

Somatosensory cells in the parieto-occipital area V6A of the macaque

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The aim of this study was to assess whether neurones of area V6A, a part of Brodmann's area 19, are modulated by passive somatosensory stimulations. Extracellular activity was recorded in four awake *Macaca fascicularis* while passive tactile stimulations of the skin and passive rotations of the joints were performed in complete darkness and under eye movement control. Out of 240 V6A

units, 78 (32%) were modulated by somatosensory stimulations. The majority of somatic receptive fields were located on both proximal and distal parts of the contralateral arm. V6A somatosensory cells may play a role in the feedback control of the actual state of the arm while reaching its target in peripersonal space. *NeuroReport* 13:2113–2116 © 2002 Lippincott Williams & Wilkins.

Key words: Area 19; Arm reaching; Awake monkeys; Behavioural neurophysiology; Grasping; Joint rotation; Passive somatosensory responses; Posterior parietal cortex; Superior parietal lobule; Tactile stimulation

INTRODUCTION

Somatosensory can be evoked in areas SI and SII as well as in several areas of the posterior parietal cortex, as in Brodmann's areas (BA) 5 [1–3] and 7 [3–5], located in the superior and inferior parietal lobules, respectively, and in ventral intraparietal area (VIP) [6,7] and medial intraparietal area (MIP) [6], hidden within the intraparietal sulcus (Fig. 1a).

Recently, a new area has been described in the caudalmost part of the superior parietal lobule: area V6A [8,9] (Fig. 1a). V6A is a visual area that also contains cells modulated by oculomotor [10] and skeletomotor [11,12] activities in darkness. As V6A is sited at the interface between classic visual and somatosensory areas of the brain, we wanted to assess whether it contains also neurones modulated by passive somatosensory stimulations. The results of this study indicate that this is the case.

MATERIALS AND METHODS

Experiments were carried out in accordance with National and European laws on care and use of laboratory animals and were approved by the University of Bologna Bioethical Committee.

Four behaving *Macaca fascicularis* were used. A detailed description of training, surgical and recording procedures, as well as anatomical reconstruction of recording sites, is reported elsewhere [9]. The following is a brief description of procedures not used in that report.

During the training period, animals were manipulated and touched on the whole body by the experimenter and were rewarded with water and fruits during manipulation. At the end of training they had become used to the manipulation and stayed quiet throughout the entire period of somatosensory stimulation.

Extracellular recordings from area V6A were performed while the monkeys were seated in a primate chair with the head fixed. Single unit activity or small clusters of neurones were recorded every 300–500 µm within V6A while passive somatic stimulations were applied. Somatosensory stimuli as manual soft touching, palpation of deep tissue and joint rotation at different velocities were carried out by the experimenter that stood behind the animal. Stimuli were delivered on both sides of the body.

As all experiments were performed with the monkey's head fixed, responses to neck rotation were not tested. When a cell responded to joint rotation, it was carefully checked whether skin stimulation around the joint was responsible for the neural activity. We assumed that the responses to light tactile stimuli were cutaneous in origin where there was no evidence that responses were due to deep tissue stimulation or joint rotations. However, the criteria we used were operational, so that this does not exclude the possible participation of other somatosensory afferences, including muscle proprioceptions.

As V6A is a visuomotor area containing visual neurones as well as non visual cells modulated by eye or arm movements [8–12], care was taken to rule out visual, arm and eye influences on cell discharges. In order to exclude

