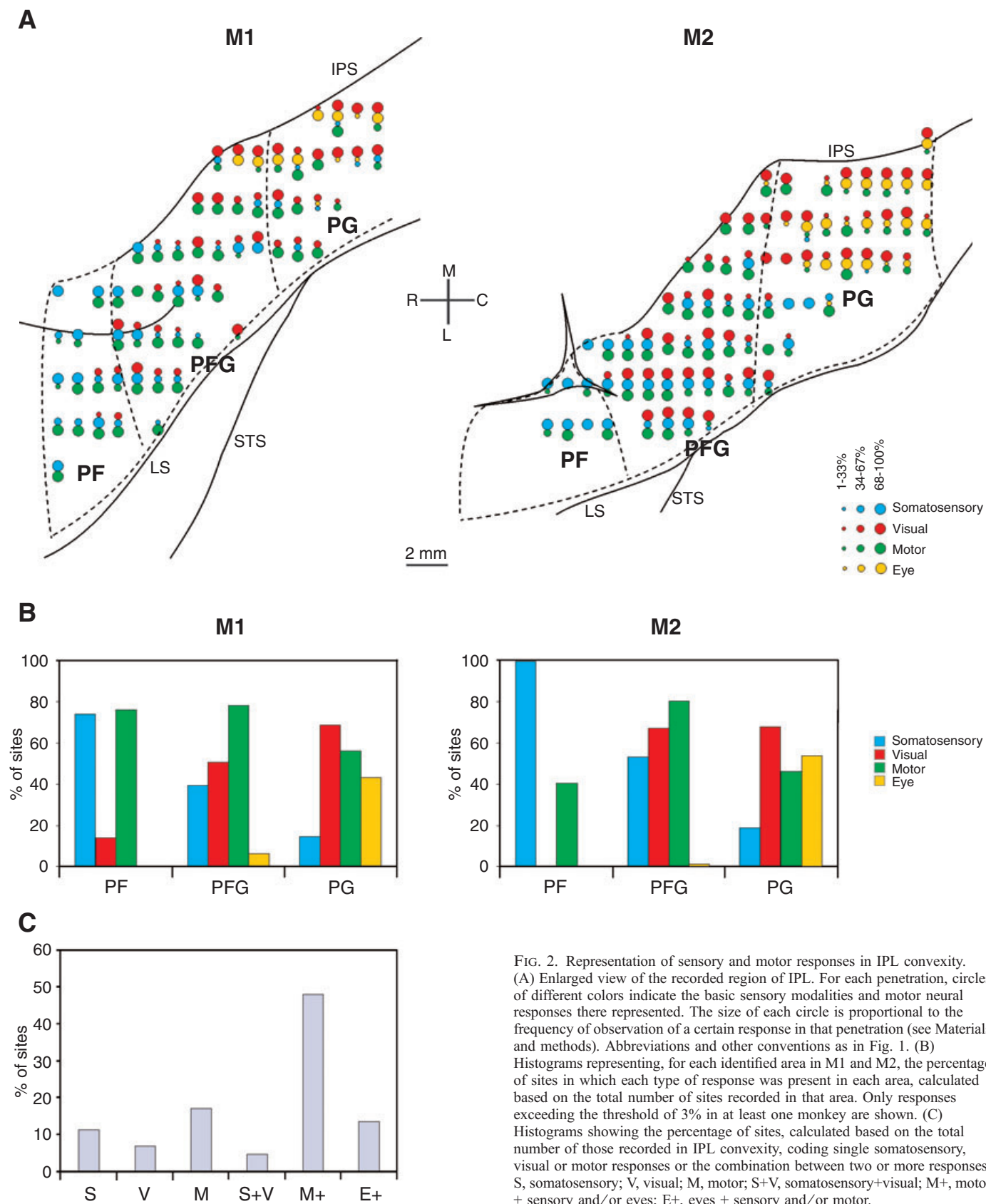
FIG. 2. Representation of sensory and motor responses in IPL convexity. (A) Enlarged view of the recorded region of IPL. For each penetration, circles of different colors indicate the basic sensory modalities and motor neural responses there represented. The size of each circle is proportional to the frequency of observation of a certain response in that penetration (see Materials and methods). Abbreviations and other conventions as in Fig. 1. (B) Histograms representing, for each identified area in M1 and M2, the percentage of sites in which each type of response was present in each area, calculated based on the total number of sites recorded in that area. Only responses exceeding the threshold of 3% in at least one monkey are shown. (C) Histograms showing the percentage of sites, calculated based on the total number of those recorded in IPL convexity, coding single somatosensory, visual or motor responses or the combination between two or more responses. S, somatosensory; V, visual; M, motor; S+V, somatosensory+visual; M+, motor + sensory and/or eyes; E+, eyes + sensory and/or motor.

Somatosensory responses (blue) are mainly present in the rostral half of the explored region, while visual responses (red) are evenly distributed throughout, but lacking in its very rostral part. Eye-movement-related activity (yellow) is limited to the caudalmost part of IPL.

Figure 2B illustrates the distribution of different functional properties in the three recorded cytoarchitectonic areas (PF, PFG and PG). Each shows a specific representation pattern. Area PF is characterized by a rich representation of somatosensory responses. This representation is higher than that present in both PFG and PG ($P < 0.001$ for both monkeys). In turn, area PFG has a richer representation of somatosensory responses than that of PG ($P < 0.001$ for both monkeys). Visual properties show an opposite trend. In both monkeys visual responses in area PF were poorly (M1) or not (M2) represented ($P < 0.001$ with respect to both PFG and PG), whereas they are more frequent in PFG and even more so, at least in M1, in PG ($P < 0.05$). Motor properties were strongly and widely represented in all three subdivisions of the lobule, with certain variability between the two monkeys. However, activity associated with body-parts movements was more represented in PFG than in PG ($P < 0.005$ both monkeys) and PF ($P < 0.001$ M2 only). Eye-related activity (fixation, saccades and pursuit) were almost exclusively present in PG ($P < 0.001$ with respect to both PF and PFG).

The great majority of the recorded sites showed an association between sensory and/or motor properties. Figure 2C shows the percentage of sites in which the different sensory and motor responses were present, separately or in association. The most frequent associations occurred between motor responses and one or two sensory modalities (M+). The association between two sensory modalities in the absence of any motor response (S+V) occurred less frequently.

Motor responses

Motor activity was typically observed in association with goal-directed motor acts (reaching, grasping, etc.) rather than with simple movements (arm extension, finger flexion, etc.). At least using our naturalistic approach, we were unable to find any motor neurons whose discharge could be correlated to individual movements.

The most frequently observed forelimb motor act was grasping (48% of recorded motor neurons) followed by reaching (12%). Responses related to grasping could be specific for the type of grip (Fig. 3, Unit 109, 'whole hand prehension', and Unit 28, 'precision grip'). Often, neurons discharging during grasping were also active during manipulation. Reaching neurons discharged during the extension of the arm to reach an object, but not when the arm was extended for other purposes or when the monkey grasped an object without extending the arm. An example (Unit 75) is shown in Fig. 3. Some neurons discharged during both reaching and grasping (reaching–grasping neurons). Other arm-related neurons discharged when the monkey brought a piece of food toward the mouth, but only if this motor act was carried out in relation to ingestive behavior (Fig. 3, Unit 261).

The most frequent type of mouth-related motor act was biting (Fig. 3, Unit 8). Other motor acts involving the mouth, such as licking or sucking, were also represented but to a minor extent. We found several neuronal responses correlated to the combination of two motor acts. Where these responses involved the hand and the mouth, they could occur either with the two motor acts related to the same goal ('hand and mouth grasping', Fig. 3, Unit 8) or with a logical sequence between them (e.g. bringing food to the mouth and mouth opening).

Figure 4 shows the distribution of the different types of motor acts effective in evoking the neuronal responses along the IPL (Fig. 4A) and their relative proportion in the three studied cytoarchitectonic areas (Fig. 4B). A somatotopic organization, although with a considerable degree of overlap between the adjacent motor fields, is evident. Motor acts performed with the mouth are more represented rostrally, mainly in area PF, where the percentage of sites related to biting is significantly higher than in both PFG and PG ($P < 0.001$ for M1 and M2). Area PFG is motorically characterized by the richest representation of hand motor acts with respect to that of the adjacent areas PF and PG ($P < 0.001$ for both monkeys). In the caudal area PG, reaching-related sites are more represented than in both PF and PFG ($P < 0.001$ for both monkeys). It is interesting to note that in the sectors of overlap between two motor fields (mouth/hand, hand/arm) we very often found neuronal activity related to movements performed with two effectors.

