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SHORT COMMUNICATION
Early coding of reaching: frontal and parietal association connections of parieto-occipital cortex

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Abstract

The ipsilateral association connections of the cortex of the dorsal part of the rostral bank of the parieto-occipital sulcus and of the adjoining posterior part of the superior parietal lobule were studied by using different retrograde flourescent tracers. Fluoro-Ruby, Fast blue and Diamidino yellow were injected into visual area V6A, and dorso-caudal (PMdc, F2) and dorso-rostral (PMdr, F7) premotor cortex, respectively. The parietal area of injection had been previously characterized physiologically in behaving monkeys, through a variety of oculomotor and visuomanual tasks. Area V6A is mainly linked by reciprocal projections to parietal areas 7m, MIP (medial intraparietal) and PEa, and, to a lesser extent, to frontal areas PMdr (rostral dorsal premotor cortex, F7) and PMdc (F2). All these areas project to that part of the dorsocaudal premotor cortex that has a direct access to primary motor cortex. V6A is also connected to area F5 and, to a lesser extent, to 7a, ventral (VIP) and lateral (LIP) intraparietal areas. This pattern of association connections may explain the presence of visually-related and eye-position signals in premotor cortex, as well as the influence of information concerning arm position and movement direction on V6A neural activity. Area V6A emerges as a potential 'early' node of the distributed network underlying visually-guided reaching. In this network, reciprocal association connections probably impose, through re-entrant signalling, a recursive property to the operations leading to the composition of eye and hand motor commands.

Introduction

Understanding the cerebral cortical coding of reaching requires knowledge not only of the functional properties of reach-related cells within different cortical areas, but also of the anatomical relationships among these areas.

In the last few years, considerable attention has been devoted to the parieto-occipital cortex (area PO, Colby *et al*., 1988), for which a visuomotor role has been postulated (Johnson *et al*., 1993, 1996, 1997; Tanné *et al*., 1995; Galletti *et al*., 1997; Battaglia-Mayer *et al*., 1998; Matelli *et al*., 1998; Shipp *et al*., 1998; Nakamura *et al*., 1999), both on the basis of the pattern of association connections and on the observation that cell activity in its dorsal part, area V6A (Galletti *et al*., 1996), seems related not only to visual and oculomotor functions but to arm movement as well (Galletti *et al*., 1997; Johnson *et al*., 1997; Battaglia-Mayer *et al*., 1998; Caminiti *et al*., 1998).

Our study combines physiology and anatomy to elucidate the pattern of association connections between area V6A, here characterized physiologically, and dorsolateral premotor cortex. The operations occurring in these parietal and frontal regions may in fact be regarded as potential early and late stages, respectively, of a unique information processing flow leading from vision to movement.

Different anatomical tracers were injected into area V6A and into the rostral (PMdr, F7) and caudal (PMdc; F2) dorsal premotor cortex (Matelli *et al*., 1985; Barbas & Pandya, 1987). Injections into V6A were made in cortical regions related to visuospatial processing, and to eye and arm movements, as determined through physiological recordings while monkeys performed different oculomotor and arm-reaching tasks.

Methods

Two rhesus monkeys (*Macaca mulatta*; body weights 3.7 and 3.5 kg) were used. This study was approved by the Ethical Committee of the University of Rome 'La Sapienza' and by the Ministry of Health of Italy. The physiological characterization of the area of tracer injection was performed by recording (System Echkorn, Thomas Recording, Marburg, Germany) single-cell activity extracellularly while the animals performed four different tasks. The animal's head was immobilized through a titanium head-holder and recording was made through a recording chamber. Both were previously emplanted under aseptic conditions and sodium pentobarbital anaesthesia (25 mg/kg, i.v.). In the instructed-delay reaching task (IDR), a red centre light was first presented and the animal fixated and touched it with the

