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"Space coding by premotor cortex"

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Research Note

Space coding by premotor cortex

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Summary. Many neurons in inferior area 6, a cortical premotor area, respond to visual stimuli presented in the space around the animal. We were interested to learn whether the receptive fields of these neurons are coded in retinotopic or in body-centered coordinates. To this purpose we recorded single neurons from inferior area 6 (F4 sector) in a monkey trained to fixate a light and detect its dimming. During fixation visual stimuli were moved towards the monkey both within and outside the neurons's receptive field. The fixation point was then moved and the neuron retested with the monkey's gaze deviated to the new location. The results showed that most inferior area 6 visual neurons code the stimulus position in spatial and not in retinal coordinates. It is proposed that these visual neurons are involved in generating the stable body-centered frame of reference necessary for programming visually guided movements.

Key words: Body-centered visual receptive fields – Space coding – Visually guided movements – Premotor cortex – Macaque monkey

Introduction

One of the fundamental problems in programming visually guided movements is the necessity to construct a body-centered frame of reference. Visual input originates from images on the retinas and, due to the point-to-point organization of visual pathways, most visual centers, including the occipital cortical areas, maintain a retinotopic organization. On the other hand, movements must be directed towards locations in space with respect to the body and therefore the motor system must encode space in body-centered coordinates.

In this article experiments will be presented in which we tested whether neurons in monkey inferior area 6, and precisely in its F4 sector (Matelli et al. 1985), had receptive fields coded in retinotopic or body-centered coordinates. F4 is a premotor area which receives a cortical input from the inferior parietal lobule (Matelli et al. 1986), a cortical region which plays a fundamental role in space perception and visually guided behavior (Lynch 1980; Hyvarinen 1982), and projects to the motor cortex (Matsumura and Kubota 1979; Muakkassa and Strick 1979; Matelli et al. 1986). Previous experiments have shown that in F4 many neurons respond to visual stimuli presented in the monkey's peripersonal space (Gentilucci et al. 1988). Furthermore, a large number of F4 neurons discharge during arm-reaching movements. F4 appears therefore an area in which the retinotopic frame of reference, typically found in the posterior cortical areas, is likely to have been changed into a body-centered frame.

Methods

The experiments were carried out on a macaque monkey (Macaca nemestrina). Animal preparation and recording procedures were the same as described in previous experiments (for details see Gentilucci et al. 1988; Rizzolatti et al. 1988). During the recordings the monkey was seated in a primate chair with its head fixed. Single neurons were recorded using tungsten microelectrodes. The microelectrode used for recording was also used for electrical intracortical microstimulation (train duration = 50 ms, pulse duration = 2 ms, frequency = 250 Hz, current intensity 3 to 40 μA).

Once a neuron was isolated we examined its discharge during the animal's active movements. The neuron's responsiveness to somatosensory and visual stimuli was then assessed and the tactile and visual receptive fields plotted. In order to map the visual receptive fields, three dimensional objects were moved towards the animal along different directions.

After "clinical" characterization, the neuron's activity was studied during a fixation task. A light emitting diode (LED) served as fixation point. The LED was placed 1 m in front of the monkey. Its azimuth and elevation could be varied. The monkey was trained to press a bar, which turned the LED on, and to fixate the LED until it dimmed. The LED dimming occurred after a delay which varied between 1.8 and 2.2 s. The monkey was rewarded if it maintained the fixation until dimming and released the bar during dimming (800 ms). There were control trials in which no stimuli were presented during the fixation task and experimental trials in which a moving device (a robot arm) was moved towards the animal.

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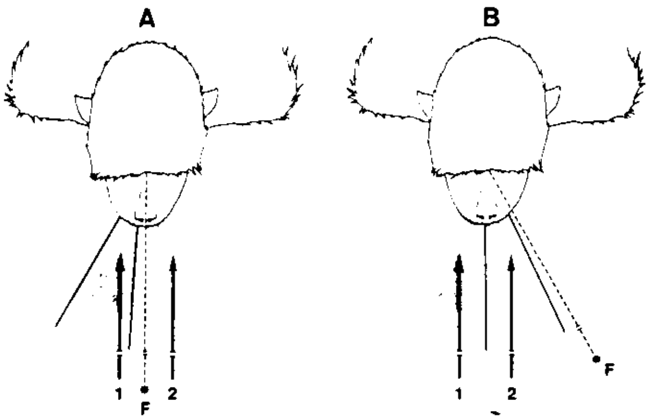

Fig. 1 A, B. Schematic representation of the procedure employed to classify receptive fields. Two hypothetical receptive fields, one coded in retinotopic coordinates (space between the continuous lines), the other coded in body-centered coordinates (shadowed area) are shown. In **A** the monkey fixates centrally. The two fields are in register. In **B** the monkey fixates eccentrically (30° to the left). The retinotopic field follows the eyes, while the body-centered field remains anchored to the head. F = fixation point. The thick arrows indicate the trajectories of the robot arm

The robot arm started at a distance of 60 cm from the animal, approached the animal's head (speed 40 cm/s), and reversed movement direction a few centimeters from the monkey's fronto-orbital plane. The robot arm movement started 200 ms after the illumination of the fixation point. Control trials and experimental trials were presented in blocks.