Somatosensory responses

Touch and proprioception are both represented in the IPL recorded region. The most represented somatosensory submodalities are 'deep touch' (57%), followed by 'light touch' (14%) and 'joint' (6%) mobilization. A consistent percentage of neurons responded to more than one submodality (23%).

In agreement with previous studies (Leinonen & Nyman, 1979; Leinonen *et al.*, 1979), the neuronal receptive fields (RFs) were typically large. With regard to location, about half of them were located on the contralateral side of the body, and the other half were bilateral. The highest percentage of RFs, calculated based on the total number of sites in which somatosensory responses were found, was on the face (48%), followed by those on the hand (28%) and then by those on the arm (10%). Other RFs were located also on the trunk and the leg. A small percentage of RFs involved non-contiguous body-parts (e.g. arm–leg) or could cover a large body area.

Figure 5A shows the distribution of somatosensory RFs in IPL. A rough somatotopic organization appears to be present in the rostral half of the lobule with the oro-facial RFs located anteriorly, and the forelimb RFs located more posteriorly. The representation of the two RFs, however, partially overlaps. Inside the forelimb representation a clear subdivision between a hand and an arm sector is not evident.

Figure 5B shows the proportion of somatosensory responses related to specific body-parts in the three cytoarchitectonic areas. The percentage of sites responsive to oro-facial stimulation is higher in PF than in the other two areas ($P < 0.001$ for both monkeys), and in PFG relative to PG ($P < 0.05$ for both monkeys). Sites responsive to hand stimulation are more represented in PFG than in PF ($P < 0.001$ for M2) and PG ($P < 0.01$ for both monkeys).

Visual properties

A variety of visually responsive neurons were found in the recorded region of IPL. Some were purely visual neurons, whereas others also discharged in association with body-parts or eye movements. Of 423 visually responsive neurons, 82% were tested for the possible presence of motor properties. Of these, 80% showed motor responses, related either to body-parts (60%) or to eye (20%) movements, with the remaining 20% not showing any motor response.

Visually responsive neurons were assigned to different categories according to the type of visual stimulus most effective in activating them. Their properties will be described below. The description order is based on their frequency in the recorded region.

Unit 109
Monkey reaches and grasps an object with whole-hand

Unit 28
Monkey reaches and grasps an object with precision-grip

Monkey reaches and grasps an object with precision-grip

Monkey reaches and grasps an object with side-grip

Unit 75
Monkey extends the arm and reaches a piece of food

Unit 261
Monkey grasps food and brings it into the mouth

Monkey extends the arm and reaches an object

Monkey grasps food and places it near the mouth

Monkey extends the arm and pushes a screen

Monkey grasps food and smells it

Unit 8
Monkey reaches and grasps a piece of food

Monkey bites food

1 s

FIG. 3. Examples of IPL neurons responding during execution of different motor acts. In each panel, the rasters and histograms represent the neuron response during a single experimental condition. The histogram represents the neuronal activity averaged across ten trials. The activity is aligned with the moment at which the monkey touches the target object with the hand or the mouth. All units were recorded in area PFG, but Unit 8 was recorded at the border with area PF and Unit 75 near the border with area PG. Abscissae: time in ms (bin width, 20 ms). Ordinates: firing rate in spikes/s.
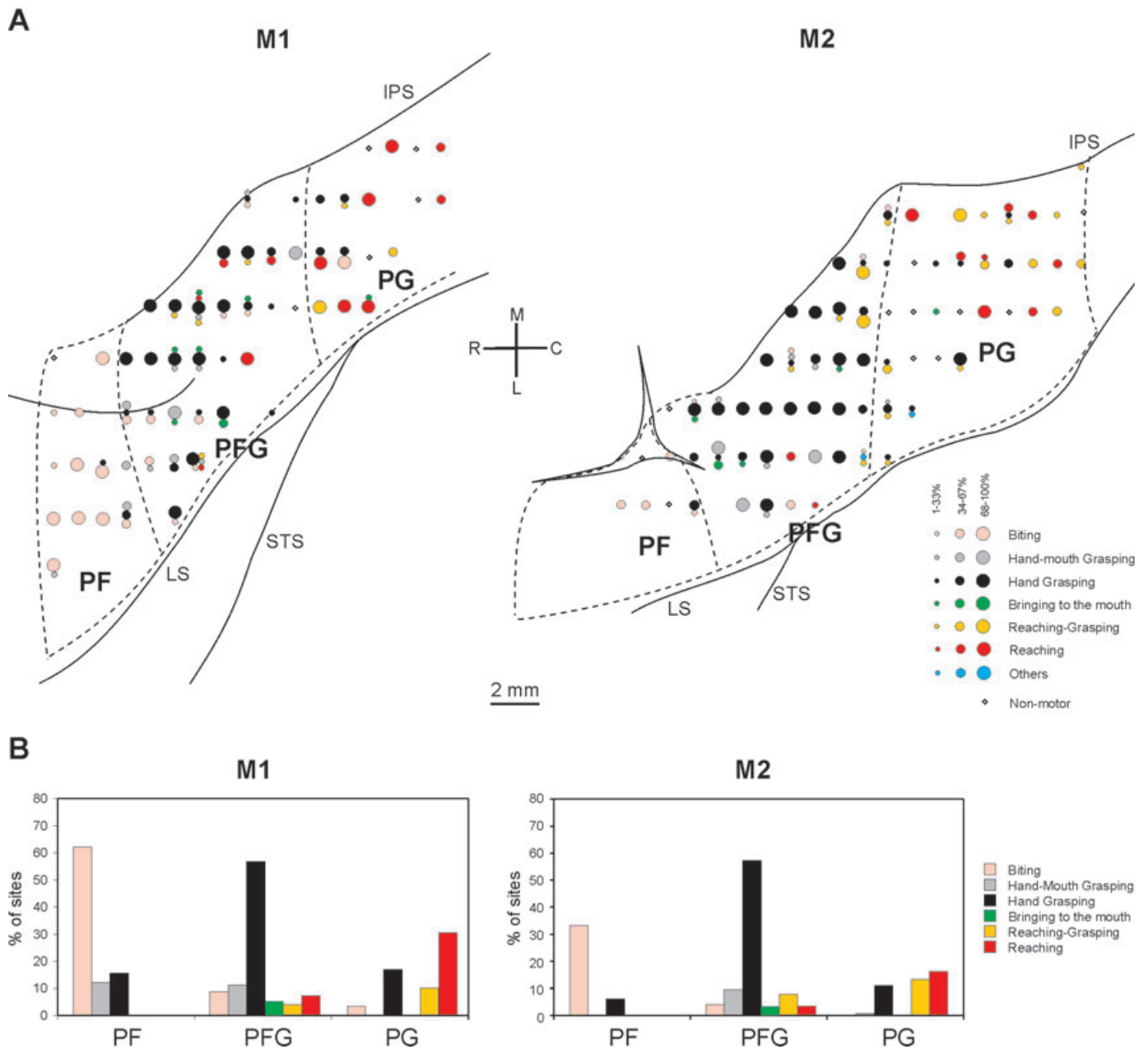
Motor responses

A

B

FIG. 4. Representation of motor responses in IPL convexity. (A) Different types of motor responses are indicated with circles of different colors. Abbreviations and other conventions as in Figs 1 and 2. (B) Histograms representing, for each identified area in M1 and M2, the percentage of sites in which each type of motor response was present in each area, calculated based on the total number of sites recorded in that area. Only responses exceeding the threshold of 3% in at least one monkey are shown.

Peripersonal (*n* = 116; 27%). This category is formed by neurons responsive to 3D objects moved in the visual space within the animal's reaching distance. Peripersonal neurons can respond to stimuli moved in a tangential plane (9%), or moved in depth towards (77%) or away from (4%) the monkey. Some neurons (10%) responded independently of the plane and direction of the moving stimulus. The RFs of these neurons were generally large. The majority were bilateral (63%), the remaining being mostly contralateral (33%). Ipsilateral RFs were rare (4%). Most RFs were near the face (61%) or near the forelimb (19%). Other RFs (16%) were located near the trunk and/or the leg and, in

some cases, included the whole body. The large majority (77%) of peripersonal neurons also showed tactile responses. The location of their visual RF always corresponded to that of the tactile RF. Seventy per cent of peripersonal neurons were also tested during execution of active movements. This showed that 53% of them also discharged in relation to body-parts movements. An example of a peripersonal neuron is shown in Fig. 6.