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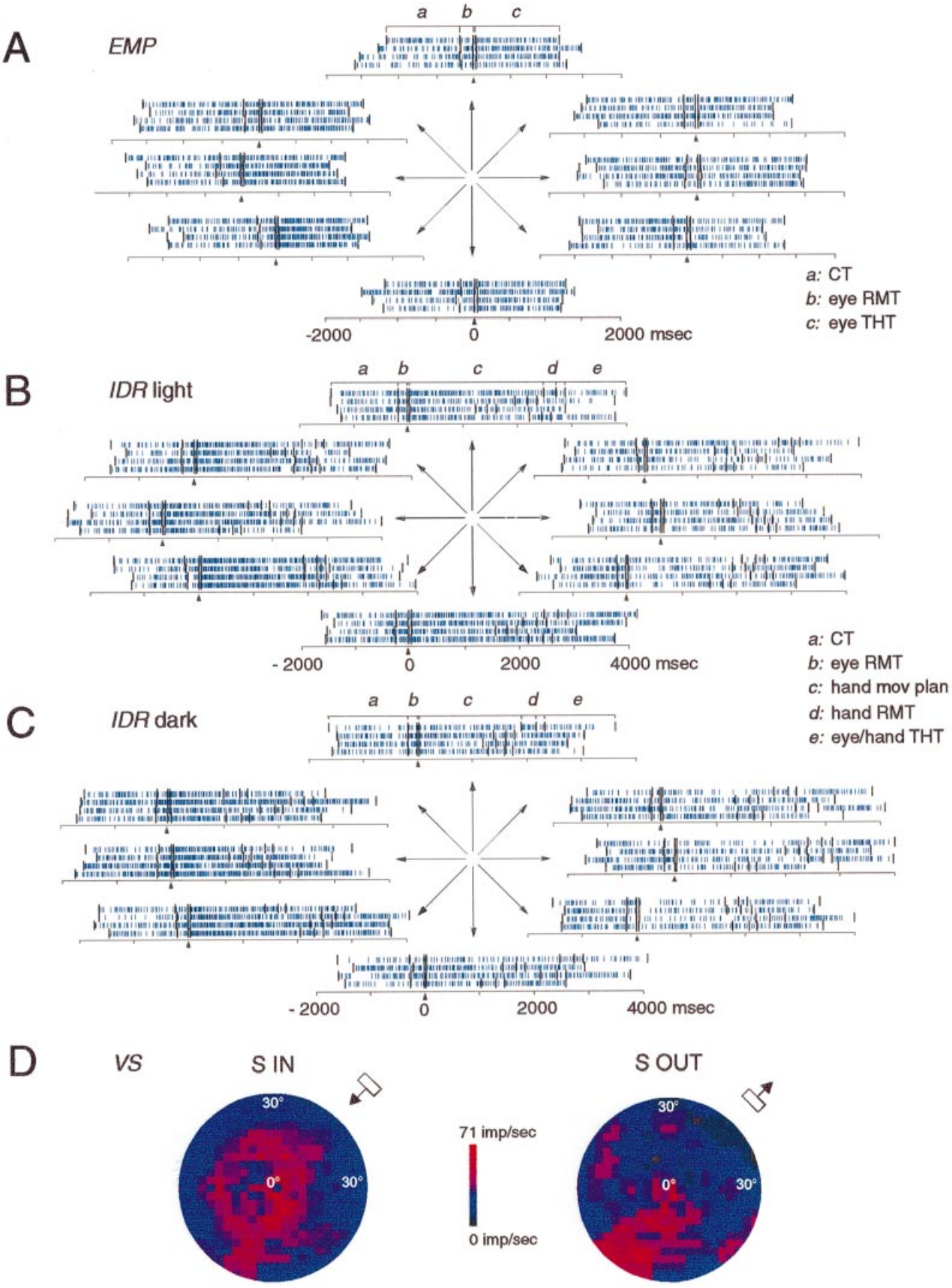

FIG. 1. (A–C) Rasters of four replicas of cell activity recorded from a prototypical neuron at the injection site in area V6A, during the EMP (A), and IDR light and dark (B and C) tasks. Rasters are aligned to onset of eye movement (arrow under temporal axis). CT, RMT, THT indicate, respectively, control time, reaction + movement time, target holding time; 'hand mov plan' indicates planning of intended hand movement. (D) Colour-coded maps of impulse activity showing the visual receptive field of the same cell during inward (S IN) and outward (S OUT) stimulus motion in the visual field, obtained from cell activity during the visual stimulation task (VS).