Eye movements were controlled using the magnetic search coil technique (Fuchs and Robinson 1966). Breaks of fixation during testing interrupted automatically the trial. The three-dimensional trajectory of the moving stimulus with respect to the animal's head was reconstructed using a computerized movement recording system (ELITE system, Ferrigno and Pedotti 1985). This system as used in the present experiment, consists of two infrared TV-cameras and a processor which elaborates the video images in real time and reconstructs the 3-D position of infrared reflecting markers. The markers used for reconstructing the robot arm trajectories were placed at the center of the head-holder and near the tip of the moving stimulus. Neck, arm, and upper trunk muscle activity was recorded unipolarly with stainless steel electrodes.

Four basic experimental situations were used to determine whether the receptive fields of the recorded neurons were coded in retinotopic or body-centered coordinates. They are shown in Fig. 1. In A1, the monkey fixated centrally and the robot arm was moved towards the animal across the neuron's receptive field. In A2, the fixation point remained unchanged, but the robot arm was moved outside the receptive field. In A1 and A2 the retinotopic and body-centered frames were in register. In B, the fixation point was shifted and the robot arm was moved along the same trajectories as in A. If the receptive field were retinotopically organized, its position should change with the eyes. Thus, the neuron would now respond in B2 but not in B1. In contrast, if the receptive field were coded in body-centered coordinates, the neuron responses should not be affected by the change of gaze. The responses should remain present in B1 and absent in B2.

The extension in depth of the visual receptive fields was assessed on the basis of the beginning of the neuron responses to the robot arm. In order to calculate the response initiation, response histograms were constructed and then filtered using a noncausal, low-pass, moving average filter (9 terms, one term = one bin). The first bin of a series of at least five successive bins with progressively increasing values was considered as the response initiation.

Results

The inferior part of area 4 and inferior area 6 (see Fig. 2) were electrically stimulated from the central sulcus to the arcuate sulcus. Distal movements were found near the central sulcus followed, rostrally, by proximal and axial movements. Further rostrally, proximal and then distal movements were again evoked. The transition from the caudal to the rostral movement representation was accompanied by the disappearance of neurons which responded to proprioceptive stimuli and by their substitution with neurons activated by tactile stimuli. This change in functional properties coincides with the border between F1 (area 4) and F4 (Gentilucci et al. 1988). All units described in this study were found in area F4 as functionally defined. Neurons recorded more laterally (oro-facial representation of F4), more rostrally (F5), and more medially (neurons unresponsive to tactile stimuli, possibly F2) were not included in the present analysis.

A total of 170 F4 neurons were studied. In agreement with previous data (Gentilucci et al. 1988), most of these neurons ($n = 131$) responded to tactile stimuli, and many ($n = 107$) could be driven by visual stimuli. Thirty-five neurons with stable, reliable visual responses were analyzed for enough time to classify them as retinotopic or body-centered. Twenty-eight of these neurons were coded in body-centered coordinates, 7 neurons were retinotopic. The term body-centered coordinates as used here indicates neuron's receptive fields anchored to the head and/or the trunk. A differentiation between craniotopic coordinates and coordinates related to the trunk was impossible because of the head fixation.

An example of a body-centered neuron is shown in Fig. 2. In A1 the monkey looked straight ahead and the robot arm was moved inside the neuron's receptive field. In A2 the monkey was still looking straight ahead but the robot arm was moved outside the receptive field. In B1 and B2 the gaze was deviated 30° to the left. In spite of this, the responses remained present in B1 and absent in B2. If the field were retinotopic the response would be expected to appear in B2 (see Fig. 1). C and D are controls. The first shows that the receptive field did not change position when the gaze was deviated 30° to the right. The second illustrates the background activity in the absence of receptive field stimulation. Note that in A1, B1 and C, in spite of large variation in gaze angle the intensity of the response and its spatio-temporal characteristics remained the same.

All body-centered neurons responded to tactile stimuli, with the tactile field located predominantly on the face. Visual receptive fields were in register with tactile receptive fields. The extension in depth of the visual fields was 19 ± 7 cm. The largest field extended for 35 cm, the smallest for 5 cm. Visual fields were exclusively contralateral to the recorded side in 18 of the 28 body-centered neurons, exclusively ipsilateral in 3 neurons, and bilateral in 7 neurons.