Visual fixation (*n* = 66; 16%). This comprises neurons active during object fixation (see Mountcastle *et al.*, 1975). Most neurons of this category (56%) responded stronger when the fixated object was of
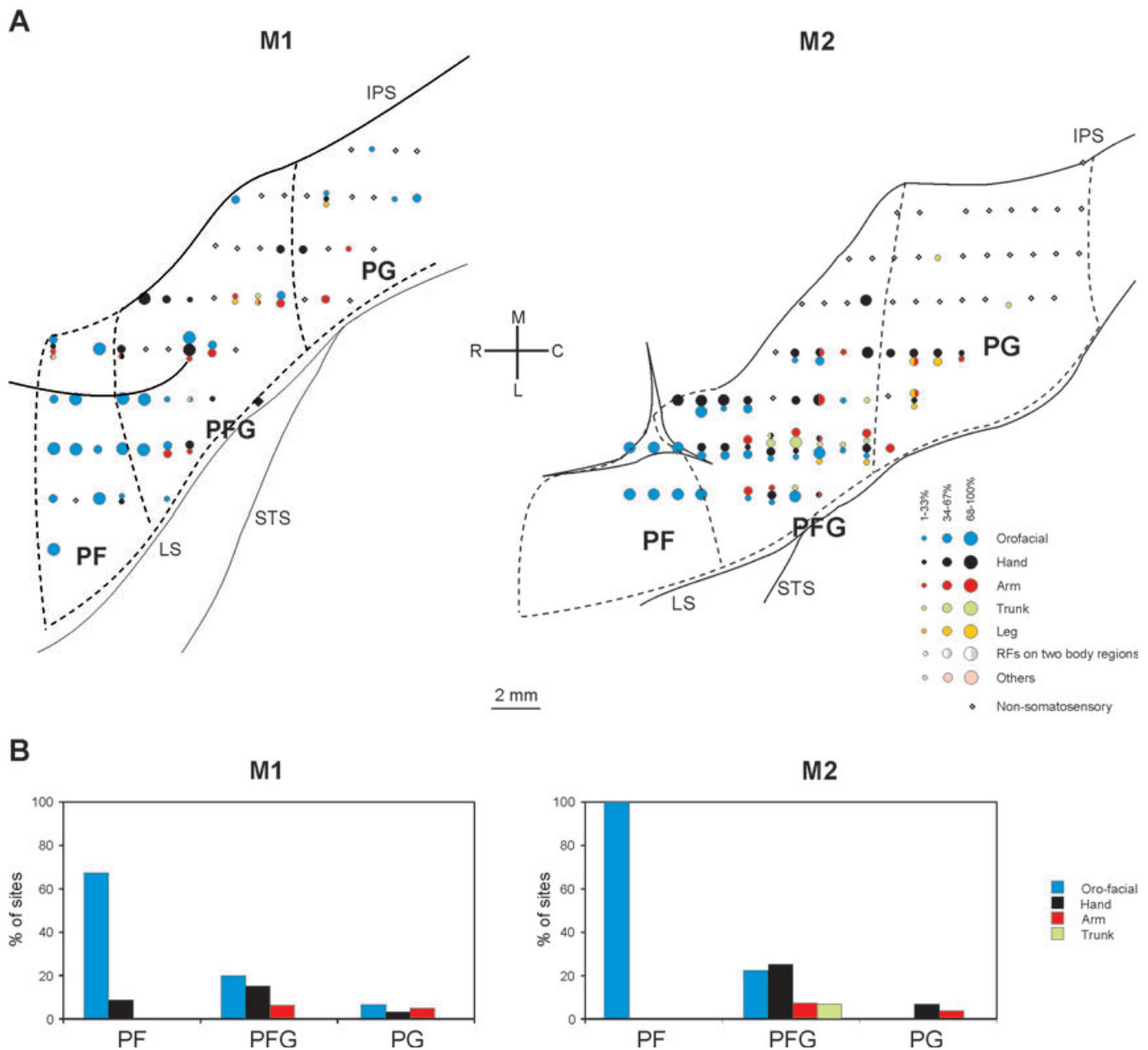
Somatosensory responses

FIG. 5. Representation of somatosensory responses in IPL convexity. (A) Circles of different colors indicate the different body-parts on which the somatosensory RFs are located. Circles divided in sectors indicate that a single receptive field covers more than one body-part. Abbreviations and other conventions as in Figs 1 and 2. (B) Histograms representing, for each identified area in M1 and M2, the percentage of sites in which each body-part RF location was represented in each area, calculated based on the total number of sites recorded in that area. Only responses exceeding the threshold of 3% in at least one monkey are shown.

interest, e.g. food, or when fixation was followed by an arm-reaching movement towards it. The responses of these neurons were not influenced by object distance or spatial position with respect to the body. These neurons did not respond during free gaze exploration of the environment.

Object presentation (*n* = 65; 15%). This comprised neurons responding to the presentation of 3D objects independently of object spatial location. These neurons did not respond to moving objects. Many of these neurons were selective for specific object size and shape. The majority of object presentation neurons (83%) were tested

also during execution of active movements, revealing that 88% of them have also motor properties. A set of object presentation neurons responded stronger when the presented object was of interest to the animal (Fig. 6, Unit 139).

Mirror neurons (*n* = 57; 13%). A detailed description of the properties of this category of neurons is presented in a separate section at the end of the Results.

Moving objects (*n* = 55; 13%). Neurons of this category responded to moving objects, but not to object static presentation. Some of them responded only to objects moved in the far space, others in both the far
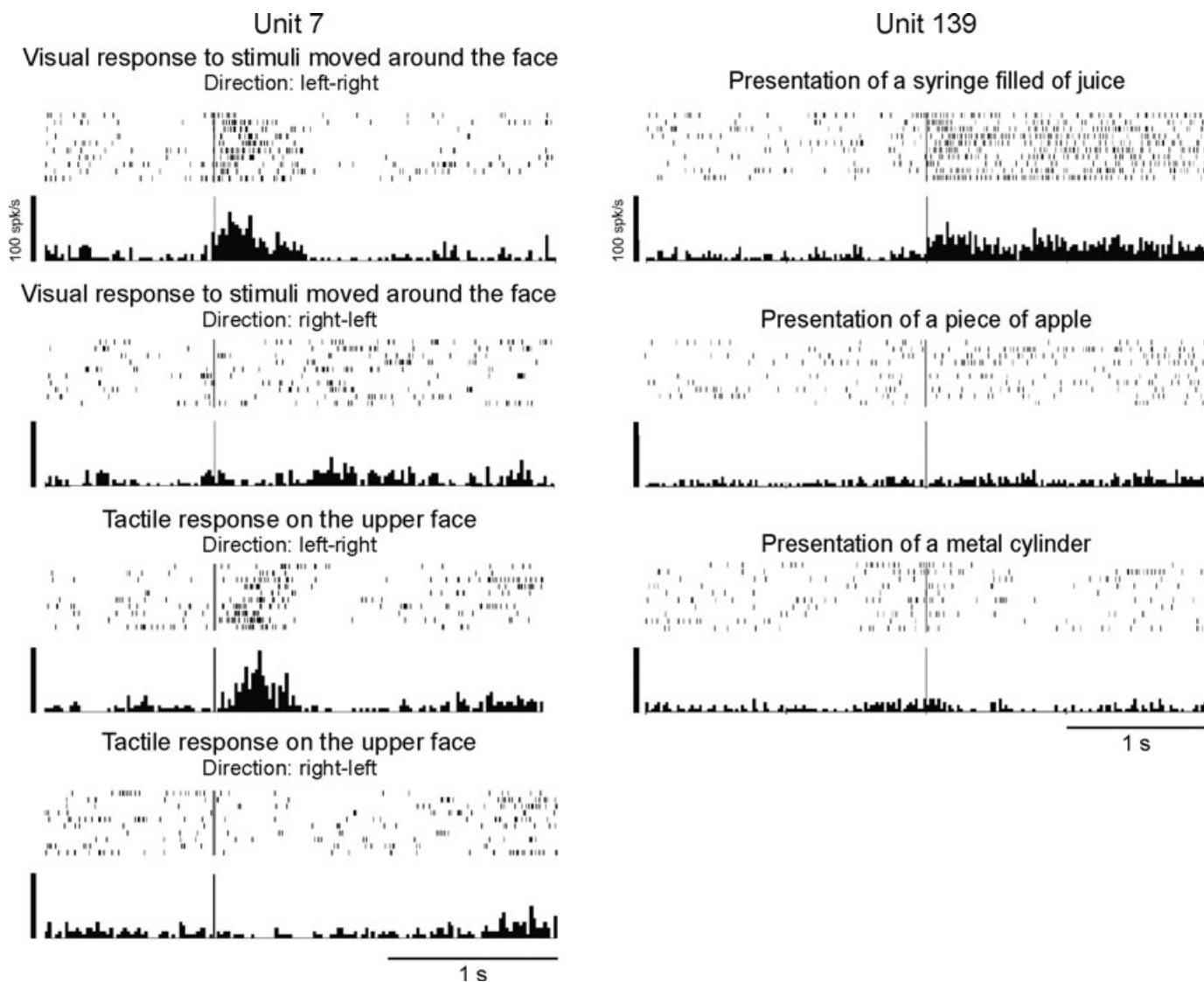
Unit 7