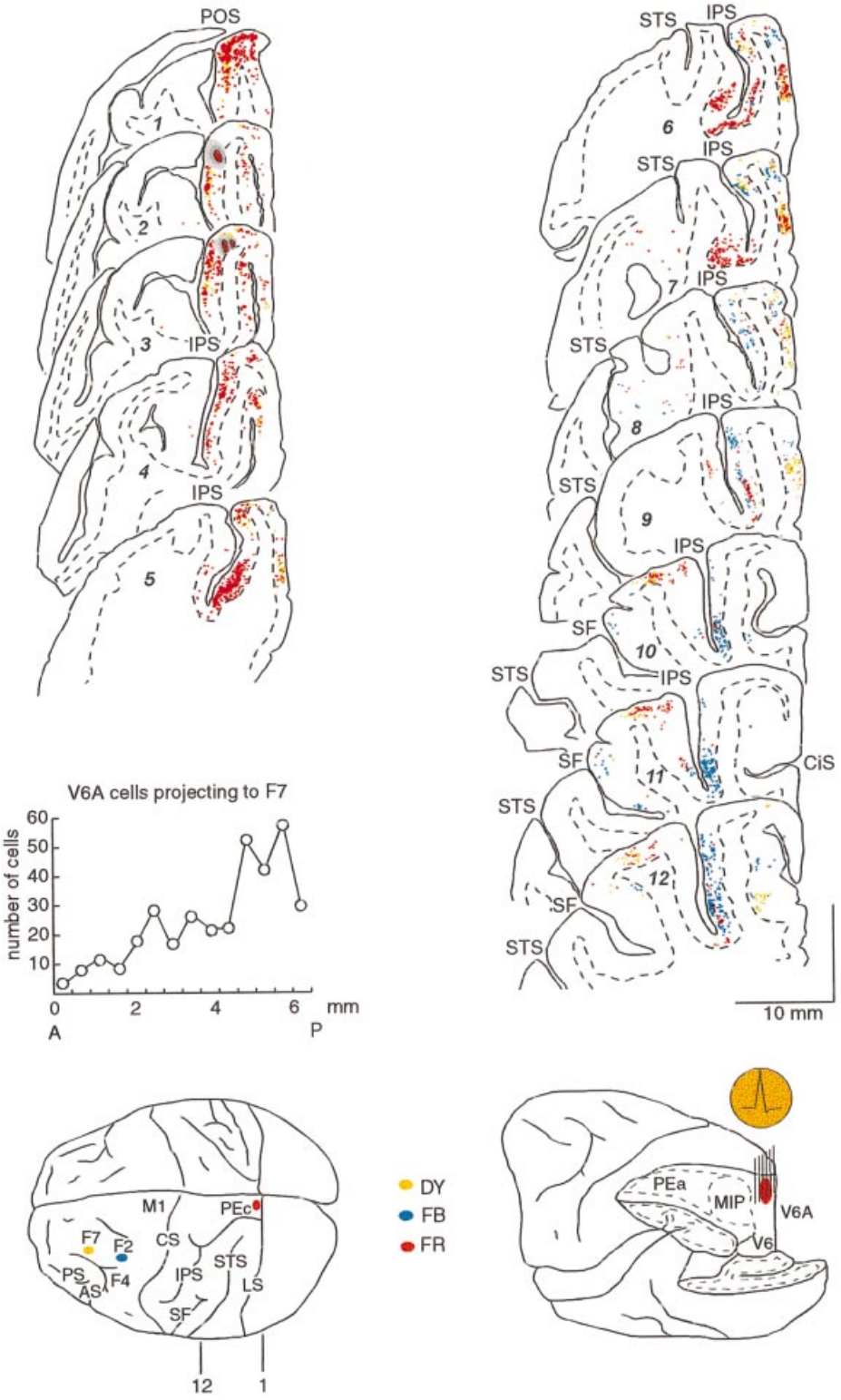

FIG. 2. Distribution of retrogradely-labelled parietal cells projecting to V6A (red dots), PMdr (yellow dots) and PMdc (blue dots), after injections of FR (red oval in V6A), DY (yellow oval in PMdr) and FB (blue oval in PMdc), as indicated in the brain figurines of the lateral views of the hemisphere. AS, arcuate sulcus; CiS, cingulate sulcus; CS, central sulcus; IPS, intraparietal sulcus; LS, lateral sulcus; POS, parieto-occipital sulcus; PS, principal sulcus; SF, Sylvian fissure; STS, superior temporal sulcus; In the figurine on the right, large parts of the parietal and occipital lobe have been removed to show the location of the areas of the medial bank of the intraparietal sulcus and of the rostral bank of the parieto-occipital sulcus (redrawn with modifications from Galletti *et al*., 1996), where the physiological characterization (orange circle including an action potential) of the injection site was performed. MIP indicates the medial intraparietal area. In each individual section, continuous and interrupted lines indicate, respectively, the pial surface and the border between layer VI and white matter; injection sites are represented as coloured spots (central core), surrounded by the halo (dark grey) of diffusion, and by the region of high cellular labelling (light grey); the number indicates the approximate level of section, as shown in the brain figurine. The locations of the cortical areas discussed in the text are drawn in the brain figurines of the lateral and mesial views of the hemisphere. The histogram shows the number and antero-posterior distribution of cells in area V6A retrogradely labelled by the injection in F7.

hand during the control time (CT 1–1.5 s), after which one of eight peripheral targets was lit green. This was the beginning of the instructed-delay time (IDT). Within variable eye reaction and movement time (RMTe), the eye moved to the green target and remained there for the rest of the trial. During the entire IDT, the animal was required to withhold the arm movement until the green target turned red. This was the go-signal for the hand to move to the target within the given hand reaction time (RTh, 0.5 s upper limit) and hand movement time (MTh, 1 s upper limit), and to stay there with the eyes for a variable eye-hand target holding time (THTeh, 1–1.5 s). Monkeys performed the task under both normal light (*l*) conditions and in total darkness (*d*). These reaching tasks separated in time eye from arm motor contributions to cell activity and assessed the relationships between cell activity and preparation for intended arm movement (during IDT), execution of arm movement (RT + MT = RMT) and arm position, both in the presence and in the absence of

visual feedback of hand position and movement in the visual field. In the eye movement and position task (EMP), a visual fixation point was presented at the centre of the workspace. During fixation, one of eight peripheral targets was lit and the central fixation point was extinguished. Within given eye reaction and movement times (RTe, 0.5 s upper limit; MTe, 1 s upper limit), the animals made a saccade to the target and kept fixation there for a variable eye target holding time (THTe, 1–1.5 s).

In all of the above three tasks (IDR, IDT and EMP), the target was randomly selected from eight possible locations on a virtual circle, at 25 ° visual angle eccentricity. In the visual stimulation task (VS) the animal was required to fixate a central fixation point while a visual stimulus was moved in one of 16 directions, inward (IN) toward the fovea and outward (OUT) from the fovea to the periphery of the visual field. Stimuli were white solid bars (3.27×7.60 °) or bars of static or dynamic random dots, and were moved at constant speed (25 °/s), while the monkey kept fixation. Stimulus orientation was always orthogonal to the direction of movement.

