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A new field in monkey's frontal cortex: Premotor ear-eye field (PEEF)

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ABSTRACT

In macaque monkey, area 8B is cytoarchitectonically considered a transitional area between the granular Brodmann area 9, rostrally, and the rostral part of the dorsal agranular Brodmann area 6, caudally. As for electrophysiological data, microstimulation of area 8B evokes ear and/or eye movements; unit activity recording shows neurons encoding different auditory environmental stimuli and ear and/or eye movements. Moreover, visual attentive fixation modulates the discharge of auditory environmental neurons and auditory-motor neurons. As for anatomical data, area 8B is connected with auditory cortical areas, superior colliculus and cerebellum. Current functional and anatomical evidences support that area 8B is a specific Premotor Ear-Eye Field (PEEF) involved in auditory stimuli recognition and in orienting processes. In conclusion, we suggest that PEEF could play an important role in engaging the auditory spatial attention for the purpose of orienting eye and ear towards the sound source.

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1. Introduction

If we observe the natural behaviour of a predator tracking a prey, for example a cat tracking a mouse, and at the same time a sound occurs, we may note two different behaviours: the cat maintains its gaze on the mouse and orients its ears towards the sound source; or breaks his attention and orients gaze and ears towards the sound source. A similar behaviour is seen in human beings everyday, for example, when conversing with a colleague someone else says our name. Simply put, how do we have the ability to listen to, and follow, one speaker in the presence of others (Cherry, 1953). Two of these common aspects are the ability to perceive sound localization, *Where*, and the ability to pay attention to a particular sound, *What*, which is a dynamic cognitive process (Haykin and Chen, 2005).

In this review, we focus our attention on macaque monkey's area 8B. This area is considered cytoarchitectonically as a transitional area between the granular Brodmann area (BA) 9, rostrally, and the

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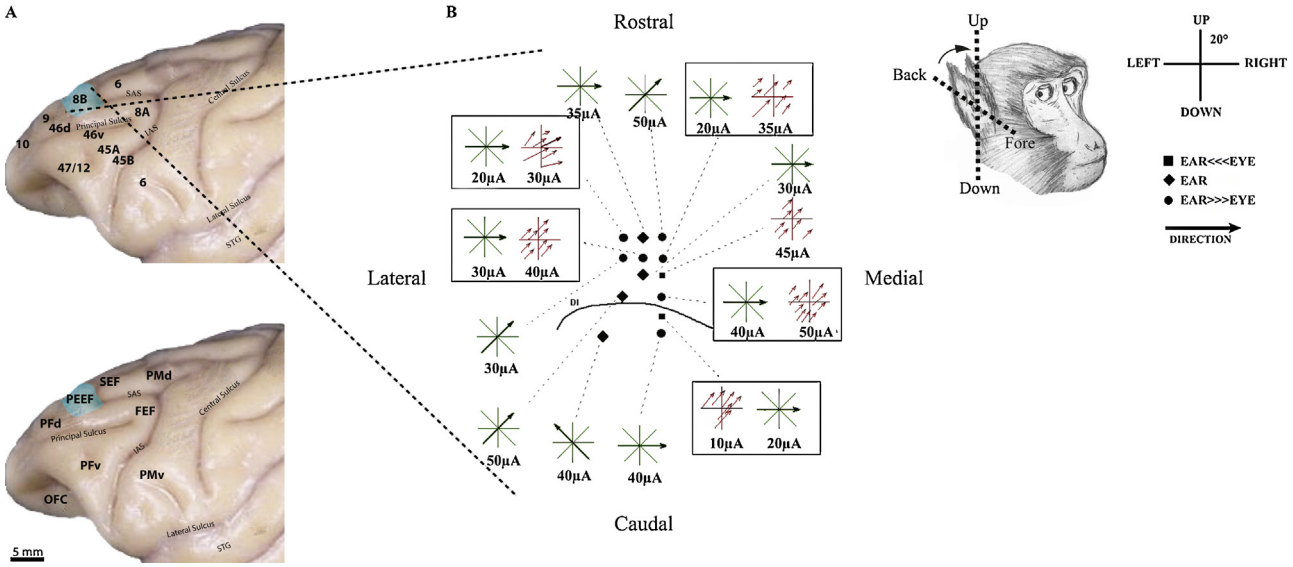