Visual response to stimuli moved around the face
Direction: left-right

Unit 139

Presentation of a syringe filled of juice

Visual response to stimuli moved around the face
Direction: right-left

Presentation of a piece of apple

Tactile response on the upper face
Direction: left-right

Presentation of a metal cylinder

Tactile response on the upper face
Direction: right-left

1 s

1 s

FIG. 6. Examples of two IPL neurons belonging to the peripersonal (Unit 7) and object presentation (Unit 139) categories. In Unit 7 (recorded in PFG) the visual responses are aligned with the moment in which the stimulus starts to move toward the monkey face, while the tactile responses are aligned with the beginning of tactile stimulation. In Unit 139 (recorded in the caudal part of area PFG) the visual responses are aligned on object presentation. Other conventions as in Fig. 3.

and the near space. Discharge of these neurons was largely independent of stimulus location relative to the monkey's body. The majority of neurons (87%) of this category preferred objects moved along a linear trajectory in a tangential plane. Twenty-three per cent had a preference for horizontal directions, 37% for vertical directions and 6% for oblique directions, while 34% did not show directional preference. The remaining neurons (13%) responded to objects moved along a circular trajectory. Sixty-three per cent of moving objects neurons were tested also for their motor properties. This showed that 71% of them were movement-related.

Space-related ($n = 41$; 10%). Neurons of this category responded to static and/or moving stimuli presented in a specific space sector. Unlike peripersonal neurons, the distance from the monkey at which the object was presented was not crucial for triggering the response of space-related neurons. The RFs of these neurons were typically large. They were located in the contralateral space (49%) or extended bilaterally (44%). The lower half of visual space was far more represented (56%) than the upper half (5%). The remaining 39%

comprised neurons responsive in both the lower and the upper half of the visual space. Seventy-three per cent of moving objects neurons were tested also for their motor properties. The results showed that 80% of them discharge in association with either body-parts or eye movements.

Biological motion ($n = 22$; 6%). This category was formed by neurons responding to the head, trunk or limb movements performed by the experimenters. None of them showed motor responses.

Figure 7A shows the distribution of visual properties along the IPL convexity. It is evident that different types of visual responses are often present in the same penetration and are widely distributed along the lobule, except for its rostralmost part. The different categories of visual responses are, however, differently distributed in the various areas (Fig. 7B). Visual responses are relatively rare in PF. Only in a few penetrations and limited to M1 were peripersonal or mirror responses recorded. Area PFG is characterized by a rich representation of both peripersonal and mirror properties that exceed those present in the other areas (peripersonal: M1, $P < 0.05$ vs. both areas, M2,
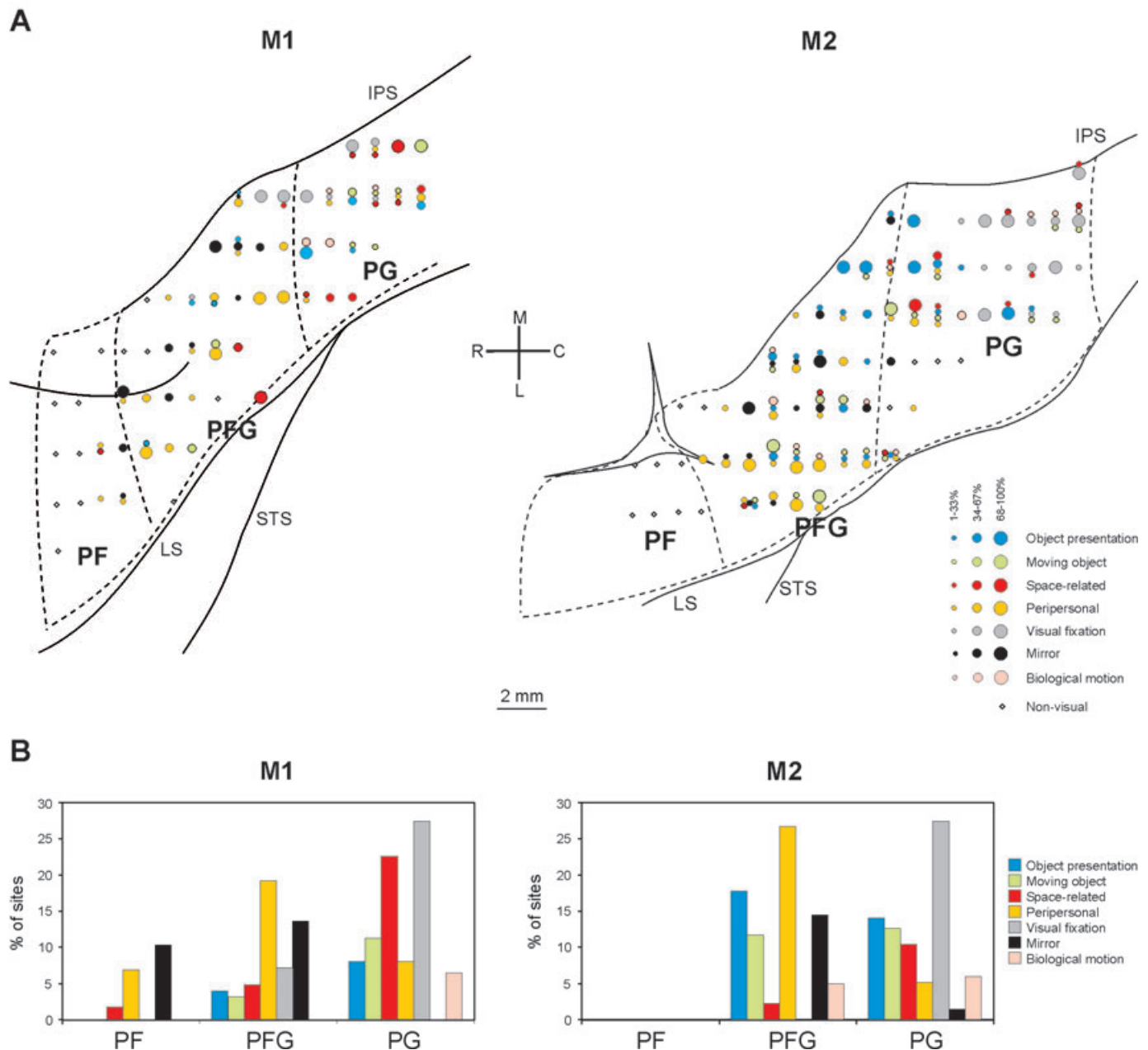
Visual responses

A

B

FIG. 7. Representation of visual responses in IPL convexity. (A) Circles of different colors indicate the different types of visual responses. Abbreviations and other conventions as in Figs 1 and 2. (B) Histograms representing, for each identified area in M1 and M2, the percentage of sites in which each type of visual response was present in each area, calculated based on the total number of sites recorded in that area. Only responses exceeding the threshold of 3% in at least one monkey are shown.

$P < 0.001$ vs. both areas; mirror: M1, $P < 0.001$ vs. PG, M2, $P < 0.005$ vs. both areas). These two categories of neurons often overlap, with a tendency for the mirror neurons to be located more frequently in IPL medial part. The caudalmost part of the recorded region (area PG) is characterized by a representation of space-related and visual fixation responses, both categories being more frequent here than in both PF and PFG ($P < 0.005$). Object presentation and moving objects neurons were present in PFG and PG, but absent in area PF.

