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SHORT COMMUNICATION
Arm Movement-related Neurons in the Visual Area V6A of the Macaque Superior Parietal Lobule

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Abstract

Area V6A is a cortical visual area located in the posterior face of the superior parietal lobule in the macaque monkey. It contains visual neurons as well as neurons not activated by any kind of visual stimulation. The aim of this study was to look for possible features able to activate these latter neurons. We tested 70 non-visual V6A neurons. Forty-three of them showed an arm movement-related neural discharge due to somatosensory stimulation and/or skeletomotor activity of the upper limbs of the animal. The arm movement-related neural discharge started before the onset of arm movement, often before the earliest electromyographic activity. Thus, although the discharge is probably supported by proprioceptive and tactile inputs it is not fully dependent on them. Arm movement-related neurons of area V6A seem to be well equipped for integrating motor signals related to arm movements with somatosensory signals evoked by those movements. Taking into account also the visual characteristics of V6A neurons, it seems likely that area V6A as a whole is involved in the visual guiding of reaching.

Introduction

The superior parietal lobule (SPL) of the macaque monkey contains Brodmann's areas 5 and 7 and is known to be mainly involved in the analysis of somatosensory signals (Stein, 1991). However, in its caudalmost region, i.e. in the anterior bank of the parieto-occipital sulcus, it also contains the most medial part of area 19, a cortical visual association area (Brodmann, 1909). Extracellular recordings from this cortical region in anaesthetized and paralysed animals have distinguished a visual area, the parieto-occipital area (PO), ventrally, from a cortical region dorsal to it, where visual neurons have been reported to be less responsive to visual stimulation (Colby *et al.*, 1988). Recent recordings in awake animals have confirmed that in the most medial part of area 19 at least two cortical visual areas are present: area V6 (PO) ventrally and area V6A dorsally (Galletti *et al.*, 1991, 1996a). According to the last studies both areas contain highly responsive visual neurons, but area V6A also contains neurons that are not visually responsive at all. The presence of both types of neurons is a functional characteristic of area V6A that distinguishes it from area V6.

A question arises about the function that non-visual neurons may have in a cortical visual area like V6A. It has already been reported that at least some of them are activated by oculomotor activities involved in the control of gaze direction, like saccadic eye movements and steady fixation towards particular directions in the visual field (Galletti *et al.*, 1991, 1995). What we have done in this study is to look for other possible features able to activate these neurons. Since area V6A abuts dorsally the caudalmost part of area 5, which is known to be involved in the analysis of somatosensory inputs and somatomotor activities (Kalaska, 1991), a possibility exists that this type of input and/or activity influences V6A neurons as well. The present data show that this is the case.

Materials and methods

Two macaque monkeys (*Macaca fascicularis*) were used. A detailed description of training, surgical and recording procedures, as well as of visual stimulation, anatomical reconstruction of recording sites and animal care, is reported elsewhere (Galletti *et al.*, 1995, 1996a). The following is a brief description of them and of procedures not used in those reports.

The animals sat in a primate chair facing a large (80 × 80°) tangent screen. Monkeys performed a fixation task with the head restrained. Single neurons from the posterior face of the SPL were extracellularly recorded using Elgiloy microelectrodes (Suzuki and Azuma, 1976). Eye positions were recorded by an infrared oculometer (Bach *et al.*, 1983). The sample rate for action potentials was 1 kHz and that for eye position 100 Hz.

The receptive fields of visual neurons were mapped using visual stimuli rear-projected on the screen facing the animal. The cell's sensitivity to oculomotor activity was tested by displacing the fixation point on the screen in darkness, in order to evoke saccades or

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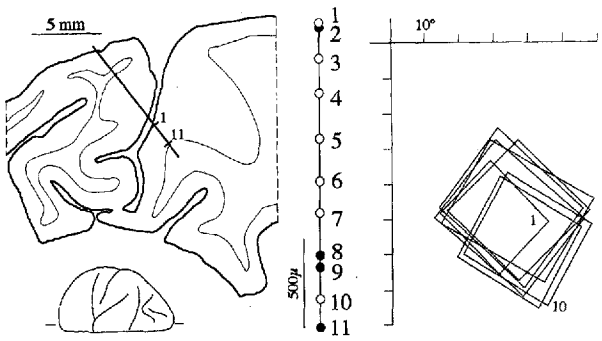

FIG. 1. Type of neurons encountered in a penetration through area V6A. (Left) Parasagittal section of the brain with the reconstruction of a microelectrode penetration passing through area V6A (1–11). (Middle) Cell types and their locations along the penetration. Empty and filled circles mark locations of visual and non-visual cells respectively. (Right) Receptive field sizes and locations of visual neurons encountered along the penetration. All receptive fields were in the lower contralateral quadrant of the visual field.