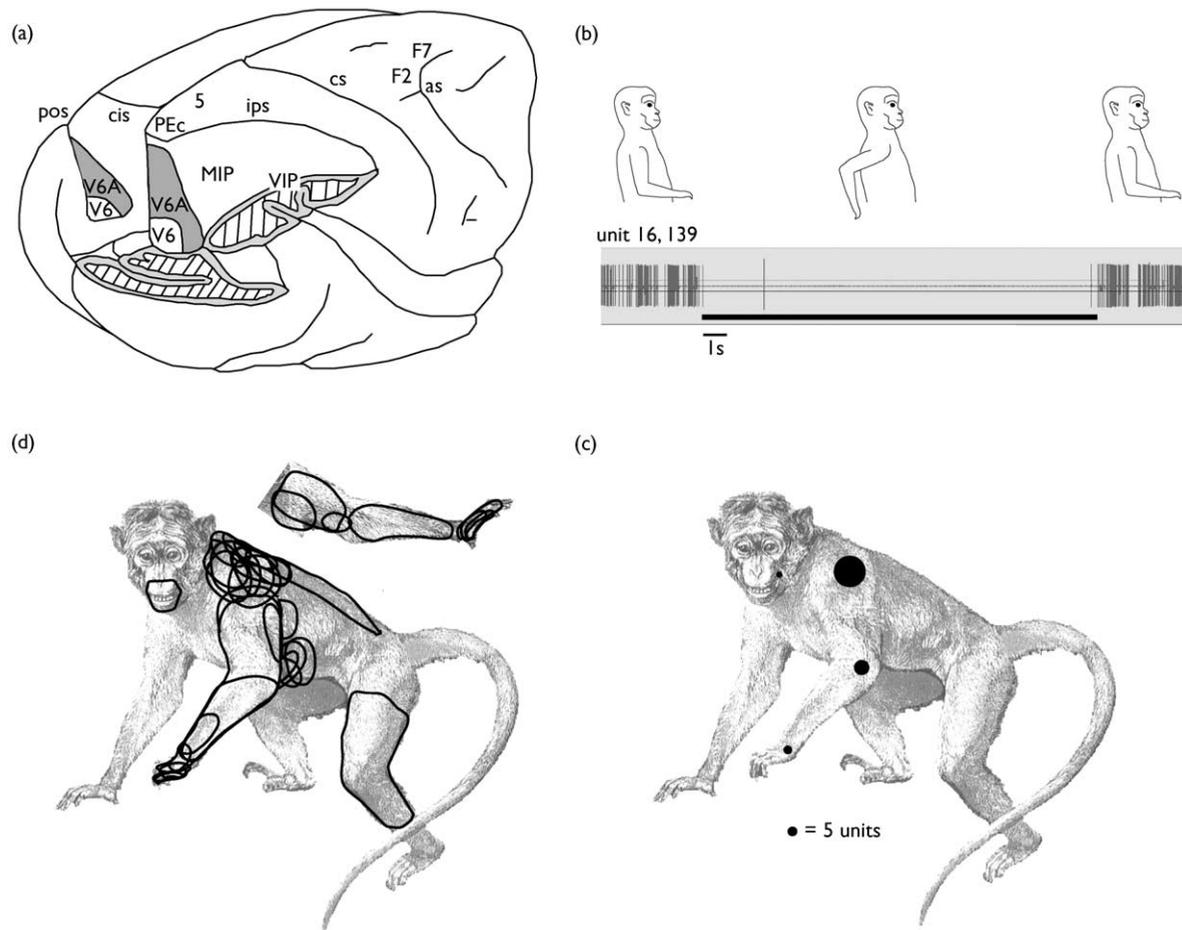


Fig. 1. (a) Postero-lateral view of the macaque brain partially dissected to reveal the anterior banks of the parieto-occipital (pos) and intraparietal (ips) sulci of the right hemisphere, as well as part of the mesial wall of the left hemisphere. The locations of areas V6 [24], and V6A [9] (this latter shown in grey) in the anterior bank of pos, areas PEc and 5 in the exposed surface of the superior parietal lobule, MIP [6,14] and VIP [6,14] in the ipsilateral side and areas F2 and F7 [25] in the frontal cortex are also reported. cs, central sulcus, cis, cingulate sulcus, as, arcuate sulcus. (b) Example of a cell modulated by rotation of the contralateral shoulder. The audio band of the videoclip below animals' silhouettes indicates the activity of the recorded cell (vertical bars are action potentials). Horizontal thick bar below the audio band indicates the period during which the arm was behind. (c) Location of joints modulating V6A cells. Each black dot indicates the joint that modulates V6A cells. The size of the dot is proportional to the number of modulated units. (d) Body locations of V6A tactile receptive fields. Above the animal, the internal surface of the left arm is reported to show locations of tactile receptive fields in that part of the body. Note that receptive fields are all reported on the left part of the body.

visual influences, somatosensory stimulations were performed in complete darkness. In addition, in the interval between two batteries of somatosensory stimuli, a light was turned on in order to avoid dark adaptation. Eye movements were continuously monitored, using an infrared oculometer [13] to check whether they were responsible for neuronal discharges. Finally, food or other objects of interest were presented to the animal to evoke arm reaching movements to check whether cell responses were arm movement-related discharges [11,12].

The somatosensory stimulations were monitored by an infrared video camera. This camera recorded the animals' movements on the video band of VHS tapes (25 frames/s) and the concurrently recorded neuronal activity on the audio band (44 kHz) of tapes. VHS tapes were digitized and stored on mini DV cassettes using a digital camcorder (Sony model TRV300E) connected with VHS player. QuickTime

movies were made using digital editing software (Apple Final Cut Pro, version 3) that allowed us to view the digitized video clips in real time or frame-by-frame. The software displayed also a strip chart of the actual spike train in a separate window (audio band), allowing us to compare video frames with firing patterns.

RESULTS

A total of 240 single cells or cell clusters recorded from area V6A were tested with passive somatosensory stimulations. A clear modulation of the neural discharge was observed in 78 cases (32%). Somatosensory-sensitive neurones were classified into four categories, as shown in Table 1, according to the submodality they were responsive to.

'Joint' neurones were activated by joint rotation. Figure 1b shows the behaviour of a joint cell modulated by the

Table 1. Categories of V6A somatosensory-sensitive neurones.