The stimuli used as targets for hand and/or eye movement or for visual stimulation were presented on a computer monitor fitted with a touch screen (MicroTouch Systems, Wilmington, MA, USA) used to control hand position. Eye position was controlled through the scleral search coil (Remmel Labs, Ashland, MA, USA) technique.

At the end of the neurophysiological recording session, the animals were anaesthetized (sodium pentobarbital, 25 mg/kg i.v.). The fluorescent tracers were injected with a Hamilton microsyringe. Four injections (0.15 µL each) of FluoroRuby (FR, 10% in saline; Molecular Probe, Eugene, OR, USA), were made in V6A, in the dorsal part of the rostral bank of the parieto-occipital sulcus (Fig. 2, brain figurines), at 2 and 4 mm depth. Four injections (0.15 µL each) of Fast blue (FB, 2% in saline; Sigma, St Louis, MO, USA) and of Diamidino yellow (DY, 2% in saline; Sigma) were made in PMdr (F7) and PMdc (F2) (Fig. 2, brain figurines), respectively. The postinjection survival period lasted 20 days for the first animal and 26 days for the second one. During the first week, the animals were given antibiotics.

Monkeys were then anaesthetized with sodium pentobarbital (25 mg/kg, i.p.) and perfused with 0.9% saline followed by 4% paraformaldehyde in 0.1 M phosphate buffer (pH 7.2). After removal, the brains were postfixed in the same fixative. They were then placed in a solution of 30% buffered sucrose until they sank. The brain blocks were cut in the coronal plane. Sections were cut at both 80 and 40 µm, in an alternating pattern. The 80-µm sections were mounted on gelatin-coated slides, air-dried and coverslipped for fluorescent labelling analysis. The adjacent sections (40 µm thick) were stained with thionin (0.025%) for cytoarchitectonic analysis. The borders of different frontal and parietal areas were drawn by using criteria defined elsewhere (Pandya & Seltzer, 1982; Matelli *et al*., 1985; Johnson *et al*., 1996; Picard & Strick, 1996).

For each animal, a series of coronal sections at 240 µm intervals was plotted using a computer-based plotting system. The X and Y coordinates of labelled neurons, injection sites of tracers, microelectrode penetrations and other landmarks were plotted through a computer microscope.

Results

Neurophysiological data

Figure 1 illustrates the activity of a prototypical neuron recorded at the injection site. A repeated-measures analysis of variance (ANOVA) showed that, in the EMP task, cell activity was related ($P < 0.001$) to both direction of saccadic eye movement (RMTe = RTe + MTe) and eye position in the orbit (THT). In the IDR tasks (Fig. 1B and C), significant directional modulation ($P < 0.001$) occurred during eye movement, preparation and execution of arm movement and combined eye-hand holding on the target (THTeh), under both light and dark conditions. Significant light-dark differences ($P < 0.005$) were observed in all these epochs. This suggests that in addition to eye-related signals, this cell encodes information about arm motion and position in the visual field. Coherently, in the VS task (Fig. 1D) cell activity was significantly ($P < 0.001$) modulated during both inward and outward stimulus motion. The visual receptive field was large, included the fovea and extended to the periphery of the visual field. The inward stimulus motion revealed the existence of the ipsilateral component of the receptive field.

Cell modulation in the dark during planning of arm movement, the arm movement itself and static posture is suggestive of a genuine relationship of cell activity to arm-related signals. However, this modulation could be attributed to the eye position signals, because during these epochs the position of the eye covaried with the direction of intended arm movement during the delay-movement time, as well as with the actual hand movement and/or position on the peripheral targets. Thus, the directional modulation during these arm-related epochs of the IDR*d* was compared with that during static eye holding on the targets (THTe of the EMP task). In these two conditions the positions of the eyes remained constant and possible effects on cell activity of hand movement and/or static position in the visual receptive field could be excluded, as the activity was recorded in the dark. Therefore, potential differences of cell activity across these epochs could safely be attributed to planning and/or execution of arm movement, and/or to arm static position on the target. Significant differences ($P < 0.001$) of directional modulation occurred during planning of intended arm movement only. In conclusion, the activity of this neuron was modulated by eye position and movement direction, preparation for arm movement, direction of arm motion and position in the visual field. These combinatorial properties were typical of all neurons (77 cells studied in all above tasks) recorded in this area, although the combination of response properties differed from neuron to neuron.

Neuroanatomical data

Because both the diffusion of tracers at the injection sites and the retrograde labelling were qualitatively similar in the two animals, results from only one of them are illustrated.

Retrograde tracer injections

Injection of FR. The injections of FR were all in the cortex of the rostral bank of the parieto-occipital sulcus and around its crown. Rostro-caudally, the local labelling involved about 4.8 mm of cortex, from the crown of the sulcus to about 5.5 mm depth. Mediolaterally, it occupied all the cortex of the exposed flat part of the parieto-occipital junction (Fig. 2, figurines *2* and *3*).