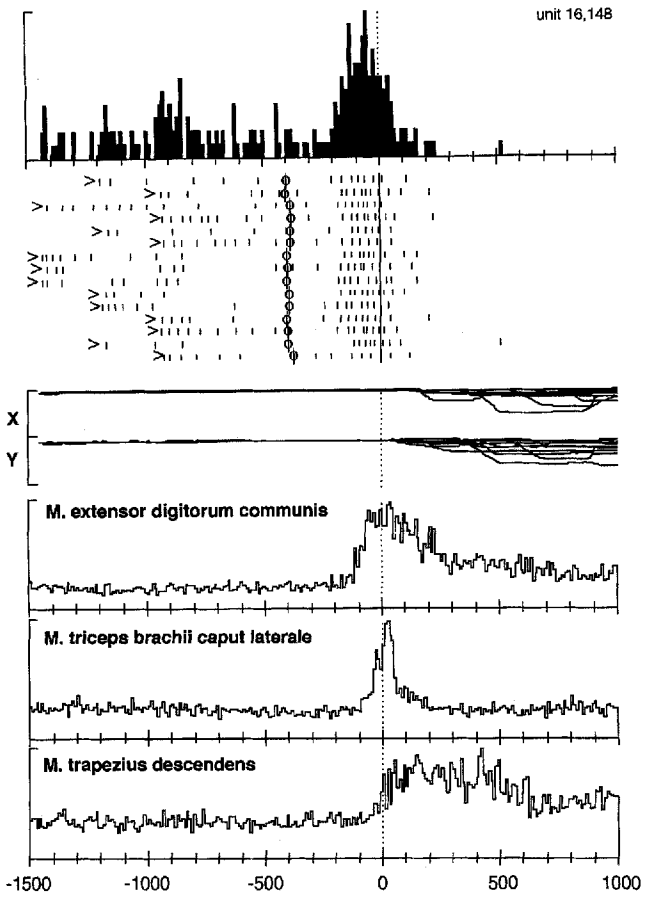

FIG. 2. Arm movement-related neuron recorded from area V6A. (Top) Peristimulus time histogram and raster displays of impulse activity. The signs > and Φ in the raster displays indicate the beginning of single trials and the 'go' signal for arm movement respectively. The neural activity is aligned on movement onset. (Middle) Recordings of *x* and *y* components of eye position. (Bottom) Electromyographic activities from muscles of the forearm (extensor digitorum communis), proximal part of the arm (triceps brachii caput laterale) and shoulder/neck/trunk (trapezius descendens). The cell shown in this figure is cell 8 in Figure 1. Scales: peristimulus time histogram, 50 imp/s; oculogram, 60°; electromyographic activity, arbitrary units; abscissa, 100 ms per division.

tracking eye movements towards different screen positions. Possible modulation of neural discharge by skeletomotor activity was tested in different ways. Stereotyped arm movements of very small amplitude (~1 cm) were elicited in each trial during the fixation task, when the animal pulled a lever to begin the trial and pushed it after task detection (change in colour of the fixation light). A microswitch connected to the lever signalled almost instantly the pull–push movement. The lever was out of the view of the animal and in a central position in front of its chest. We forced the animal to use either the left or the right arm, not allowing the unused arm to access the lever. While working, the animal's hand was constantly on the lever. Larger and more complex arm movements were elicited by presenting at arm distance small pieces of apple in different regions of space in front of the animal, and by allowing it to reach and grasp them. Videotape recordings were used to analyse the correlation of arm movements towards different directions in space with neural discharges.

The cell's sensitivity to somatosensory stimulation was assessed by light touches of the hair and skin, light or deep pressure on the tissues, and slow or fast rotations of the limb joints. In the first training sessions, the animal tried to withdraw the limbs whenever it was touched, but at the end of the training and during recording sessions it was quiet and compliant, so it was possible to test the effect of passive somatic stimulation on the activity of the recorded neurons.