	Size of receptive field			Total <i>n</i> (%)
	Contralateral	Ipsilateral	Bilateral	
Joint	41	5	0	46 (59)
Skin	10	1	4	15 (19)
Deep	13	0	0	13 (17)
Joint + tactile	3	1	0	4 (5)
Total <i>n</i> (%)	67 (86)	7 (9)	4 (5)	78

Joint, skin, deep refer to neurones activated by soft touching of the skin, palpation of subcutaneous tissues, or joint rotations, respectively.

rotation of the shoulder. When the shoulder was passively rotated, the cell showed a brisk inhibition each time the arm was brought behind by the experimenter. The inhibition was well evident also when the monkey spontaneously brought his arm behind. The cell had a sustained discharge when the monkey maintained the arm relaxed on a plate, near his chest and outside the visual field. When the arm was behind, the cell became silent and the activity increased again when the arm returned to the initial position. As shown in Fig. 1c, the large majority of joint cells were modulated by rotation of the shoulder (31/46); others cells were modulated by the elbow (5/46), wrist (1/46), and jaw (1/46). Eight units were activated by movements of more than one joint of the upper limb, but only one of these was a single cell, the others being cell clusters.

'Skin' neurones were activated by light tactile stimulation of the skin. As shown in Fig. 1d, their receptive fields were mainly located on the arm (4/15), hand (4/15), and parts of the trunk near the arm (5/15). One cell had receptive field on the leg, and one on the muzzle.

'Deep' neurones were activated by deep pressure of subcutaneous tissues. As shown in Fig. 1d, their receptive fields were located on the arm (6/13), on the parts of the trunk near the arm (6/13), and on the hand (1/13).

We also found four cell clusters activated by more than one somatosensory modality (joint + tactile), but no one of the 26 single cells we studied responded to more than one type of somatosensory modality.

Almost all somatosensory receptive fields (75/78) were located on the upper limbs or in regions of the trunk close to the arm, and the overwhelming majority (86%) was located on the contralateral part of the body.

The majority of somatosensory cells (68/78) had tactile receptive fields located in the proximal part of the arm or was modulated by rotation of a proximal joint of the upper limbs. The proximal/distal gradient was different between joint and tactile cells: 40 joint cells were activated by rotation of the shoulder and 5 by the wrist, 17 tactile neurones had the receptive fields on the upper arm or nearby regions and 7 on the hand.

As shown in Fig. 1d, 28 of 32 tactile receptive fields covered small parts of the arm (seven were restricted to the hand) or of the trunk. Only two receptive fields covered the entire arm, one the leg and one the back, but none of these was a single unit.

DISCUSSION

The present data show that in area V6A about one third of the tested neurones were activated by passive somatosen-

sory stimulations, as joint rotation, light touch or deep pressure of the upper limbs, or of parts of the trunk close to them.

The proportion of V6A neurones sensitive to passive somatosensory stimulations (32%) is similar to that of area 7 [3–5], but much lower than that observed in areas 5 [1–3] and VIP [6,7]. In V6A, neurones sensitive to joint rotations are more represented with respect to those sensitive to tactile stimulations (50/32). Similar results have been observed in area 5 [1–3], whereas in VIP only skin responses were found [6,7]. Cells in area 5 often show complex somatosensory receptive fields that include several joints and body parts, as well as different somatosensory submodalities, whereas V6A cells are activated by only one joint or submodality.

The somatic representation in area V6A is far from complete, being mainly restricted to the upper limbs. The same restriction to the upper limbs has been observed in the somatic representation of area MIP [6]. Like V6A, area MIP is a bimodal visual/somatosensory area [6], but contrary to V6A the visual cells of MIP are insensitive to the direction of movement of visual stimuli, and its somatic representation represents mostly the distal part of the arm [6]. Among the other areas of the posterior parietal cortex containing somatosensory cells, areas 5 [1–3] and 7 [3–5] represent the entire body, while area VIP mainly the head [6,7].

In all posterior parietal areas, including V6A, somatosensory receptive fields are mainly contralateral. The size of tactile receptive fields is quite small in V6A cells, while it ranges from small to large (up to the whole trunk or limbs) in cells of areas 5 and 7 [1–5].

Possible sources of somatosensory input to V6A could be other cortical areas showing somatosensory properties and known to be connected with V6A, as areas MIP, VIP, P_{Ec}, and the premotor area F2 [14–16]. Among these areas, MIP seems to be a candidate as it represents both proximal and distal parts of the contralateral forelimb [6], like V6A. Another candidate could be the rostro-ventral part of F2, as it too represents proximal and distal parts of the arm [17] and is just the part of F2 connected with V6A [15,16,18].

Subcortical connections might represent another source of somatosensory information for V6A. It is known that pulvinar and lateral posterior nucleus in the thalamus also convey somatosensory information [19,20] and project to posterior parietal cortex [21], but at present it is unknown whether V6A is among the posterior parietal areas that are targets of these thalamic afferents.

CONCLUSION

On the basis of functional characteristics and anatomical connections of V6A, it has been repeatedly suggested that this area is involved in the visual guidance of arm reaching movements [8,9,11,12,15,16,22,23]. It has been suggested that activity in V6A is not exclusively visual, but presumably represents a blend of visual-somatomotor signals [8,11,12,23]. This paper is the first study to confirm that V6A activity does have a somatosensory component. Somatosensory inputs come from both proximal and distal parts of upper limbs, suggesting that somatosensory cells of V6A monitor the arm position and movement during

reaching out for things and grasping, activities that are congruent with the functional role proposed for area V6A.

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