Fig. 1. Microstimulation map of area 8B. (A) Upper: area 8B localization within the macaque monkey's frontal lobe. SAS, Superior Arcuate Sulcus; IAS, Inferior Arcuate Sulcus; STG, Superior Temporal Girus. Bottom: Functional map of monkey's frontal lobe. PEEF, Premotor Ear-Eye Field; SEF, Supplementary Eye Field; FEF, Frontal Eye Field; PFd, Prefrontal Dorsal Cortex; PFv, Prefrontal Ventral Cortex; OFC, Orbito Frontal Cortex; PMd, Premotor Dorsal Cortex; PMv, Premotor Ventral Cortex; SAS, Superior Arcuate Sulcus; IAS, Inferior Arcuate Sulcus; STG, Superior Temporal Girus. (B) Representation of ear, eye, and both ear and eye movements evoked with a current threshold equal or lower than 50 µA. DI, dimple. Green arrow represents the mean direction of ear movement. The red arrows represent the direction of eye movements in each site (modified by Bon and Lucchetti, 1994).

rostral part of the dorsal agranular BA 6, caudally (Von Bonin and Bailey, 1947).

First, we will review recent electrophysiological data. In particular, we will describe results of microstimulation, unit activity recording and lesion studies in area 8B.

Second, we will review recent anatomical data showing connections with auditory cortical areas, superior colliculus and cerebellum.

Considering current functional and anatomical evidence we propose that area 8B is a specific field involved in the recognition of auditory stimuli and in ear and eye orienting processes. We suggest that area 8B might play an important role in the hierarchical organization of the auditory network. This is the reason why we proposed to rename area 8B, summing up its functional characteristics: "Premotor Ear-Eye Field", acronym PEEF (Bon et al., 2009; Lucchetti et al., 2008).

2. Cytoarchitecture

In macaque monkey area 8B is considered cytoarchitectonically as a transitional area between the granular BA 9, rostrally, and the rostral part of the dorsal agranular BA 6, caudally (Von Bonin and Bailey, 1947) (Fig. 1A). The first scientist, who identified this area, was Walker (1940), and successively Von Bonin and Bailey (1947) and Matelli et al. (1991) confirmed his findings. Some neuroanatomists considered area 8B as the dorso-mesial caudal part of BA 9 (Barbas et al., 1999; Barbas and Pandya, 1989; Pandya and Yeterian, 1990). Petrides and Pandya (1999) re-examined, in a comparative cytoarchitectonic analysis, the dorsolateral prefrontal cortex of the human and the macaque brain. They identified an area interposed between BA 9 and the dorsal part of BA 6 and following Walker (1940) they defined this area as 8B.

In the original paper they described this area as follows:

> "Its posteroventral part is located in the rostralmost section of the superior limb of the arcuate sulcus. Dorsally, it extends up to the midline, and it continues medially as far as the border of the cingulate sulcus. In this area, layer II is well defined and blends gently with layer III. Layer III is sparse and contains small- to medium-sized pyramidal neurons; only a few neurons in this layer are as large as those encountered in 8A. Layer IV is poorly developed and layer V almost blends with layer VI. A few darkly stained cells can be distinguished in layer Va".

3. Neurophysiology

3.1. Microstimulation

Electrophysiological investigation of area 8B started with the Ferrier's (1875) experiments. In those experiments the author electrically stimulated a large frontal region: area 9, 8B, 8A, area 46 and dorsal area 6 and evoked eye movements. Later Levinsohn (1909) used electric stimulation to evoke eye movements in dorsal area 6 and ear movements in area 8B. Many years later an explosion of investigations pointed out relevant neuronal characteristics of area 8A (FEF), and the rostral part of dorsal area 6 (SEF). For a detailed vision about FEF and SEF see Tehovnik et al. (2000), and about the cortical and subcortical networks see Lynch and Tian (2006). Area 8B was neglected until 1994, when experiments of microstimulation and unit activity recording in macaque monkey pointed out the role of this area in ear and eye motor control in spontaneous, i.e. not-reinforced, behaviours (Bon and Lucchetti, 1994). Microstimulation in some sites evoked only ear movements or only eye movements; in other locations it evoked both ear and eye movements by varying the intensity of electrical stimulation (Fig. 1B). The electrically evoked ear movements were forward, or backward or oblique (upward-forward; upward-backward). The evoked eye movements were mostly fixed vector saccades, contralateral and with an upward orientation of about 45 degrees. If we consider only the sites where the threshold was equal or lower than 50 µA, mostly of the evoked ear movements were dependent on the ear position at the beginning of stimulation.

3.2. Unit activity recording

As for unit activity recording, Bon and Lucchetti (1994) found several kinds of neurons discharging either before ear movements,