Electromyographic activity (EMG) was monopolarly recorded with surface electrodes from 14 muscles of the arms, shoulders, neck and trunk in different sessions; seven electrodes were put on the right and seven on the left side. The raw EMG signals were filtered and recorded digitally at 1 kHz and then resampled at 100 Hz. The EMG and neural recording sessions were performed separately. The onsets of the rectified EMG and neural activities were calculated from peristimulus time histograms (PSTHs) of correct trials with a bin width of 10 ms. PSTHs were aligned on the onset of arm movement, and calculations were made with respect to the 500 ms time-window preceding this onset. From the first 20 data points (i.e. 200 ms) the mean and the standard error were calculated and used to construct an upper 95% confidence level. The onset of either EMG or neural activity was defined as that point preceding the arm movement where the PSTH was continuously above the confidence level.

Electrode tracks and the approximate location of each recording site were reconstructed on parasagittal sections of the brain on the basis of marking lesions and several other cues. Cells were assigned to area V6A on the basis of the functional criteria illustrated in Galletti *et al.* (1996a).

Results and discussion

In area V6A, typically, both visual and non-visual neurons were encountered along the same penetration, as shown in the example of Figure 1. Many V6A neurons, either visual or non-visual in nature, were activated by the oculomotor activities involved in changes of gaze direction. In the penetration shown in Figure 1, for instance, neurons 2, 8, 9, 10 and 11 were of this type. The receptive field organization and the gaze- and gain-field characteristics of V6A neurons have been fully described in previous papers (Galletti *et al.*, 1991, 1995, 1996a). In this study we tested the sensitivity of V6A neurons to somatosensory stimulations and/or skeletomotor activities. In order to reduce the possibility that visual stimulations were responsible for the observed changes in discharge rate, we decided to restrict our study to non-visual neurons only. Figure 2 shows the results of one of these tests. The animal was looking at a spot of light in darkness while performing the fixation task. Its hands were

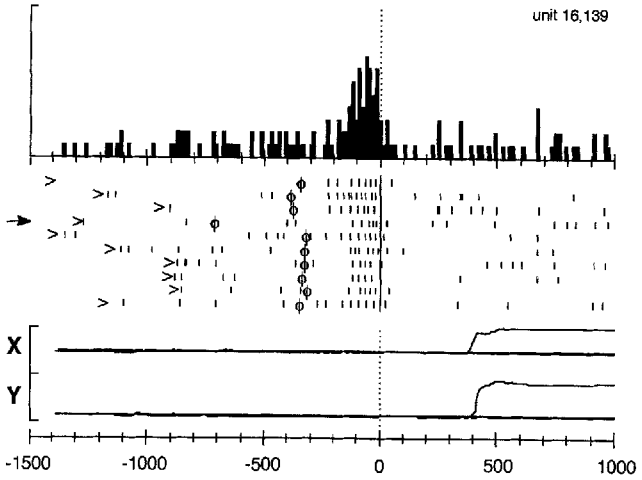

FIG. 3. Arm movement-related neuron recorded from area V6A. Details as in Figure 2. The arrow indicates a trial with a very long reaction time. Scales: peristimulus time histogram, 80 imp/s; other scales as in Figure 2.

out of its field of view. The cell in this record showed a clear increase in discharge rate ~200 ms before the onset of arm movement each time the animal pushed the lever during the fixation task. This neuron, as many other arm movement-related neurons of area V6A, was also activated by the pull movement of the arm at the beginning of each trial. In Figure 2, the last part of the neural discharge related to the pull movement of the arm can be seen in the raster display of each trial after the marker for the start of the trial (indicated by the symbol > in the figure).

Of a total of 70 non-visual neurons recorded from area V6A, clear modulation of the neural discharge to pull–push active movements was observed in 43 cases. In 17 of them passive somatic stimulations were also clearly effective: modulation of the neural activity was observed with rotations of arm joints (shoulder, elbow and/or wrist; $n = 13$), and/or a light touch of the skin of the arm ($n = 8$) in relaxed animals. In 22 cases we were not able to discriminate between the modulating effect of passive and active limb movements, although active movements often seemed to be more effective than passive ones. Finally, in four cases active arm movements strongly modulated neural discharge while passive ones were not effective.

Twenty-four of the 43 arm movement-related neurons were affected by movement of the contralateral arm, eight by the ipsilateral arm and 11 by both of them. While not all the arm movement-related neurons showed strong responses to lever pushing or pulling, all of them were optimally activated by natural arm movements evoked by presenting a piece of apple to the animal. Clear spatial tuning was often observed, i.e. the neural discharge was modulated only when the arm was directed towards particular regions of the animal's peripersonal space. Videotape recordings documented this behaviour, but our experimental setup was inadequate to quantitatively study this phenomenon. Further experiments are planned for this purpose.