Somatosensory-motor and visuo-motor associations

Frequently an association was found between specific types of movements (mouth, hand, arm, eyes) and specific sensory responses. Penetrations characterized by activity associated with hand and mouth motor acts were also characterized by somatosensory responses to stimulation of the mouth and the hand and by peripersonal or mirror visual responses. Penetrations characterized by activity associated with arm motor acts showed somatosensory responses to stimulation

of the arm, hand and mouth and peripersonal, visual fixation and object presentation visual responses. Finally, penetrations characterized by neuronal activity related to eye movements rarely showed somatosensory responses, instead frequently presenting an association with visual fixation and with space-related visual responses (Supplementary material Tables S1 and S2). An association between visual and somatosensory responses in neurons devoid of motor properties was very rare (< 5%).

Mirror neurons

As mentioned in the Introduction, besides investigating the functional organization of IPL, the aim of the present study was increasing our present knowledge of IPL mirror neurons. Unlike other categories of IPL neurons, mirror neurons have been not reported in classical studies of this region (Mountcastle *et al.*, 1975; Hyvärinen, 1981) and, in recent studies, their properties have been described either in very general terms (Fogassi *et al.*, 1998; Gallese *et al.*, 2002) or in relation to some specific properties (Fogassi *et al.*, 2005).

The database of the present study consists of 134 single mirror neurons, all studied both for their motor and for their visual properties (37 in M1 and 97 in M2). They were recorded in part during the initial phase of the experiment largely devoted to IPL mapping (*n* = 57) and in part in a subsequent phase specifically aimed to investigate their functional properties (*n* = 77).

The definition of a mirror neuron was that used in previous studies on the ventral premotor cortex (Gallese *et al.*, 1996). Mirror neurons are neurons that respond when the animal both performs a given motor act and when it observes a similar motor act done by the experimenter. They do not respond or respond only very weakly to object presentation and to mimicking of motor acts without the target object.

Visual responses

Mirror neurons responded to the observations of hand, mouth, or mouth and hand motor acts done by the experimenter. As shown in Table 2 the majority of them responded to the observation of a single motor act performed with the hand (58%). Other neurons responded to the observation of two motor acts performed with the hand (25%). Finally, another set of neurons responded to the observation of mouth or both mouth- and hand-related motor acts (17%).

Examples of neurons responding to the observation of hand motor acts are shown in Fig. 8 (Unit 78 and Unit 33). Unit 78 discharged during the observation of hand grasping, but did not show any discharge when the observed act was mimed, or during simple presentation of food. Unit 33 responded to the observation of object manipulation, while its activity was much weaker during hand grasping observation. No discharge was present during food presentation. For a few neurons (*n* = 4) the observation of hand motor acts (grasping or manipulation) when performed by two different persons gave a stronger response than when performed by a single person. Figure 9 shows an example of this type of neuron (Unit 93), and also illustrates a mouth–hand mirror neuron (Unit 58).

The responses of mirror neurons were usually present regardless of the distance at which the experimenter performed the motor act. A set of neurons (12 of 21 tested) showed directional sensitivity, i.e. their discharge was stronger when the observed motor act was performed by the experimenter in a rightward or leftward direction, independent of the space sector in which it was performed. Other neurons (five of 23 tested) showed space preference (with respect to a body-centered

TABLE 2. Mirror neurons subdivided according to the effective motor acts observed

Neuron category	M1	M2	M1 + M2
Responsive to hand-related motor acts			
Single motor acts			
Grasping	7 (19)	23 (24)	30 (22)
Manipulating	2 (5)	5 (5)	7 (5)
Breaking or tearing	2 (5)	3 (3)	5 (4)
Taking away	2 (5)	2 (2)	4 (3)
Placing	3 (8)	3 (3)	6 (4)
Two hands interacting	7 (19)	13 (13)	20 (15)
Trying to grasp		4 (4)	4 (3)
Others	1 (3)		1 (1)
Subtotals (single motor acts)	24 (65)	53 (55)	77 (58)
Two motor acts			
Grasping/manipulating	2 (5)	8 (8)	10 (7)
Grasping/holding	3 (8)	4 (4)	7 (5)
Grasping/placing		5 (5)	5 (4)
Grasping/others	1 (3)	5 (5)	6 (4)
Manipulation/others		6 (6)	6 (4)
Subtotals (two motor acts)	6 (16)	28 (29)	34 (25)
Responsive to mouth or mouth/hand-related motor acts	7 (19)	16 (16)	23 (17)
Grand totals	37 (100)	97 (100)	134 (100)
Direction sensitivity	4 (11)	12 (12)	16 (12)
Spatial field	3 (8)	2 (2)	5 (4)

Values are expressed as *n* (%).

frame of reference), discharging more strongly when the motor act was performed on the right or the left of the monkey. An example of a neuron with a preference for the contralateral side is shown in Fig. 9, lower panel (Unit 372).

The discharge of many mirror neurons appeared to be modulated by the monkey's gaze. In the great majority of them (41/61) the optimal discharge was present when the monkey directly looked at the experimenter's action. When the monkey was not looking at the action, the response was weak or absent altogether. However, because the eye movements were not recorded in the present study, these data require confirmation.

Mirror neurons have been found mainly in area PFG (see above) with no clear spatial segregation between hand and mouth neurons showing different properties. Furthermore, neurons belonging to different categories could be found in the same penetration and even at the same site level.

Congruence between visual and motor responses

Of 134 mirror neurons, 124 were studied for long enough to establish a relationship between visual and motor responses. The results showed that in most of them there was a clear relationship between the observed motor act they responded to and the effective executed motor act. Using their congruence as a classification criterion, we subdivided the mirror neurons into four classes (see di Pellegrino *et al.*, 1992; Gallese *et al.*, 1996): strictly congruent (29%), broadly congruent (54%), logically related (6%) and non-congruent (11%).

'Strictly congruent' neurons are those in which the effective observed and executed motor act correspond in terms of both general goal (e.g. grasping) and the way in which the motor act was executed (e.g. precision grip), while 'broadly congruent' neurons show a similarity but not identity between the effective observed and executed motor act (e.g. observed whole hand or precision grip and executed precision grip).

Unit 78

Experimenter grasps food

Experimenter mimes grasping

Food presentation

Monkey reaches and grasps food

Unit 33

Experimenter manipulates an object

Experimenter grasps an object

Food presentation

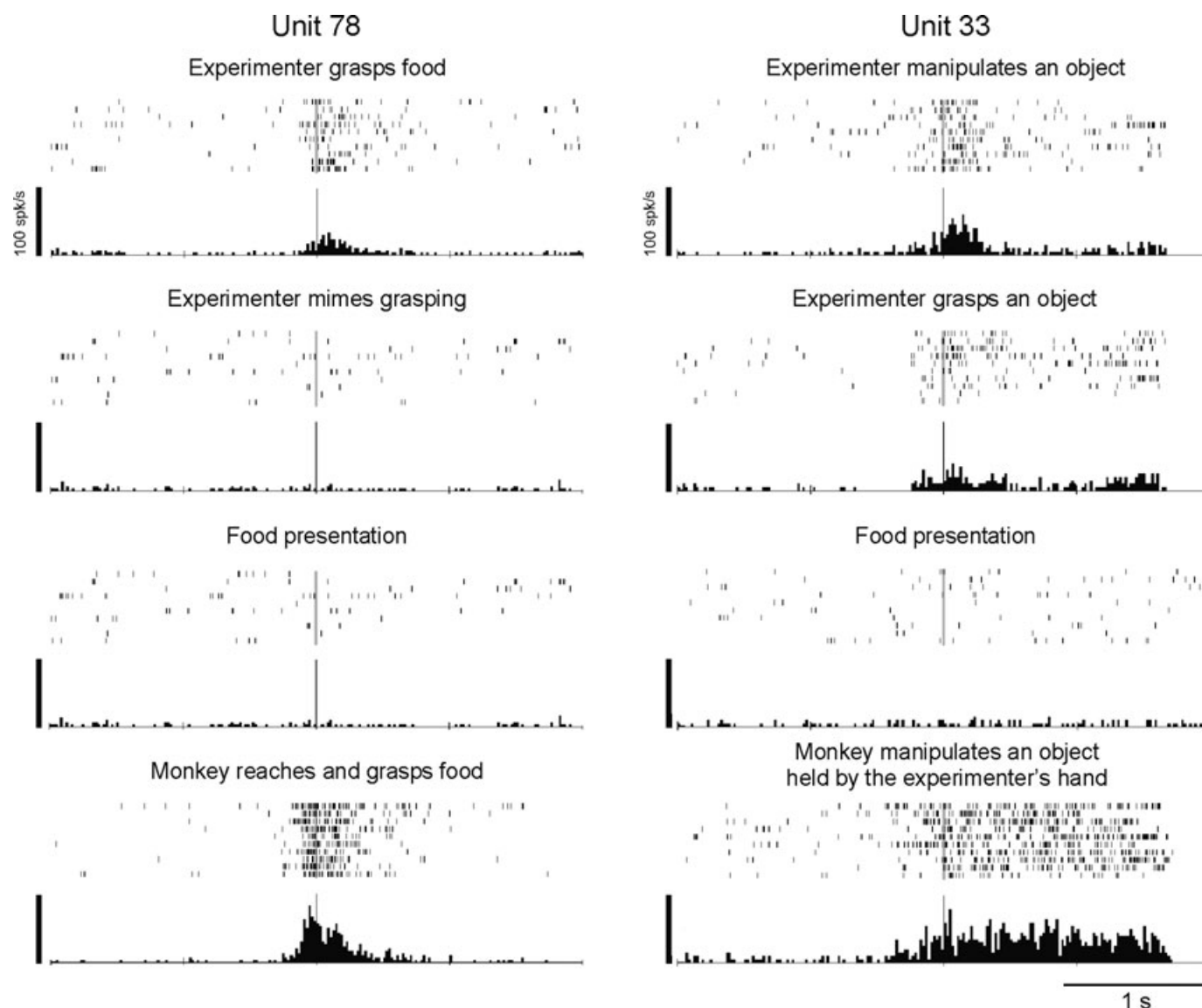### Monkey manipulates an object held by the experimenter's hand