Injection of DY. The local labelling of the injections of DY was found medial to the medial limb of the arcuate sulcus (Fig. 3, figurines *7* and *8*). It extended for about 6.4 mm rostro-caudally, around the crown of the sulcus and in the upper part of its bank. Injections were within PMdr (F7).

Injections of FB. The cores and halos of the four injections of FB were all contained within PMdc (F2; Fig. 3, figurines *2* and *3*), lateral to the precentral dimple, and extended rostro-caudally for about 6 mm, up to the spur of the arcuate sulcus, which in this animal was unusually long.

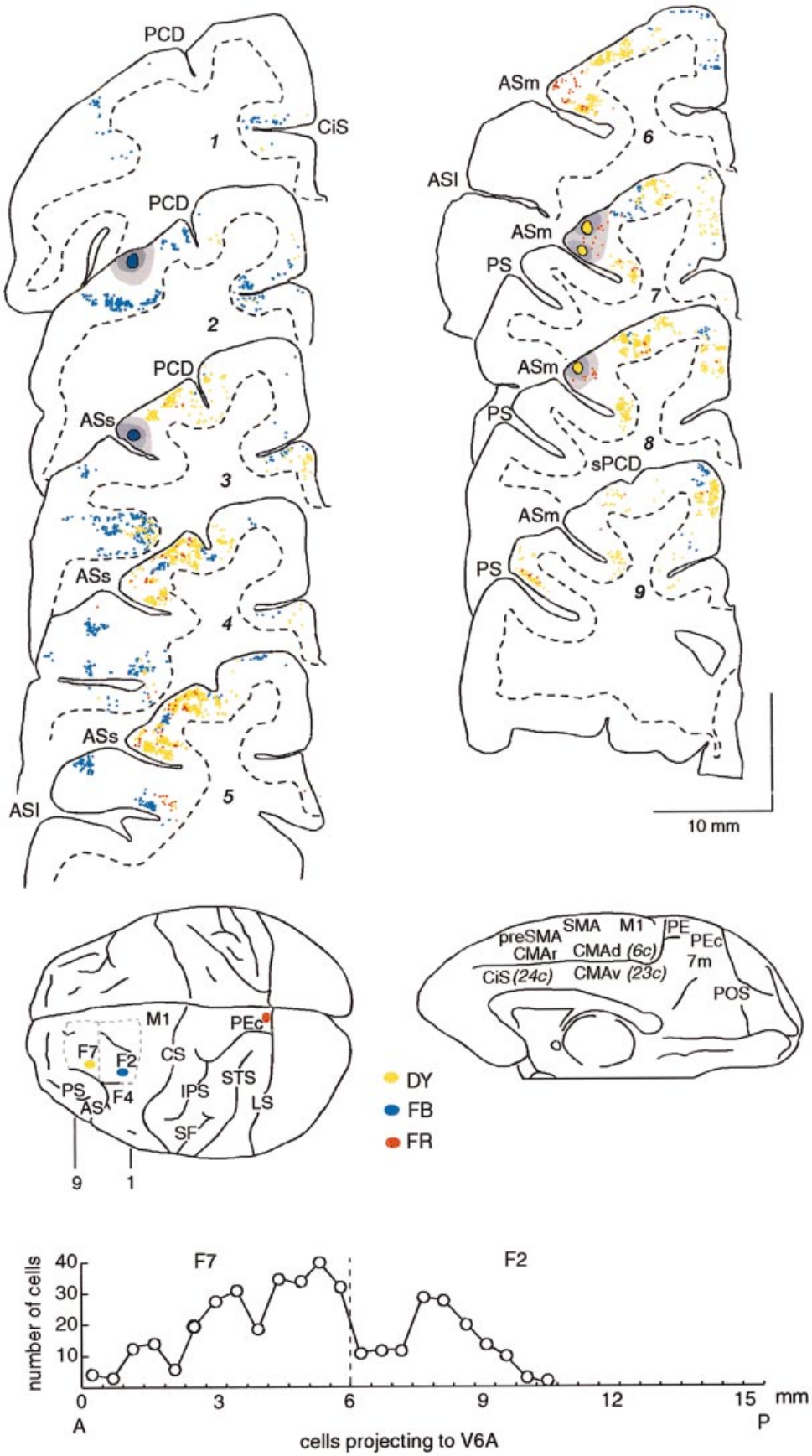

FIG. 3. Distribution of retrogradely labelled frontal cells projecting to V6A, PMdr, and PMdc. The histogram shows the number and antero-posterior distribution of cells in areas F7 and F2 retrogradely labelled by the injection in V6A. ASi, lateral limb of the arcuate sulcus; ASm, medial limb of the arcuate sulcus; ASs, spur of the arcuate sulcus; CiS, cingulate sulcus; PCD, pre-central dimple; other conventions and symbols as in Fig. 2.

Thus, the injection sites of DY and FB were separated in space and no overlap of the areas of diffusion of the two tracers was observed.