In most neurons ($n = 16$) the shift of gaze did not modify the intensity of visual responses. In other cells, however, although the receptive field remained anchored

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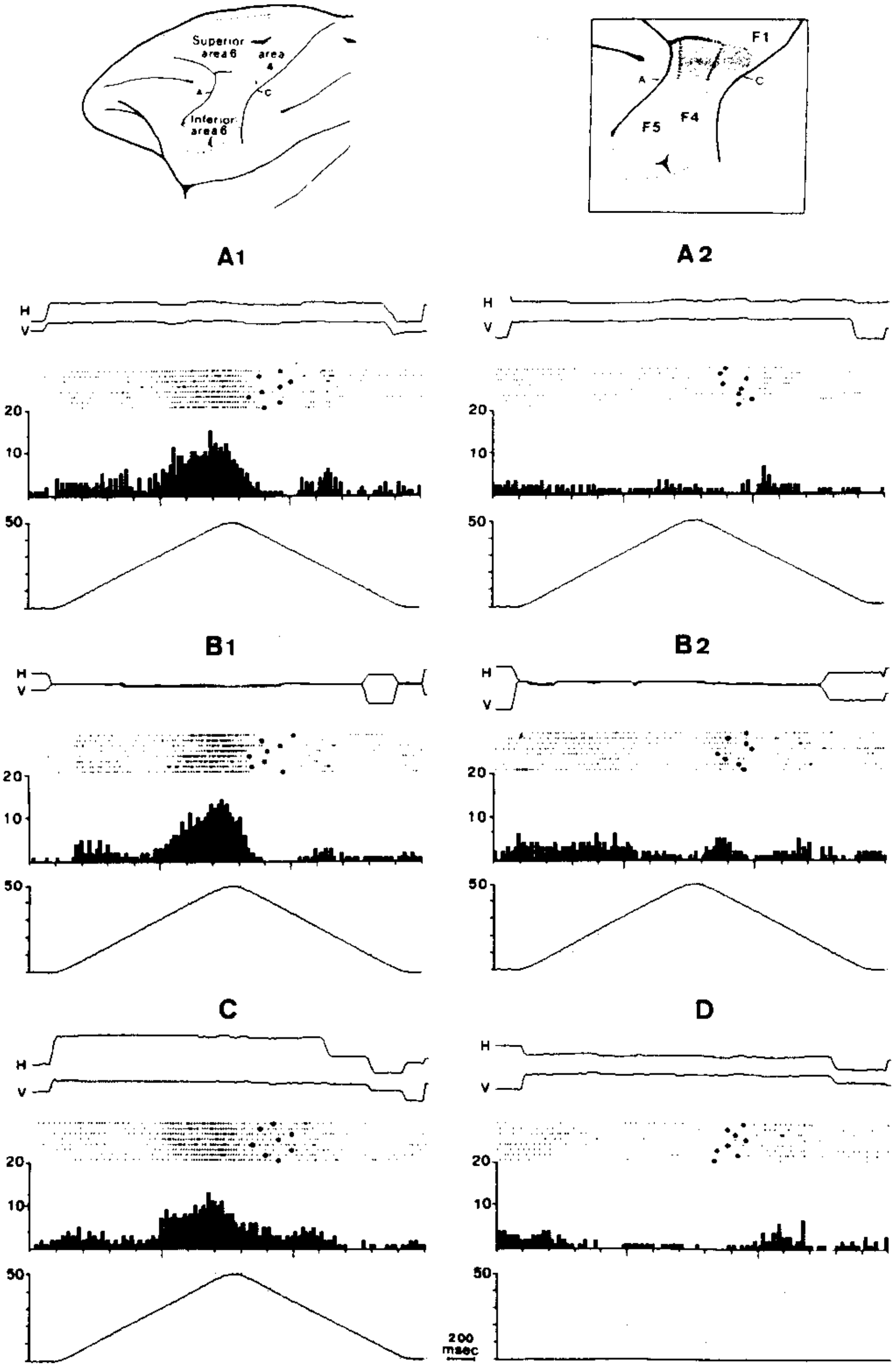