1 s

FIG. 8. Examples of two IPL mirror neurons responding to the observation of hand motor acts. The neural activity occurring during the observation of goal-directed or mimed motor acts performed by the experimenter is aligned with the moment in which the hand touches the target object or a support without the object, respectively. The neural activity occurring during food presentation is aligned with the moment at which food is introduced in the visual field. The activity occurring during movement execution is aligned with the moment at which the monkey touches the food/object with the hand. Both neurons were recorded in PFG. Other conventions as in Fig. 3.

A small number of neurons fell in the category of 'logically related'. These neurons do not show congruence between the seen and the executed motor act, but they appear to be logically linked, in so much as the effective executed motor act could be interpreted as a logical consequence of the effective observed one (e.g. visual placing and motor grasping). For the interpretation of this atypical class of mirror neurons see the Discussion.

The last class ('non-congruent') comprised neurons that either showed only a visual similarity between the observed and the executed motor act (e.g. visual response to manipulating, motor response during grasping) or did not exhibit any clear congruence between them (e.g. visual response to tearing, motor response during grasping).

In agreement with the lack of segregation of mirror neurons belonging to different categories, no topographic segregation was found between neurons showing different congruence.

Discussion

Here we have examined the functional organization of IPL convexity and related it to the cytoarchitectonic parcellation of this region. Our data confirmed the presence of a general somatotopic pattern based on the distribution of the motor responses, as originally outlined by Hyvärinen (1981). Furthermore, they showed that the somatosensory and visual responses are not homogeneously distributed in IPL and, most interestingly, that they are much more frequently associated with motor activity than one to another.

One of the most important findings of the present study is that each of the identified cytoarchitectonic subdivisions – PF, PFG and PG – is characterized by a specific pattern of neuronal properties. This evidence allowed us to consider these cytoarchitectonic fields as three distinct anatomo-functional areas.

Finally, we confirmed the presence of mirror neurons in IPL, showing that they are mainly concentrated in PFG and that their
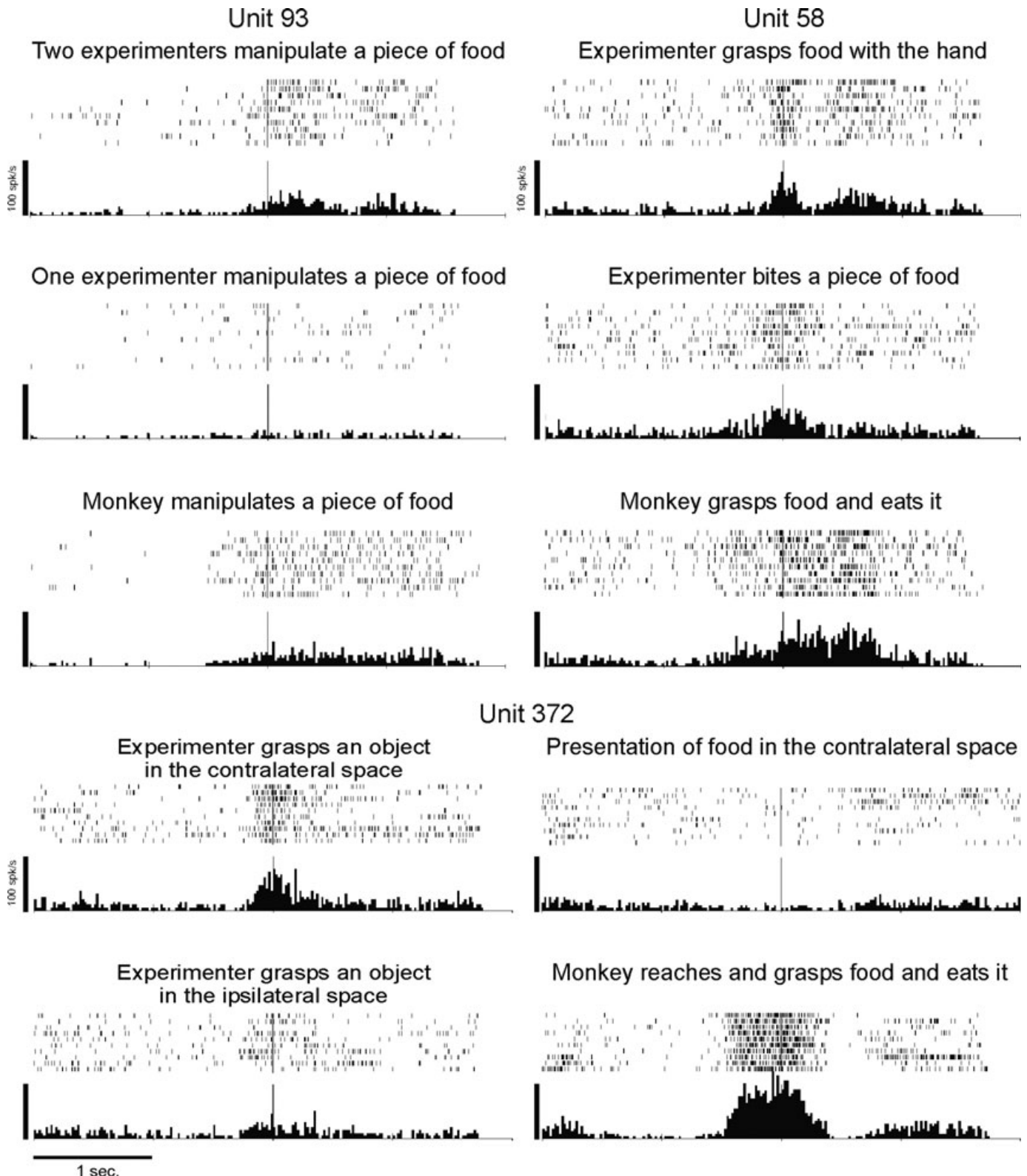
FIG. 9. Examples of IPL mirror neurons responding to observation of hand (Unit 93 and 372) and hand/mouth motor acts (Unit 58). Neural activity occurring during the observation of the motor acts performed by the experimenter is aligned with the moment at which his hand or mouth touches the target object. The neural activity occurring during food presentation is aligned with the moment at which food is introduced in the visual field. The activity occurring during movement execution is aligned with the moment at which the monkey touches the food/object with the hand. All neurons were recorded in PFG. Other conventions as in Fig. 3.

features are remarkably similar to those of mirror neurons originally described in ventral premotor cortex.

Anatomical and functional organization of IPL

Although the three studied areas of IPL convexity have many features in common, there are also clear differences among them in the motor acts and sensory responses represented. We first discuss the functional properties of each area, and later present some considerations on the operational aspect that they have in common.