Tangential distribution of retrogradely-labelled cells in frontal and parietal cortices

Cell projecting to V6A. In the parietal lobe, the highest number of cells retrogradely labelled by FR was observed in the crown and medial bank of the parieto-occipital (Fig. 2, figurines *1* and *2*) and intraparietal sulci (IPS) in the medial intraparietal area (MIP; Fig. 2, figurines *5–7*). Another population of labelled neurons was found in the lateral intraparietal area, in the cortex of the lateral bank of the IPS (Fig. 2, figurines *5–7*). Rostrally, cells projecting to V6A were found in area PEa, in the medial bank of the IPS (Fig. 2, figurines *8–10*), as well as in area 7a (Fig. 2, figurines *10* and *11*) in the cortex of the exposed part of the inferior parietal lobule (IPL), and in the ventral intraparietal area (VIP) around the fundus of the IPS (Fig. 2, figurine *11*). Labelled cells were also observed in area PEc, in the posterior part of the superior parietal lobe (SPL; Fig. 2, figurines *5* and *6*), and were found in abundance in area 7m (Fig. 2, figurines *5–9*), in the cortex of the medial wall of the hemisphere.

In the frontal lobe, cells projecting to V6A were scant at the rostralmost regions examined, in pre-supplementary motor area (pre-SMA) or in prefrontal cortex (Fig. 3, figurines *8* and *9*). Their number increased moving caudally and laterally into PMdr (F7), where they occupied a region including the exposed part of the dorsolateral frontal cortex, up to the crown and bank of the medial limb of the arcuate sulcus (Fig. 3, figurines *6–8*). Their number finally decreased more caudally, approaching PMdc (F2; Fig. 3, figurines *3–5*) where, however, another discrete population was found close to the spur of the arcuate sulcus. A population of labelled cells was also found in area F5 in the caudal bank of the lateral limb of the arcuate sulcus (Fig. 3, figurines *4* and *5*).

Cell projecting to PMdr (F7). In the parietal cortex, significant numbers of cells labelled by DY were found in area V6A (Fig. 2, figurines *1–4*), as well as in areas PEc (Fig. 2, figurines *5–7*), MIP (Fig. 2, figurines *5–7*), 7m (Fig. 2, figurines *5–9*) and, to a lesser extent, in 7a (Fig. 2, figurines *10* and *11*).

In the frontal cortex, cells projecting to PMdr (F7) were consistently found in the pre-SMA (Fig. 3, figurines *7–9*); in PMdr (F7) itself, both in the exposed dorsolateral frontal cortex and in the medial bank of the medial limb of the arcuate sulcus (Fig. 3, figurines *6–9*); in PMdc (F2; Fig. 3, figurines *3–5*) and in area F5 (Fig. 3, figurines *4* and *5*), in the cortex of the caudal bank of the lateral limb of the arcuate sulcus (Fig. 3, figurines *3–5*). Labelled neurons were also found in the anterior ventral cingulate motor area (CMAv, Picard & Strick, 1996), in the cortex of the ventral bank of the cingulate sulcus (CiS in Fig. 3, also see the sulcus in figurines *3* and *4*).

Parietal cells projecting to PMdc (F2) were found in area MIP (Fig. 2, figurines *5–7*) and PEa (Fig. 2, figurines *8–11*), with few in area 7b, in the dorsal bank of the caudamost part of the Sylvian fissure (Fig. 2, figurines *10* and *11*). Another population of labelled cells was found in areas PEc (Fig. 2, figurines *6–8*), and 7m (Fig. 2, figurines *8* and *9*).

Frontal cells projecting to PMdc (F2) were found in the dorsal and ventral walls of the cingulate sulcus, in the cingulate anterior dorsal (CMAd, 6c) and ventral (CMAv, 23c) motor areas (Fig. 3, figurines *1–4*; Picard & Strick, 1996), in SMA (Fig. 3, figurine *6*), in the region flanking the precentral dimple (PCD) (Fig. 3, figurines *2–4*), and in area F5 (Fig. 3, figurines *3–5*). Labelled cells were also found in M1.

Discussion

An intricate pattern of association connections links area V6A with different parietal and frontal regions. All superior parietal areas except area 5d (PE) project to V6A. These projections originate from MIP, PEc, 7m and PEa. Smaller contributions come from 7a, VIP and LIP in the IPL.

The main source of frontal projections to V6A is PMdr (F7), although some arise also from PMdc (F2) and F5 (see also Matelli *et al.*, 1998) as well. Frontal projections of V6A are mainly addressed to PMdr (F7). In this study, we saw little V6A projection to PMdc (F2). V6A projects to PMdc (F2) in its ventro-rostral part and around the precental dimple (Matelli *et al.*, 1998). These regions were not injected in our animals.

PMdr (F2) is the target of other parietal projections that originate from 7m, MIP and, to a lesser extent, from PEc. These results conform to those already shown by previous studies (Cavada & Goldman-Rakic, 1989a,b; Johnson *et al.*, 1993, 1996; Tanné *et al.*, 1995; Matelli *et al.*, 1998). The frontal projections to PMdr (F7) originate from pre-SMA, PMdc (F2) and from area F5.

