Functional properties of premotor area F5a: a single-unit study

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BACKGROUND

Functional data demonstrate that area F5 of the macaque ventral premotor (PMv) cortex is involved in different aspects of goal-directed motor control *(Rizzolatti G. et al. 1996)*. Recent architectonic data show that F5 consists of three fields, referred to as the anterior (F5a), posterior (F5p) and convexity (F5c) subdivisions of F5 (Figure 1) *(Belmalih A. et al. 2009)*. A recent fMRI study on awake monkeys shows that both F5c (where "mirror" neurons are located) and F5a are activated by action observation *(Nelissen K. et al. 2005)*.

There are no single-neuron data available on the motor properties of F5a. However, considering its architectonic organization and the known functions of premotor areas, it is likely that F5a neurons do have motor properties.

To explore this issue, we performed an electrophysiological mapping of this area at the single-neuron level.

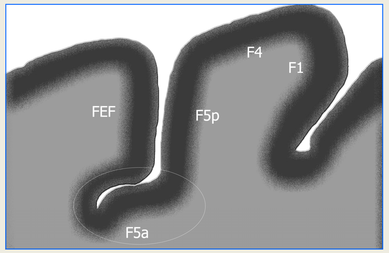


Fig.1. Schematic representation of the location of F5a in the arcuate sulcus

METHODS

A circular recording titanium chamber, with an inner diameter of 20 mm was placed on skull covering the premotor region of the left hemisphere from the iAS to the cortical convexity close to the central sulcus. In this way FEF, F5 and sulcus were accessible for the recordings (Figure 2).

Intracortical microstimulation (ICMS) and naturalistic testing were used to:

- precisely characterize the location of the anterior and posterior banks of the iAS and of the adjacent convexity cortices in order to identify possible breakthrough points for the electrode to reach the fundal part of iAS where area F5a is located;

- identify deeper anatomical landmarks as the profile of iAS and periarcuate cortices, according to the functional properties displayed by the neurons encountered as the electrode was slowly advanced through the cortex (Figure 2).

. test the functional properties of F5a neurons

Naturalistic Testing

Functional properties of neurons were tested as follow:

1-Somatosensory properties: tactile stimuli were gently and deeply applied to the skin and hair of the animal.

2-Visual properties: static or moving 3D objects of different size and shape were presented at different spatial locations and distances from the monkey, together or without a human hand.

3-Motor responses: the monkey was asked to perform different actions on the objects, such as grasping, manipulating, holding, pulling, etc. Eye-related movements were studied with the monkey gazing at a target object moving in the space.

4-Mirror-like responses: object-related, non-object related and mimicked actions performed by the experimenter were observed by the monkey.

5-Other properties: if needed, each F5a neuron was systematically studied by using additional tests varying on an ad hoc basis.

Criteria and functional characteristics described by *Umiltà M.A. et al. (2001)*, were used to distinguish areas and regions.

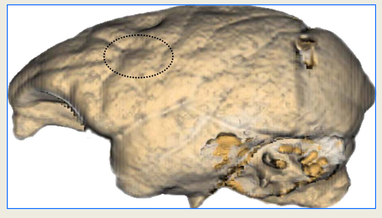


Fig.2. Brain area covered by recording chamber.