Area PF

The motor acts most represented in area PF are grasping-with-the-mouth and licking. Associated with them are, typically, somatosensory responses to stimuli applied to the face or the mouth. These neural properties are consistent with anatomical studies showing that PF is closely connected with the mouth fields of somatosensory areas SI and SII, with the lateral part of ventral premotor cortex as well as with rostral areas of IPS (Petrides & Pandya, 1984; Rozzi *et al.*, 2006).

Visual responses are very rare in PF. When present, they are mainly related to the observation of actions performed by others or to stimuli moving in the peripersonal space. In line with the paucity of visual responses, no clear connections appear to exist between area PF and visual areas. PF mirror properties could therefore depend on connections of PF with the adjacent area PFG or with the ventral premotor area F5 and, as far as peripersonal visual responses are concerned, on connections with area VIP and F4 (Petrides & Pandya, 1984; Rozzi *et al.*, 2006).

In summary, the predominance of somatosensory-motor associations found in PF suggests an important role of this area in organizing eating behavior, with neurons providing somatosensory information instrumental to the execution of appropriate food-related or explorative mouth motor acts.

Area PFG

The motor acts mostly represented in area PFG are hand motor acts and, in particular, hand grasping. Responses related to hand motor acts are frequently associated with tactile responses to stimuli applied not only to the hand but also to the mouth, and with proprioceptive stimulation mainly involving arm flexion. Neurons with similar sensory-motor associations have been reported by Yokochi *et al.* (2003). The hand–mouth linkage found in PFG suggests that this area plays a role in linking hand and mouth motor acts so to achieve a fluent way for grasped food to be brought to the mouth. The presence in PFG of neurons coding the bringing-to-the-mouth motor act (see Fig. 3, unit 261) supports this view.

These sensory-motor properties are consistent with anatomical data showing that PFG is connected with the hand representation of SII–PV complex, and with ventral (F5 and F4) and dorsal (F2) premotor areas (Petrides & Pandya, 1984; Neal *et al.*, 1990; Rozzi *et al.*, 2006). Interestingly, PFG is also directly connected with the spinal cord (Galea & Darian-Smith, 1994; Rozzi *et al.*, 2006).

In addition, PFG is richly endowed with neurons responding to visual stimuli. The most represented among them are peripersonal, object presentation and mirror neurons. The richness of visual responses in PFG is consistent with anatomical findings showing that this area is richly connected with visual (MST, middle superior temporal) and polysensory areas of the superior temporal sulcus (Seltzer & Pandya, 1978; Andersen *et al.*, 1990; Rozzi *et al.*, 2006).

The large majority of neurons responding to peripersonal visual stimuli also respond to tactile stimuli (see also Hyvärinen, 1982).

Furthermore, more than half of them are also active during active movement. This suggests that convergence of different sensory modalities on the same motor neuron is more frequent than a mere sensory–sensory association. A convergence of different sensory modalities on neurons coding motor acts has been previously described also in the premotor cortex (Gentilucci *et al.*, 1983; Fogassi *et al.*, 1996a, b; Graziano *et al.*, 1997). The presence of peripersonal neurons in both PFG and premotor cortex, anatomically connected with it (Petrides & Pandya, 1984; Rozzi *et al.*, 2006), suggests an important role for this circuit in the organization of goal-directed actions in space. Graziano & Cooke (2006) described neurons with visual peripersonal receptive fields coding avoiding behaviors in area VIP. We have not found, however, neural responses in PFG related to avoidance behaviors.

A considerable number of neurons in PFG responded to visual presentation of objects. The large majority of them also had motor responses. Although a detailed description of the properties of these neurons (such as that which may be achieved employing specific tasks) was outside the scope of the present study, it is interesting to note that similar properties have been previously described in the intraparietal area AIP. In this area the 'visuomotor' neurons become active both during the observation of a specific object and during the execution of the grip appropriate for that object, thus accomplishing the visuomotor transformation necessary for object grasping (Taira *et al.*, 1990; Murata *et al.*, 2000; see also Jeannerod *et al.*, 1995). This interpretation of the function of AIP neurons is most likely also valid for the object-related neurons of area PFG, given the rich connections between the two areas.

In PFG we also observed that objects similar for their physical characteristics but having a different behavioral value (e.g. food vs. solid object) could elicit a different neural response (see Fig. 6, Unit 139). This finding suggests that object-related visual responses of IPL convexity neurons could be related not only to object affordances but also to the meaning of the object to be acted upon. This interpretation is supported by anatomical findings showing that area PFG is connected, in addition to ventral prefrontal (Petrides & Pandya, 1984; Cavada & Goldman-Rakic, 1989b; Rozzi *et al.*, 2006) and infero-temporal cortex (Boussaoud *et al.*, 1990; Webster *et al.*, 1994; Borra *et al.*, 2007), also to subcortical limbic structures (Kievit & Kuypers, 1975; Selemon & Goldman-Rakic, 1988).

The association between action observation and hand motor acts is discussed in a separate section devoted to mirror neurons.

In summary, area PFG appears to be a crucial node for the organization of hand and hand-to-mouth actions, aimed to manipulate and interact with objects on the basis of their physical properties, their location in peripersonal space and their behavioral value.

Area PG

In area PG, the motor act most represented is arm reaching. The presence of this type of motor response is in line with the anatomical connections of this area with the caudal part of the superior parietal and cingulate cortices (areas PEc, MIP, V6A, PEci and area 23), including the functionally defined parietal reaching region (PRR; see Andersen & Buneo, 2002), and with both dorsal (F2) and ventral (F5) premotor cortices (Petrides & Pandya, 1984; Rozzi *et al.*, 2006). It is interesting to note that although we did not use a specific experimental paradigm to study oculomotor responses in detail, eye-related activity is also present in PG. This finding is in agreement with the results of experiments by Battaglia-Mayer *et al.* (2007) showing neurons related to eye–hand coordination in the posterior half of the IPL. It is worth noting that their recording region,

although mostly located more caudally, partially overlaps with that of the present study, confirming our observations. Interestingly, no significant connections have been found between PG and the oculomotor areas LIP and FEF (frontal eye field) (Rozzi *et al.*, 2006). Thus, its eye-related responses most likely depend on its strong connections with area Opt (not explored in the present study), in turn connected with area LIP. Opt most likely corresponds to the eye-related region described in previous studies (Mountcastle *et al.*, 1975; Lynch *et al.*, 1977; Andersen *et al.*, 1990; Battaglia-Mayer *et al.*, 2005; Raffi & Siegel, 2007).

Somatosensory responses in area PG are sparse while visual responses are widely represented. The latter consist mainly of responses during fixation, presentation or movement of objects and space-related responses, consistent with PG connections with the visual area MST and with the multisensory areas of STS (Tpt and STP) (Pandya & Sanides, 1973; Seltzer & Pandya, 1984; Andersen *et al.*, 1990; Rozzi *et al.*, 2006). Interestingly, as in area PFG, visual responses are often modulated by the behavioral value of the object, or when this was the target of a subsequent arm reaching or eye movement.

Taken together, these data suggest that the possible functional role of PG neurons is the organization and control of 'reaching-with-the-arm and the eye' at the limit between the peri- and extrapersonal space, using several visual information sources about the position, motion and behavioral values of the target stimuli.

Common operational features of IPL convexity

The general organization of IPL convexity described indicates, on the one hand, that different cytoarchitectonic areas play different functional roles, and on the other, that a certain degree of overlap between different functional properties is present, possibly depending on the strong, reciprocal connections between IPL adjacent areas (Pandya & Seltzer, 1982; Rozzi *et al.*, 2006). These connections could accomplish an important functional role in allowing the sequential activation of motor acts occurring in body-centered pragmatic spaces, in order to orchestrate more complex actions. To give an example, an action whose aim is eating, will typically start with food fixation (far space), followed by reaching, grasping and manipulating, and then by bringing the food to the mouth (peripersonal space), biting and chewing. This idea is consistent with the deficits in the organization of eye, arm and hand movements observed following IPL lesion (Ettlinger & Kalsbeck, 1962; Faugier-Grimaud *et al.*, 1978; Lynch, 1980; Rizzolatti *et al.*, 1985) and with the frequently associated spatial impairments of the different pragmatic spaces (Denny-Brown & Chambers, 1958; Heilman *et al.*, 1970; Eidelberg & Schwartz, 1971; Lynch, 1980; Deuel, 1987).