PMdc (F2), thanks to its connections with parietal areas 7m, MIP, PEa and, to a lesser extent, V6A, can serve as an intermediate link between early parietal and subsequent motor cortical mechanisms for the control of reaching.

Area V6A receives visual inputs from different extrastriate areas, such as V3, V3A, V5 and V6 (Shipp *et al.*, 1998). Its frontal projections are addressed to PMdr (F7) which, from previous studies, appears related to arm reaching to visual targets only in a rather loose way (Johnson *et al.*, 1996). This rostral premotor region is linked to PMdc (F2), whose neural activity is instead highly correlated with arm position and movement direction (Caminiti *et al.*, 1991) and is modulated by eye position signals (Boussaoud *et al.*, 1998).

The parietal connections of V6A are mainly made with areas such as 7m, MIP and PEa, which all project to dorsal premotor cortex. Neural activity in these parietal areas is highly correlated to arm position and movement direction (Johnson *et al.*, 1996; Ferraina *et al.*, 1997a,b). In area 7m, reach-related activity is influenced by eye position signals (Ferraina *et al.*, 1997a,b) and, as predicted by previous studies (Caminiti *et al.*, 1996; Wise *et al.*, 1997; Battaglia-Mayer *et al.*, 1998), this is also true for MIP (Snyder *et al.*, 1998).

In our study, before tracer injections, area V6A was characterized physiologically (Battaglia-Mayer *et al.*, 1998; Caminiti *et al.*, 1998). Preliminary analysis shows that its neurons combine visual, eye- and arm-related information relevant to visual reaching (see also Galletti *et al.*, 1997). This combinatorial mechanism of V6A does not seem to directly influence premotor or parietal areas linked to motor cortex, such as PMdc (F2) or 5d (PE), but mainly cortical regions such as parietal areas 7m, MIP and PEa, and frontal areas such as PMdr (F7), which all project to PMdc (F2). Therefore this last area is a crucial frontal node between vision and movement, while V6A emerges as an 'early' node in the combinatorial mechanisms underlying reaching and as a potential source of visual and eye position signals to cortico-cortically related parietal and frontal areas (see also Tanné *et al.*, 1995). The link between V6A and frontal cortex is reciprocal and may represent a cortical substrate whereby information about arm position and movement direction influences its neural activity (Galletti *et al.*, 1997; Johnson *et al.*, 1997; Battaglia-Mayer *et al.*, 1998; Caminiti *et al.*, 1998).

Therefore, the distributed system for visual reaching is characterized anatomically by the reciprocity of association connections linking its different nodes, and physiologically by the recursive nature of their interactions, probably due to re-entrant signalling. This mechanism

may be responsible for the combination along a continuum of functional properties (Johnson *et al*., 1996; Battaglia-Mayer *et al*., 1998; Caminiti *et al*., 1998) of retinal-, eye- and arm-related directional and positional information underlying coding of reaching, and suggests that no specific processing step can be solely attributed to any individual area.

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Abbreviations

CT, control time; *d*, total darkness; DY, diamidino yellow; EMP, eye movement and position task; FB, fast blue; FR, FluoroRuby molecular probe; IDR, instructed-delay reaching task; IDT, instructed-delay time; IN, inward from the periphery of the visual field toward the fovea; IPL, inferior parietal lobule; IPS, intraparietal sulcus; *l*, normal light condition; LIP, lateral intraparietal area; MIP, medial intraparietal area; MTe, movement time (eye); MTh, movement time (hand); OUT, outward from the fovea to the periphery of the visual field; PMdc (F2), caudal dorsal premotor cortex; PMdr (F7), rostral dorsal premotor cortex; PO, parieto-occipital cortex; RMTe, reaction and movement time (eye); RTe, reaction time (eye); RTh, reaction time (hand); SMA, supplementary motor area; THTe, eye target holding time; THTeh, eye-hand target holding time; VS, visual stimulation task; VIP, ventral intraparietal area.

References

Barbas, H. & Pandya, D.N. (1987) Architecture and frontal cortical connections of the premotor cortex (area 6) in the reshus monkey. *J. Comp. Neurol.*, **256**, 211–228.

Battaglia-Mayer, A., Ferraina, S., Marconi, B., Bullis, J.B., Lacquaniti, F., Burnod, Y., Baraduc, P. & Caminiti, R. (1998) Early motor influences on visuomotor transformations for reaching. A positive image of optic ataxia. *Exp. Brain Res.*, **123**, 172–189.

Boussaoud, D., Jouffrais, C. & Bremmer, F. (1998) Eye position effects on the neuronal activity of dorsal premotor cortex in the macaque monkey. *J. Neurophysiol.*, **80**, 1132–1150.

Caminiti, R., Ferraina, S. & Battaglia Mayer, A. (1998) Visuomotor transformations: early cortical mechanisms of reaching. *Curr. Opin. Neurobiol.*, **8**, 753–761.

Caminiti, R., Ferraina, S. & Johnson, P.B. (1996) The source of visual information to the primate frontal lobe: a novel role for the superior parietal lobule. *Cereb. Cortex*, **6**, 319–328.