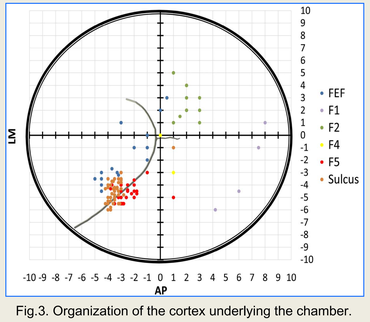
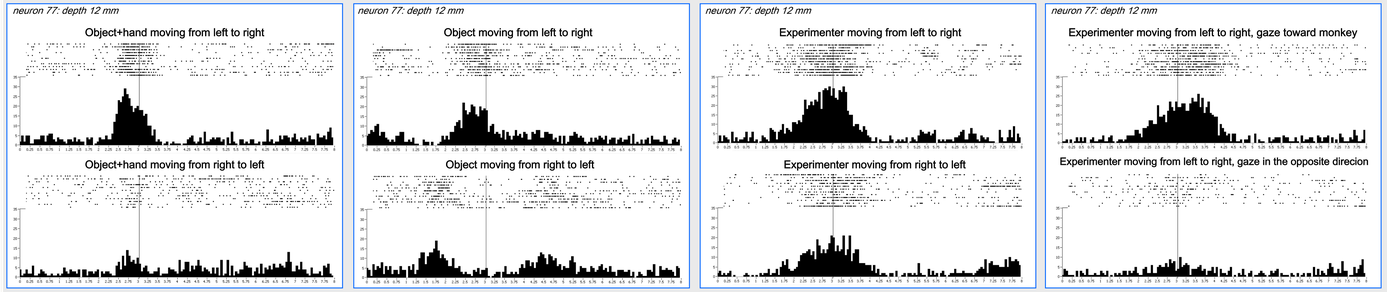


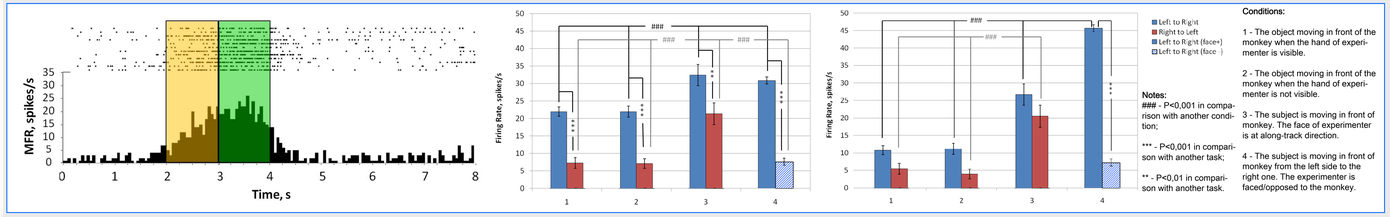
Fig.3. Organization of the cortex underlying the chamber.

RESULTS

Here we report preliminary data from 138 penetrations made in PMv. Functional mapping and depth of electrode recordings indicate that 46 units from 44 penetrations were F5a neurons.

Almost 2/3 of these neurons had complex activity correlated with eye-movements. Among 46 tested neurons 65% had eye-related movement properties and 13% had hand-related motor properties, they discharged when the monkey performed a particular grasping. Visual responses were direction-selective in 21% of cases and stronger when elicited by biological motion, but did not have any clear motor counterpart. There was no or weak response to voluntary saccades, while some of these neurons discharged at the presentation of a particular 3D objects or moving objects. In the last case the response was typically stronger for the biological stimuli. In fact, some of these responses, were specific to the tangent motion of an experimenter faced to the monkey (these effects are shown at PSTH and rastergrams below). The activity of such neurons was also direction-selective, increasing when the object (or the experimenter) moved leftward rather than rightward. Similar, but lower response was found for a puppet moving in the same direction.





CONCLUSIONS

In this preliminary study we focused on the localization of area F5a, based on the identification of critical anatomical landmarks and the characterization of the general functional properties of the deep periarcuate regions.

1. The activity of the neurons presumably recorded from area F5a are mostly eye movement-related, in all probability because of the anatomical contiguity with FEF. In addition, some neurons were found to show discharge properties similar to those described in the superior temporal sulcus (STS), an area where cells respond to the observation of specific body part movements *(Perret D.I. et al., 1986)*.

2. These findings suggest a role for F5a as possible interface for premotor areas in a neuronal circuitry involving STS, parietal and frontal regions during action observation.

3. The “mirror” responses has not been revealed at the present time.

Our exploratory study has also evidenced some technical limitations:

a) a better online control on the depth and extent of the iAS as well as of the adjacent areas (for example, by means of an ultrasonic device) is essential to drive penetrations and correct possible electrode misplacing;

b) once localized, neurons in area F5a should be systematically studied by implementing controlled behavioral tests aiming to characterize a variety of functional properties.

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