Fig. 2A–D. *Upper part.* Left side: lateral view of the monkey left hemisphere showing motor (area 4) and premotor (area 6) cortices. Right side: enlarged view of inferior area 6. This area is formed by two sectors: F4 and F5. F1 corresponds to area 4. The shadowed area indicates the cortex explored in the present study. A = arcuate sulcus; C = central sulcus. *Lower part.* Example of a body-centered visual neuron. Each panel shows: a) horizontal (H) and vertical (V) eye movements; b) rasters illustrating the neural activity during the individual trials. The large dots indicate the fixation point dimming; c) response histograms (abscissae: time, ordinates: spikes/bin, binwidth: 20 ms); d) robot arm displacement expressed as its vector module. The ascending part of the curve indicates movement of the stimulus towards the monkey, the descending part indicates the movement away from the monkey (abscissae: time, ordinates: cm). The tactile receptive field of the neuron was located on the face contralateral to the recorded side. The visual receptive field was around the tactile one (visual receptive field width: 70°; medial border of the field coincided with the 0° gaze axis). In **A1**, **B1** and **C** the trajectory of the stimulus, moved inside the receptive field, was along a parasagittal plane 7 cm lateral to the head midline; the direction reversed when the stimulus was 4 cm from the orbital plane. In **A2** and **B2** the trajectory was identical to **A1** but on the opposite side of the midline (outside the receptive field). **D** Control trials. No moving stimulus was presented. Fixation point: **A1**, **A2**, and **D** = 0°; **B1** and **B2** = 30° to the left; **C** = 30° to the right. Note the constancy of the response onset following the start of stimulus movement. The response onset corresponded approximately to a distance of 25 cm from the orbital plane. The responses in **A1**, **B1**, and **C** did not differ statistically one from another (one-way ANOVA: independent variable number of spikes per bin. $F < 1$)

to the body, the background discharge rate and the intensity of response to visual stimuli varied with gaze location. With few exceptions the pattern was the following. The background discharge rate was the lowest when the gaze was deviated away from the receptive field and was the highest when the gaze was aligned with the spatial position of the field. In contrast, the visual response intensity was maximal when the gaze was away from the field and was minimal when it was directed towards the field.

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Changes in muscle activity related to visual stimulation were never observed. In contrast a tonic increase in the activity of neck muscles ipsilateral to the fixation side was constantly associated with gaze deviation. Electric stimulation of F4 produces neck movements, but never eye movements (this experiment, see also Gentilucci et al. 1988). It is likely, therefore, that the increase in discharge rate with different gaze positions reflected the activity of neurons which control neck muscles rather than neurons related to oculomotor control.

Nineteen out of 28 body-centered neurons fired in association with bar release. Some of these neurons fired also during reaching arm movements. Informal testing showed that proximal arm movements, head turning movements, and combined arm-reaching and head-turning movements were the motor responses observed in body-centered neurons. Neurons related to distal movements were never observed.

Discussion

A stable visual frame of reference is necessary for programming visually guided movements, for integrating visual information over fixations and for generating a stable visual world despite eye movements. There is no agreement however on how a stable frame is achieved (Feldman 1985). Although there are isolated reports of neurons whose receptive fields appear to be independent of eye position (Schlag et al. 1980; Gentilucci et al. 1983; Pigarev and Rodionova 1986, 1988; Battaglini et al. 1990), the hypothesis has been advanced that the stable frame of reference is the result of a computation that involves retinotopic neurons rather than an explicit space coding due to neurons with body-centered receptive fields (Andersen et al. 1985; Bruce 1988; Goldberg and Bruce 1990). For the oculomotor system it has been proposed that, when there is dissonance between retinal vector of a stimulus and the movement vector of the saccade necessary to acquire that stimulus, a change occurs in the topographical location of the retinal receptive field. This remapping, (possibly based on a vector subtraction) is thought to be responsible for the correct acquisition of a target (Bruce 1988; Goldberg and Bruce 1990). Another solution is based on the observation that in some posterior cortical areas there are retinotopic neurons whose activity is modulated by the eye position (Andersen and Mountcastle 1983). The computation of stimulus position in retinal coordinates and that of the eye in the orbit would provide sufficient information to localize an object in space (Andersen et al. 1985; Galletti and Battaglini 1989).

The present findings clearly demonstrate that the primate nervous system can code space directly. In area F4 the great majority of neurons which are responsive to visual stimuli had receptive fields organized in body-centered rather than in retinotopic coordinates. Space is therefore explicitly coded at the single neuron level. It is hardly coincidental that retinotopic coding disappears in an area such as F4, which is involved in the programming of arm and other body movements. On the contrary it is likely that the programming of limb and head movements demands a more direct way of coding space than one based on the continuous updating of eye position. This is not to say that there are no other ways of achieving a stable visual frame of reference. It is quite possible that the saccadic system may use an indirect way of coding space. If one considers that the areas that provide a stable (eye-position independent) spatial frame are usually involved in motor control (Rizzolatti and Gallese 1988), the interesting possibility arises that space is coded differently in different cortical areas and that a particular spatial code depends upon the computational requests of the effectors that a given area controls.

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Erratum

Exp Brain Res (1992) 88:455–458

H. Sato and H. Noda

An error unfortunately occurred in the title of the above article. The correct title is:

Saccadic dysmetria induced by transient functional decortication of the cerebellar vermis

6.