Caminiti, R., Johnson, P.B., Galli, C., Ferraina, S. & Burnod, Y. (1991) Making arm movements within different parts of space: The premotor and motor cortical representation of a coordinate system for reaching to visual targets. *J. Neurosci.*, **11**, 1182–1197.

Cavada, C. & Goldman-Rakic, P.S. (1989a) Posterior parietal cortex in rhesus monkey: I. Parcellation of areas based on distinctive limbic and sensory cortico-cortical connections. *J. Comp. Neurol.*, **287**, 393–421.

Cavada, C. & Goldman-Rakic, P.S. (1989b) Posterior parietal cortex in rhesus monkey: II. Evidence for segregated corticocortical network linking sensory and limbic area with the frontal lobe. *J. Comp. Neurol.*, **287**, 422–485.

Colby, C.L., Gattass, R., Olson, C.R. & Gross, C.G. (1988) Topographical organization of cortical afferents to extrastriate visual area PO in the macaque: a dual tracer study. *J. Comp. Neurol.*, **269**, 392–413.

Ferraina, S., Johnson, P.B., Garasto, M.R., Battaglia-Mayer, A., Ercolani, L., Bianchi, L., Lacquaniti, F. & Caminiti, R. (1997a) Combination of hand and gaze signals during reaching: activity in parietal area 7m of the monkey. *J. Neurophysiol.*, **77**, 1034–1038.

Ferraina, S., Garasto, M.R., Battaglia-Mayer, A., Ferraresi, P., Johnson, P.B., Lacquaniti, F. & Caminiti, R. (1997b) Visual control of hand-reaching movement: activity in parietal area 7m. *Eur. J. Neurosci.*, **9**, 1090–1095.

Galletti, C., Fattori, P., Battaglini, P.P., Shipp, S. & Zeki, S. (1996) Functional demarcation of a border between areas and V6A in the superior parietal gyrus of the macaque monkey. *Eur. J. Neurosci.*, **8,** 30–52.

Galletti, C., Fattori, P., Kutz, D.F. & Battaglini, P.P. (1997) Arm movement-related neurons in the visual area V6A of the macaque superior parietal lobule. *Eur. J. Neurosci.*, **9**, 410–413.

Johnson, P.B., Ferraina, S., Bianchi, L. & Caminiti, R. (1996) Cortical networks for visual reaching: Physiological and anatomical organization of frontal and parietal lobe arm regions. *Cereb. Cortex*, **6**, 102–119.

Johnson, P.B., Ferraina, S. & Caminiti, R. (1993) Cortical networks for visual reaching. *Exp. Brain Res.*, **97**, 361–365.

Johnson, P.B., Ferraina, S., Garasto, M.R., Battaglia-Mayer, A., Ercolani, L., Burnod, Y. & Caminiti, R. (1997) From vision to movement: cortico-cortical connections and combinatorial properties of reaching-related neurons in parietal areas V6 and V6A. [In Their, P. & Karnath, O. (eds), Parietal Lobe Contributions to Orientation in 3D Space.] *Exp. Brain Res.*, **25 Suppl.**, 221–236.

Matelli, M., Govoni, P., Galletti, C., Kutz, D. & Luppino, G. (1998) Superior area 6 afferents from the superior parietal lobule in the macaque monkey. *J. Comp. Neurol.*, **402**, 327–352.

Matelli, M., Luppino, G. & Rizzolatti, G. (1985) Patterns of cytochrome oxidase activity in the frontal agranular cortex of the macaque monkey. *Behav. Brain Res.*, **18**, 125–136.

Nakamura, K., Chung, H.H., Graziano, M.S.A. & Gross, C.G. (1999) Dynamic representation of eye position in the parieto-occipital sulcus. *J. Neurophysiol.*, **81**, 2374–2385.

Pandya, D.N. & Seltzer, B. (1982) Intrinsic connections and architectonics of posterior parietal cortex in the rhesus monkey. *J. Comp. Neurol.*, **204**, 196–210.

Picard, N. & Strick, P.L. (1996) Motor areas of the medial wall: a review of their location and functional activation. *Cereb. Cortex*, **6**, 342–353.

Shipp, S., Blanton, M. & Zeki, S. (1998) A visuo-somatomotor pathway through superior parietal cortex in the macaque monkeys: Cortical connections of areas V6 and V6A. *Eur. J. Neurosci.*, **10**, 3171–3193.

Snyder, L.H., Batista, A.P. & Andersen, R.A. (1998) Change in motor plan, without a change in the spatial locus of attention, modulates activity in posterior parietal cortex. *J. Neurophysiol.*, **79**, 2814–2819.

Tanné, J., Boussaoud, D., Boyer-Zeller, N. & Rouiller, E.M. (1995) Direct visual pathways for reaching movements in the macaque monkey. *Neuroreport*, **7**, 267–272.

Wise, S.P., Boussaoud, D., Johnson, P.B. & Caminiti, R. (1997) Premotor and parietal cortex: Cortico-cortical connectivity and combinatorial computations. *Annu. Rev. Neurosci.*, **20**, 25–42.