Sensory-motor transformations in IPL

The transformation of sensory information into a motor format appears to be the basic organization principle of IPL. This has been shown for two areas located in the depth of IPS, areas AIP and LIP (Taira *et al.*, 1990; Barash *et al.*, 1991a, b; Murata *et al.*, 2000; see also Andersen & Buneo, 2002), and proposed for area VIP (see Colby & Duhamel, 1996), located in the fundus of IPS. All these areas belong to specific parieto-frontal circuits (AIP-F5, VIP-F4 and LIP-FEF) (Blatt *et al.*, 1990; Stanton *et al.*, 1995; Luppino *et al.*, 1999; Lewis & Van Essen, 2000; Borra *et al.*, 2007) and are responsible for sensory-motor transformations for grasping, reaching and eye movements, respectively (see Andersen *et al.*, 1997; Colby, 1998; Rizzolatti *et al.*, 1998; Rizzolatti & Luppino, 2001).

The present data show that areas located in the convexity also play a role in the sensory-motor transformation, each of them presenting its own specific peculiarity related to the most represented effector. The rich connections of IPL convexity with the ventral premotor cortex, in addition to those with the adjacent areas of IPS (Pandya & Seltzer, 1982; Petrides & Pandya, 1984; Cavada & Goldman-Rakic, 1989a, b; Andersen *et al.*, 1990; Lewis & Van Essen, 2000; Rozzi *et al.*, 2006), support this view.

It is worth noting that the connections of the areas located inside the IPS with frontal motor areas are more specific than those of the areas located on the adjacent convexity. For example, area AIP is richly connected only with the ventral premotor area F5, while area PFG is connected with both ventral (F4 and F5) and dorsal (F2) premotor cortex. This anatomical arrangement suggests that the sensory-motor processes in which areas of IPL convexity are involved have a lesser degree of functional specificity than those of the areas located inside the intraparietal sulcus.

Goal coding of IPL motor neurons

The main feature of IPL neurons that discharge in association with body-parts movements is that, typically, they become active in relation to movements having a specific goal rather than to simple body-part displacements.

The following findings support this conclusion. First, neurons that discharge during the execution of a specific goal-directed motor act (e.g. reaching) are usually not active when similar movements (arm extension) are done for another purpose (e.g. pushing away), as shown by Unit 75 (see Fig. 3). Second, there are neurons (e.g. Fig. 3, Unit 8) that discharge when the monkey tends to achieve the same goal independently of which effector (e.g. mouth or hand) is used. Third, many neurons are active during all phases of a motor act, even when this act is constituted of different antagonistic movements. For example, the motor discharge of Unit 372 (Fig. 9) occurs during both opening and closure of the hand when the monkey grasps a piece of food.

These findings confirm previous evidence concerning the rostral part of IPL (Gallese *et al.*, 2002; Yokochi *et al.*, 2003; Fogassi *et al.*, 2005) extending it to the remaining part of the lobule and including mouth, arm and coordinated arm/hand motor acts.

Neurons coding goal rather than movements have been previously shown in the ventral (Rizzolatti *et al.*, 1988, 2004; Kakei *et al.*, 2001; Umiltà *et al.*, 2008) and dorsal (Hoshi & Tanji, 2002; Raos *et al.*, 2004) premotor cortex as well as, although in a smaller proportion, in the primary motor cortex (Alexander & Crutcher, 1990; Kakei *et al.*, 1999; Umiltà *et al.*, 2008). This similarity in terms of functional properties and the strong reciprocal anatomical connections between IPL and the premotor cortex (Petrides & Pandya, 1984; Cavada & Goldman-Rakic, 1989b; Rozzi *et al.*, 2006) strongly suggest that IPL convexity should be considered as a part of the motor system.

IPL mirror neurons

In agreement with previous reports (Fogassi *et al.*, 1998; Gallese *et al.*, 2002), the present study showed that parietal mirror neurons are located in the rostral half of IPL. On the basis of recent cytoarchitectonic criteria (Gregoriou *et al.*, 2006), it was possible to demonstrate that most of them are located in area PFG rather than in area PF, as previously assumed on the basis of macroscopic anatomical landmarks.

Most IPL mirror neurons responded to the observation of hand motor acts. These neurons, as per those described in F5 (Gallese

et al., 1996), usually generalize across many instances of stimulus presentation such as distance, action direction, hand preference, type of object to which the action is directed or space sector in which it takes place. Thus, for the parietal mirror neurons the general principle that their activation is not related to the detailed visual description of an observed motor act, but rather to those basic elements that allow one to recognize its goal, appears to be valid.

Among effective observed motor acts, grasping, either alone or in combination with other hand acts, is the most represented. The percentage of IPL neurons responding to the observation of mouth motor acts is, in contrast, low: this constitutes one of the main differences between IPL and F5 mirror neurons. Another although minor difference is the presence of a higher percentage of neurons classified as 'two-hands interaction' in IPL with respect to F5. Interestingly, we noted that some neurons of this category responded better when the two interacting hands belonged to two different individuals, suggesting that IPL can code more complex interactions than those involving an agent and an observer.

An interesting aspect of IPL mirror neurons is that the intensity of their response, or even the response itself, is rather frequently conditional upon the monkey's active observation of the experimenter's motor act, while this phenomenon is not common in F5. It appears therefore that while in the premotor cortex the peripheral vision of a motor act is sufficient to trigger mirror neurons, a considerable proportion of those in the IPL require foveation. However, further investigation with specific control of eye movements is necessary to understand this behavior better.

As in F5, most IPL mirror neurons show a clear correspondence between the observed and executed effective motor acts, suggesting that they play a role in matching another's act with one's own motor representation of that act, providing a possible neural basis for action understanding. A possible source of visual information for this matching mechanism is the STS cortex, where Perrett *et al.* (1989) found neurons responding to the observation of biological actions, but devoid of motor-related activity. Thus, area PFG could represent the first step in the organization of the mirror neuron system, while area F5 would be the next step, receiving motor act-related visual information from IPL. An alternative possibility is that both IPL and F5 receive independently the visual input describing motor acts and that they independently perform the matching between the observed and executed act. As yet, no direct anatomical connections have been found between anterior STS and area F5. This does not exclude the possibility, however, that information coming from STS can reach area F5 through indirect pathways via the prefrontal cortex.

A minority of IPL mirror neurons (logically related and non-congruent), as in F5, do not show similarity between the effective observed and executed motor acts. Thus, in a narrow sense, the responses of these neurons would not depend on the same mechanism responsible for the discharge of the majority of mirror neurons. Nonetheless, both these categories of neurons share with the other mirror neurons the property of coding motor acts, albeit different, both visually and motorically. Furthermore, in the 'logically related' neurons an observed motor act triggers the motor representation of another act, functionally linked to the observed one. Thus, it is possible that the lack of congruence among non-congruent neurons could, in further studies, be explained as a different type of visuomotor mapping.

Conclusions

All subdivisions of IPL convexity have in common the functional property of generating motor representations integrating sensory and motor inputs. These representations can be used, on the one hand, for organizing individual motor acts into actions in space, while on the other hand, they can remain at the level of pure representation subserving the understanding of space relations and others' actions in a subject-centered perspective.

This view of the function of the IPL, derived from monkey studies, is in good agreement with that based on neuropsychological findings in humans, also showing space and action deficits following IPL damage (see Heilman *et al.*, 1985; Bisiach & Vallar, 1988; De Renzi, 1989; Leiguarda & Marsden, 2000; Halligan *et al.*, 2003). The lateralization of these functions in humans obviously renders this picture more complex, but the fundamental sensory-motor organization of IPL appears to maintain its basic structure.

Supplementary material

The following supplementary material may be found on http://www.blackwell-synergy.com

Table S1. Number and percentage of penetrations characterized by motor activity related to different body-parts or to eye movements and somatosensory responses on different body parts.

Table S2. Number and percentage of penetrations characterized by motor activity related to different body-parts or to eye movements and different types of visual responses.

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Abbreviations

AIP, anterior intraparietal area; FEF, frontal eye field; IPL, inferior parietal lobule; IPS, intraparietal sulcus; LIP, lateral intraparietal area; LS, lateral sulcus; MST, middle superior temporal; PRR, parietal reaching region; RFs, receptive fields; SI, primary somatosensory cortex; SPL, superior parietal lobule; STS, superior temporal sulcus; VIP, ventral intraparietal area.

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