Arm movement-related neural discharge always started before the onset of arm movements, often before the earliest EMG activity. We recorded EMG activities from muscles of the forearm (extensor digitorum communis and palmaris longus), the proximal part of the arm (biceps brachii and triceps brachii caput laterale) and the shoulder, neck and trunk (deltoideus medialis, pectoralis major and trapezius descendens) while the animal pulled and pushed the lever during the fixation task. EMG activities started at different times in these three groups of muscles: 70–120 ms before the onset of arm movement in the forearm, 50–90 ms in the proximal part of the arm and 10–60 ms in the shoulder, neck and trunk. This phenomenon is clearly evident in the bottom part of Figure 2, where the EMG activity from one muscle of each group is reported. The activity of the neuron shown in the figure starts well before the EMG activity of forearm muscles, i.e. the earliest EMG activity in the tested muscles. Therefore, proprioceptive signals and tactile stimulations cannot fully explain the cell's activation. The fact that active arm movements were often more effective than passive movements in activating the cells seems to confirm that the movement-related discharge of these V6A neurons can be supported by proprioceptive and tactile signals, but is not fully dependent on them. Certainly it was not the case for the four cases where only active arm movements were effective.

An alternative hypothesis to explain the earliest activity of these cells should also be considered: it might have been due to a visual stimulation made before arm movement rather than to the arm movement *per se*. The 'go' signal for pushing the lever was a change in colour of the fixation light (from green to red), hence a visual stimulation which happened ~400 ms before the onset of arm movement (reaction time), i.e. ~200 ms before the onset of the cell's discharge (Fig. 2). But 200 ms is a very long delay for a cortical visual response, even in a visual association area. In fact the latency to stationary visual stimulation in area V6A is 50—70 ms (Galletti *et al.*, unpublished results). So it seems unlikely that the arm movement-related neural discharge is in fact a visual response.

We also calculated the onset of the arm movement-related neural discharge [by the method described by Commenges *et al.* (1986)] and used this value to calculate the mean latencies relative to the 'go' signal and to the movement onset. This was done on the assumption that the variances of these two means were different, the smaller variance indicating the phenomenon that was more correlated with the neural discharge. But since the monkey was forced to react as fast as possible to the 'go' signal and was well trained to do so, the two variances were generally not statistically different from one another. However, when the animal occasionally showed longer reaction times to the 'go' signal the cell's discharge was *always* temporally related to the arm movement and not to the 'go' signal itself. Figure 3 shows one example of this behaviour. In the trial indicated by an arrow the animal had a longer reaction time to the 'go' signal (the red onset indicated by ϕ in Fig. 3). The neural response remained time-linked to the movement onset instead of to the red onset. Since in this trial the animal was correctly fixating, as in all other trials, we conclude that the cell's discharge was actually due to the arm movement *per se* instead of to the visual stimulation evoking that movement. This premotor activity dealing with the arm movement, or with the animal's intention to move the arm, might be a command for initiating motor acts or an efference copy of motor commands relayed from structures commanding arm movements. The recent finding of an interconnection between the frontal lobe and area V6A (Matelli *et al.*, 1995; Shipp and Zeki, 1995) makes both hypotheses plausible.

Concluding remarks

It seems likely that the function of area V6A as a whole is the visual guidance of reaching. As a matter of fact, area V6A contains visual neurons able to encode spatial coordinates of visual targets (Galletti *et al.*, 1993, 1995), and others with high sensitivity to both the orientation and the direction of moving stimuli (Galletti *et al.*, 1991, 1996a). These characteristics are very useful for visually encoding the features and spatial location of the target to be reached, as well as the direction of movement of the animal's hand approaching the target itself. Area V6A also contains non-visual neurons finely

encoding gaze directions (Galletti *et al.*, 1995), and neurons with spatially tuned saccade-related activity (Galletti *et al.*, 1991). In addition, the present results show that it contains neurons whose activity is modulated by arm movements and is not dependent on visual information, while it is dependent on somatosensory stimulation from the arm itself. In conclusion, area V6A seems to have the machinery needed to control the correct orientation of both arm and gaze in space for executing reaching movements in the extrapersonal space and for the ongoing correction of them. This view might explain why a lesion of the parieto-occipital cortex at the level of the superior parietal lobule in man causes visuomotor ataxia (Perenin and Vighetto, 1988): the lesion strikes a region of the human brain homologous to that of the monkey brain containing area V6A (Galletti *et al.*, 1996b), so the patient loses the possibility of using visual information in order to spatially localize the target of reaching, and to correct the arm movement towards that target.

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Abbreviations

EMG	electromyography
PO	parieto-occipital area
SPL	superior parietal lobule

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